Estimating Bottlenose Dolphin Population Parameters From Individual Identification and Capture-Release Techniques

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ABSTRACT

Field studies begun in 1970 and continuing to date have identified at least three adjacent resident populations (or communities) of bottlenose dolphins along the central west coast of Florida. We have used photo-identification, mark-recapture techniques, behavioral observations, radio-tracking and brief captures for biological sampling to examine the structure and dynamics of these populations. Population designations are based on consideration of individual home ranges, social association patterns and genetics. Although the populations are relatively discrete in terms of ranges and associations, electrophoretic analyses of blood samples indicate that genetic exchange occurs between populations. Males travelling between populations appear to be the probable vectors for genetic exchange.

Most field effort has concentrated on the Sarasota dolphin population. Most of its members are identifiable from natural marks or tagging efforts over the last 20 years. This population consists of about 100 individuals. For the analyses presented here, we considered 116 dolphins identified during 1980–1987. Of these, the sex was known for 90 dolphins and the age has been estimated for 79 dolphins.

The long time span of the study and the high proportion of identifiable individuals has allowed us to estimate vital rates for this population. An annual recruitment rate to age 1 of 0.048 was countered by a minimum mortality rate of 0.010 and a mean annual loss rate from other causes of 0.029 (e.g., emigrations, mortalities for which carcasses were not recovered or undocumented changes in identifying characteristics). Immigration was infrequent, with a mean annual rate about 0.02. The mean fecundity rate was 0.144. Knowledge of maternal relationships allowed comparisons of the percentage of calves observed in the field vs the percentage of young of the year. Because of the prolonged period of association between mothers and calves, there were nearly six times as many mother-calf pairs as mothers with young of the year.

To test the effectiveness of photo-identification techniques, we compared the number of correct identifications made in the field 'by eye' against the number identified from photographs. We identified 89% of these well-marked dolphins correctly by eye. Because virtually all the dolphins were marked in the most-heavily surveyed portion of the study area, it was also possible to test the accuracy and precision of mark-recapture methods. Both the Petersen and Schnabel methods underestimated the known population size, although the Schnabel estimate was less biased. This bias was likely due to heterogeneity of sighting probabilities; different age-sex classes were shown to have different sighting probabilities.

INTRODUCTION

Individual identification can be an effective approach for collecting detailed data on population rate parameters for many free-ranging cetaceans. Repeated observations of recognizable individuals can lead to the definition of population units. Once the population units have been defined, observations of the members of the population can provide data for estimates of population abundance, recruitment through natality or immigration and losses through mortality or emigration. When the age and sex of the identifiable population members are known, it becomes possible to construct models of the dynamics of the populations.

Since 1970, we have used capture-mark-and-release techniques and photographic identification to study bottlenose dolphins (*Tursiops truncatus*) along the central west coast of Florida. As a result of these efforts, we can recognize nearly every member of a resident population of bottlenose dolphins inhabiting the inshore waters near Sarasota and Bradenton. In this paper, we present our analyses of data from long-term studies of this resident population to (1) estimate population rate parameters and (2) test some of the techniques commonly used in field measurements and abundance estimations.

METHODS

Individual identification techniques

Individual identification efforts in the Sarasota area began in 1970. Details of the development of our research program from 1970 to date have been reviewed recently by Scott, Wells and Irvine (1990a) and Wells (in press). Capture-and-release operations during 1970–89 have resulted in the marking of 156 different individuals. Dolphins were captured by encircling small schools with a 500m long by 4m deep net in waters less than 2m deep. We have used a variety of marking techniques during this study including freezebrands, plastic or fiberglass 'button' tags, roto tags, spaghetti tags and radio transmitters (Irvine and Wells, 1972; Irvine, Wells and Scott, 1982; Scott, Wells and Irvine, 1990b).

Mark-and-release captures also provided opportunities to collect additional biological data of relevance to population studies. Currently, we determine the sex, obtain a suite of standard length and girth measurements and collect blood samples for assessments of genetic relationships, health and reproductive condition from all dolphins handled for marking. In addition, we obtain a tooth for age estimation (Hohn, Scott, Wells, Sweeney and Irvine, 1989).

Of the 156 dolphins marked, 122 were residents of the Sarasota area and the other 34 were captured in adjacent areas to the north and south. Thirty dolphins were marked and released during 1970–71, 47 during 1975–76 and 118 during 1984–89. Of the 122 dolphins captured near Sarasota during 1970–89, 107 (55 females and 52 males) have been observed in the area during 1980–89.

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Natural markings have been used to identify individuals since 1970 (Irvine and Wells, 1972). Photography was used during 1970–76 to confirm identifications of tagged and naturally marked dolphins in the Sarasota area (Wells, Irvine and Scott, 1980; Irvine, Scott, Wells and Kaufmann, 1981). Beginning in 1980, we regularly surveyed the Sarasota area and adjacent waters in 5–7m boats (Wells, 1986; Wells, Scott and Irvine, 1987). During these censuses, we photographed all dolphins encountered, including both previously tagged and naturally marked animals. We used 35mm cameras with a variety of fixed and zoom telephoto lenses of up to 300mm, motordrives and databacks. We have found the best film for our situation to be *Kodachrome* 64 color slide film, shot at ASA 80. We used shutter speeds of 1/500 or faster.

Observations of naturally marked dolphins have provided some additional information on age and sex of individuals. The seasons of birth have been determined for 54 individuals and 5 frequently seen dolphins are presumed to be adult females because of their regular associations with small calves. At present, our photographic identification catalogue from the Sarasota area and the surrounding region of Florida contains nearly 500 individuals.

Population description

Radio-tracking results combined with sightings of identifiable individuals over periods up to 20 years indicate the existence of resident populations of bottlenose dolphins in the inshore waters of the central west coast of Florida. In a previous description of the dolphins' social structure (Wells *et al.*, 1987), we defined a community as being composed of those individuals

'that shared large portions of their ranges and interacted with each other to a much greater extent than with members of similar units in adjacent waters. This regional society could be considered to be a population, in the broadest sense (for example, Wilson, 1975). However, evidence indicates that this 'population' was not a closed reproductive unit and thus not a population in the strictest sense. The term community was used because it emphasized the geographic and social relationships of the individuals.'

In this paper, we use the term 'population' in this broad sense and we therefore use it interchangably with the term 'community.'

Several resident populations have been identified in Sarasota Bay and adjacent waters (Wells, 1986; Weigle, 1990). The Sarasota population ranging from Terra Ceia Bay and the southern edge of Tampa Bay southward to Siesta Key, has been the focus of our research efforts since 1970 and is the basis for the analyses presented here (Fig. 1). The Sarasota community home range includes about 100 km² of shallow bays, seagrass meadows, narrow channels and Gulf of Mexico coastal waters. With the exception of occasional absences of some adult males, most of the members of the Sarasota population can be found within this range throughout the year (Wells, 1978; 1986). Within the home range, members frequent different core areas. Females exhibit a high degree of site fidelity. Bands of females, many of whom are related (Duffield, Chamberlin-Lea, Wells and Scott, 1985; Wells *et al.*, 1987), use specific portions of the home range on a regular basis, but may range occasionally throughout the area and interact with members of other female bands. Calves of both sexes tend to remain in the community at least until they reach sexual maturity and typically longer (Wells *et al.*, 1987).
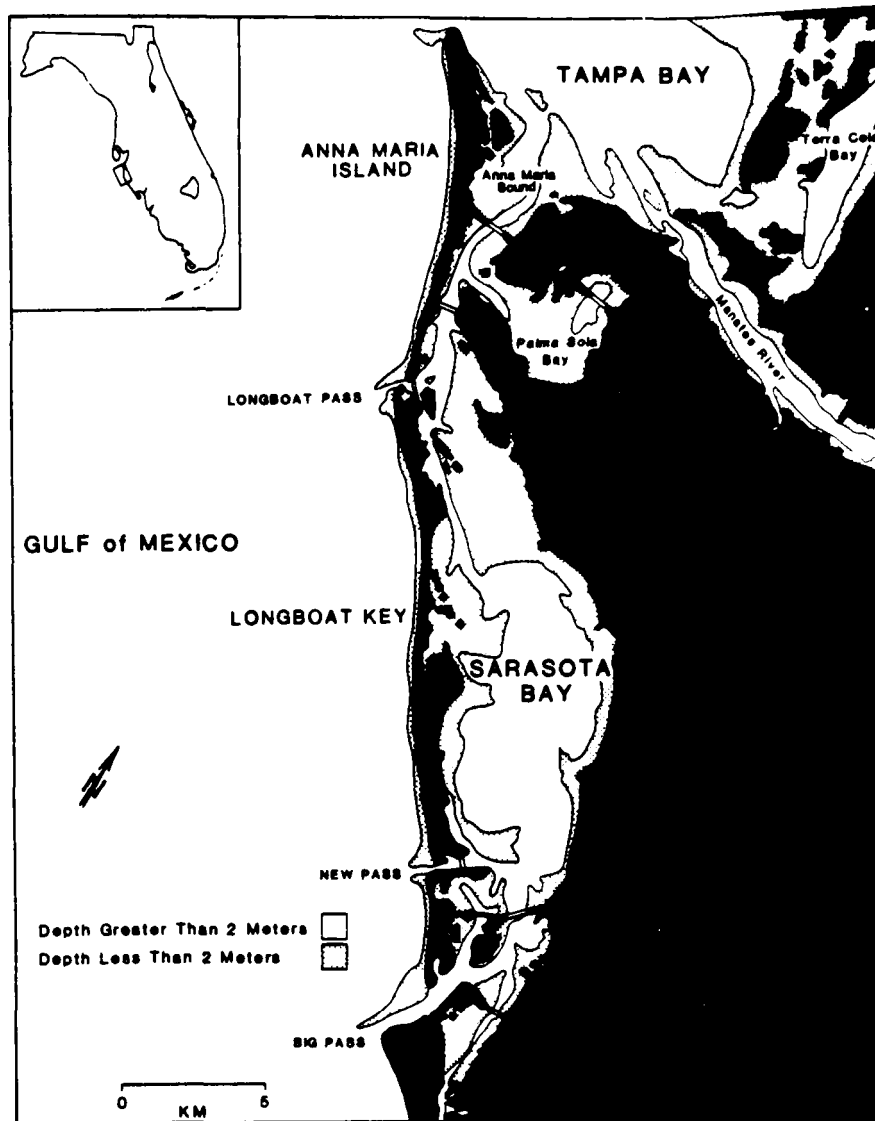

Fig. 1. Map of the Sarasota Bay study area. Inset shows the location of the region on the Florida peninsula.

Males begin to range farther as they mature, apparently traveling from one female band to another (Wells *et al.*, 1987). As adults, some males who were seen regularly as young animals may not be seen in the home range for periods of days to months, or longer. In a case involving the longest range that we have observed, a pair of adult Sarasota males was observed with a school of non-Sarasota females and young 16km north of the previously defined range of Sarasota population members. We suspect that genetic exchange may occur while males are ranging beyond the normal Sarasota home range and similarly when male 'strangers' pass through the Sarasota community range (Duffield and Wells, 1986).

Census efforts have been most consistent in the portion of the home range inhabited by the greatest number of dolphins, including Anna Maria Sound southward to Big Pass (Fig. 1). Virtually all of the regular inhabitants are well known. The waters of the extreme northern portion of the home range, including the Manatee River and Terra Ceia Bay, have not been as accessible for our small boats during regular surveys. As a result, these waters have not been surveyed as consistently and thus the individuals using these waters as their core area are not as well known as are those to the south.

The ability to recognize nearly every Sarasota community member and the observed long-term residency patterns within a stable geographical range provide an unprecedented opportunity to monitor the dynamics of a free-ranging dolphin population. Our regular photographic identification censuses from 1980 to date have been designed to monitor the presence or absence of known individuals and to document recruitment through births and immigration. Mortality data have been provided through the local marine mammal stranding program

Table 1

Roster of known individuals in the Sarasota community and the number of sightings of each one during 1980-1987 (maximum of one sighting per day). The x's indicate those dolphins that were also present during studies in 1970-1971 and 1975-1976. Of these 116 dolphins, the sex is known for 90 dolphins, and the age is known or estimated for 79 dolphins. x = Captured and observed during previous studies. a = Assumed to be present because of sightings during previous and subsequent years. (In some cases, data from 1988 were used to confirm the presence in preceding years). d = Mortality confirmed from recovered carcass.

(a) Males

No.	70-71	75-76	80	81	82	83	84	85	86	87
58	x	x	3	4	1	12	9	3	9	3
27	x	x	6	5	8	22	14	4	6	
73	x	x	a	a	5	5	4	2	4	5
112	x	x	a	a	a	1	a	a	a	1
136	x	x	a	a	a	a	1	a	a	a
3		x	11	6	27	29	20	7	13	11
11		x	10	4	21	30	21	7	13	6(d)
43		x	7	5	8	14	6	3	9	6
40		x	7	6	7	14	8	3	9	6
56		x	7	5	9	4	6	3	6	6
49		x	5	5	9	13	13	4	15	6
30		x	4	7	6	25	11	1	4	7
132		x	2	1	2	14	12	7	13	15
38		x	8	7	3	14	1(d)			
86		x	5	1						
39			4	3	11	16	11	4	6	9
6			9	7	21	36	28	5	15	10
31			7	8	16	22	13	7	12	15
34			5	3	12	16	11	4	6	9
37			5	8	10	11	8	4	6	6
44			1	3	15	15	7	7	10	4
41			6	2	8	19	17	5	10	13
74			1	a	6	2	4	2	3	3
90			1	a	a	5	10	4	18	7
82			a	1	5	3	a	1	3	a
12				6	23	35	20	6	13	8
17				3	22	32	16	7	13	11
33				4	12	23	8	2	4	1
36				2	15	16	8	6	8	5
78					5	5	2	2	2	
107					2	4	9	1	1	3
67						14	5	3	3	2
153							8	3	6	4
149							7	1	10	2
146							15	6	5	6
156							2	5	7	3
142							6	9	12	3
157							6	3	13(d)	
154							7(d)			
160								2	7	6
191								3	3	a
166										4
Total	*5*	*15*	*25*	*29*	*30*	*31*	*38*	*38*	*38*	*36*

(b) Females

No.	70-71	75-76	80	81	82	83	84	85	86	87
5	x	x	10	7	21	36	28	4	14	17
7	x	x	9	6	23	34	20	9	12	4
24	x	x	6	10	19	19	9	3	13	6
48	x	x	4	7	8	13	6	a	6	a
1		x	11	9	27	31	29	12	13	23
16		x	10	6	18	26	16	8	14	10
14		x	8	5	20	29	23	6	11	8
2		x	7	6	29	25	18	4	9	5
8		x	7	6	21	35	19	10	10	11
4		x	6	7	28	29	20	9	17	13
22		x	5	5	19	24	16	8	9	7
26		x	5	9	13	23	8	4	7	6
47		x	5	4	9	15	3	5	6	2
10		x	4	6	22	32	18	7	13	16
28		x	4	4	6	27	9	5	13	11
32		x	3	5	13	16	14	4	7	11
42		x	3	5	10	19	5	3	3	2
9		x	3	7	32	29	10	4	7	9
35		x	2	8	6	22	12	1	4	4
45		x	6	4	12	9	12	3	1	5
53		x	3	5	20					
62		x	7	8						
68			4	1	4	5	2	4	6	2
59			3	6	7	6	4	3	4	2
21			11	8	15	22	15	4	15	13
13			3	4	21	35	19	10	11	10
52			1	4	4	17	5	4	3	2
79			1	1	3	5	1	a	2	a
50				4	17	12	7	3	7	6
25				a	19	27	13	3	4	5
23				a	22	28	14	3	9	12
20					22	29	19	9	17	12
15					27	31	30	11	13	18
141					2	a	6	5	13	9
18					27	25	18	1		
61						13	13	4	9	12
51						25	9	5	13	11
147						3	1	4	6	1
91						6	1	1	3	1
151							8	1	15	4
148							8	9	9	7
140							12	8	14	10
144							9	8	13	20
145								3	9	9
164								4	3	2
159									9	16
158									1	12
170									5	a
Total	*4*	*22*	*28*	*31*	*34*	*37*	*41*	*43*	*45*	*45*

(c) Unknown sex

No.	70-71	75-76	80	81	82	83	84	85	86	87
60	x	x	3	5	7	4				
106			2	a	2	1	a	a	2	
55			4	a	19	1	3	1		
54			a	3	9	15	1	3		
29			2	4	23	16	11			
46			6	4	12	9	1			
163			1	4	4	17	1			
161			2	a	1	1				
121			4	1	1					
66			3	4	10					
122			3	5	21					
104			1	a	4					
117			9							
65			2	6	9	2	a		2	4
57			1	15	12	2				
123			3							
162				2	a	7	1		2	a
19				30	29	10				
119				a	4	1	a		2	a
120					2	a	1		3	1
155							22	18	24	29
165							1			
168							5			
171								3		
167								1		
169									9	1
Total	*1*	*1*	*13*	*15*	*16*	*14*	*15*	*10*	*7*	*6*

Table 2A

Annual reproductive rates of the Sarasota bottlenose dolphin community. The number of calves born to known mothers (b) is included in the number of known individuals (n). The number of known mature females (f) is also shown as ios the number of known births surviving to 1 year (b$_1$). The number of days a dolphin identification effort is indicated for each year (Fd=field days, Sd=survey days, Cd=capture days. A weighted average was used for the mean; a binomial variance was used to calculate the standard deviation.

	1980	1981	1982	1983	1984	1985	1986	1987	Mean	SD
n=	67	75	81	82	94	91	90	87		
f=	20	25	25	27	27	27	27	30		
b=	7	4	5	5	7	4	4	1		
b$_1$=	5	4	5	5	5	2	3	1		

Crude birth rate (b/n)

| 0.104 | 0.053 | 0.062 | 0.061 | 0.074 | 0.044 | 0.044 | 0.011 | 0.055 | 0.0089 |

Fecundity rate (b$_1$/f)

| 0.250 | 0.160 | 0.200 | 0.185 | 0.185 | 0.074 | 0.111 | 0.033 | 0.144 | 0.0244 |

Recruitment rate to age 1 (b$_1$/(n-b))

| 0.083 | 0.056 | 0.066 | 0.065 | 0.057 | 0.023 | 0.035 | 0.012 | 0.048 | 0.0085 |

Fd	22	21	77	72	55	20	34	35		
Sd	22	21	77	72	39	12	25	20		
Cd	0	0	0	0	16	8	9	15		

Table 2B

Annual mortality, survivorship and loss rates of the Sarasota bottlenose dolphin community. Deaths (d) were scored if a carcass of a known animal was found, if an animal appeared to be diseased and then subsquently disappeared, or if a calf less than 3 years old disappeared from the population. Losses (l) were scored if an animal disappeared, but the cause (mortality, emigration, or undocumented change in marking) was not known.

	1980	1981	1982	1983	1984	1985	1986	1987	Mean	SD
n=	67	75	81	82	94	91	90	87		

For dolphins > 1 year old

	1980	1981	1982	1983	1984	1985	1986	1987	Mean	SD
d=	0	0	1	0	2	1	1	1		
l=	0	2	4	2	5	2	3	0		

Minimum mortality rate (d/(n-b))

| 0.000 | 0.000 | 0.013 | 0.000 | 0.023 | 0.011 | 0.012 | 0.012 | 0.010 | 0.0039 |

Loss rate (l/(n-b))

| 0.000 | 0.028 | 0.053 | 0.026 | 0.057 | 0.023 | 0.035 | 0.000 | 0.029 | 0.0066 |

Maximum mortality rate ((d+l)/(n-b))

| 0.000 | 0.028 | 0.066 | 0.026 | 0.080 | 0.034 | 0.047 | 0.012 | 0.038 | 0.0076 |

Minimum annual survival rate (1 - (d+l)/(n-b))

| 1.000 | 0.972 | 0.934 | 0.974 | 0.920 | 0.966 | 0.953 | 0.988 | 0.962 | 0.0076 |

Annual survival rate (DeMaster and Drevenak, 1988)

| 1.000 | 0.970 | 0.934 | 0.973 | 0.918 | 0.964 | 0.953 | 0.988 | 0.961 | 0.0079 |

For young of the year

	1980	1981	1982	1983	1984	1985	1986	1987	Mean	SD
d=	1	1	0	0	2	2	1	0		

Minimum mortality rate (d$_1$/b)

| 0.143 | 0.250 | 0.000 | 0.000 | 0.286 | 0.500 | 0.250 | 0.000 | 0.189 | 0.0644 |

Maximum annual survival rate (1 - (d$_1$/b))

| 0.857 | 0.750 | 1.000 | 1.000 | 0.714 | 0.500 | 0.750 | 1.000 | 0.811 | 0.0644 |

Annual survival rate (DeMaster and Drevenak, 1988)

| 0.539 | 0.869 | 1.000 | 1.000 | 0.643 | 0.630 | 0.717 | 1.000 | 0.803 | 0.0703 |

based at Mote Marine Laboratory in Sarasota. Attempts to identify emigration have included tagging efforts and our own photographic identification surveys in Tampa Bay, the Gulf of Mexico, Charlotte Harbor and Pine Island Sound, as well as examination of identification photographs from other researchers working in Tampa Bay (Weigle, 1990) and Pine Island Sound (Shane, in press).

Data base

Data for the following analyses were collected on 336 days on the water during the period April 1980 through December 1987. Of these, 288 days were census days and 48 were capture days.

We recognized 116 dolphins as members of the Sarasota community during the period 1980–87 (Table 1). As of April 1990, 42 of these were known to be males, 48 were females and 26 were of undetermined sex. The ages of 79 dolphins were known from field observations of known mothers or were estimated from examination of growth layers in the teeth. Dolphins were added to the identification catalog over a period of years by photographing naturally marked individuals, by capturing and marking the dolphins or by observing the addition of calves to known mothers in the population. Of the 116 dolphins considered in this paper, 56 (48%) non-calves were identified from natural marks or tags during captures and surveys during 1970–80. Most of the later additions to the catalog were calves born to known mothers; 42 dolphins (36%) were first identified as calves, with 37 of these being born during 1980–1987 and the other 5 being born previously. Seven other dolphins (6%) were marked during capture operations reinitiated in 1984–85. The remaining 11 dolphins (9%) were naturally marked dolphins added to our identification catalog during 1981–85 either because natural marks were newly acquired or changed, or because they immigrated into the area.

Analyses

Population parameters were calculated for each year as detailed in Table 2. Overall means were calculated as weighted averages. A binomial variance was used to calculate the standard deviations.

POPULATION PARAMETERS

Population size and stability

We estimated the size of the Sarasota dolphin population in two ways, through direct counts of known dolphins and their calves (Table 2) and through mark-recapture (or, more accurately, mark-resight) analyses. The first technique provides a minimum estimate of the total population size because it does not account for dolphins that are not distinctively marked. The second technique takes both marked and unmarked dolphins into account and provides a point estimate with confidence limits.

The number of known individuals increased steadily during the initial compilation of the catalogue from 1980 to mid-1982 and then leveled off thereafter. With the initiation of capture and marking efforts in 1984, the number of known individuals increased markedly with the addition of newly marked dolphins. From 1984–87, the number of known individuals varied less than during the previous four years and variations could be largely accounted for by births and losses to the population (Table 2).

The results of mark-resight analyses suggest that the number of dolphins in the Sarasota population remained relatively stable at approximately 100 individuals over at least a seven-year period. Irvine *et al.* (1981) estimated that the population contained 102 dolphins in 1976 (95% CL = 90–117), based on Lincoln Index calculations. Wells (1986) calculated a Schnabel point estimate of 98 dolphins (95% CL = 89–108) in 1983, of which 82 individuals were known. Minimum estimates of the population size, based on counts of known dolphins during 1983–87, ranged from 82 to 94 individuals (Table 2).

In addition to the constancy of population estimates from mark-resight analyses, the composition of the population also remained stable. At least half of the known individuals in Table 2 (48 dolphins) were accounted for during all eight years of the period 1980–1987. A high proportion of individuals marked in the 1970s were reidentified during the 1980s: 9 of 12 dolphins (75%) marked during 1970–71 and 37 of 47 dolphins (79%) marked during 1975–76 were reidentified in the study area during 1980–87 (Table 1). If the four dolphins known to have died prior to 1980 are deducted from the total, 86% of the remaining dolphins marked in 1975–76 were reidentified.

Recruitment
Dolphins were added to the Sarasota population through births to known community members and probably through immigration.

Natality
By regularly surveying the area, particularly during and after the main calving peak (May-July), we could record the births of calves to known females and monitor their fate. A calf was defined as a presumed offspring that closely associated with an adult female, regardless of the calf's age; calves in their first year of life are referred to as young of the year. The calculated mean annual crude birth rate is 0.055 ($\pm$ SD 0.0089) based on the number of births as a proportion of the total population of known dolphins (Table 2A). This is probably a slight underestimate because on occasion calves may have been born and died before we had a chance to record them. A mean annual fecundity rate of 0.144 was calculated ($\pm$ SD 0.0244) based on the number of young of the year surviving to one year of age that were born to known mature females (Table 2A). Mature females were defined as those known to have given birth, or those indicated to be ovulating over several breeding seasons by an analysis of plasma progesterone concentrations by V. Kirby. This fecundity rate is low compared to the three- to six-year calving interval observed by Wells *et al.* (1987), because of the addition to the mature female category those that had apparently not calved but were sexually mature based on hormone levels. The mean recruitment rate to age 1 was 0.048 ($\pm$ SD 0.0085), based on the number of calves that were born and survived to an age of one year as a proportion of the total population of known dolphins (Table 2A).

The number of calves born annually varied within the Sarasota study area, ranging from a single birth recorded in 1987 to 11 births in 1988. A wide range in birth rates has been reported for other studies of bottlenose dolphins (see reviews by Leatherwood and Reeves, 1982; Perrin and Reilly, 1984), but differences from study to study in birth rates based on percentage of calves may result at least in part from a lack of information on calving intervals and the

Table 3

Age distribution of dolphins identified as calves and the fraction of the total population these age classes comprised. Calves were identified by their close association with their mother. Tagging of both the mother and calf allowed us to monitor the association of the pair even though a distinct size difference was not apparent in the field. During the time of this sample (July, 1986), all the known 3- and 4-year-olds were associated with their mothers. Because many of the 5- and 6-year-olds were independent of their mothers, we did not calculate the fraction of the population they comprised.

	Age in years						
	0-0.9	1	2	3	4	5	6
Calves	3	2	5	4	3	0	1
Fraction	0.034	0.022	0.056	0.045	0.034	-	0.011

age distribution of calves. For example, calves comprised 20% (N=18) of the Sarasota population in July 1986, while the young of the year comprised but 3.5% (Table 3).

The percentage of calves reported here (20%) is higher than values reported elsewhere for bottlenose dolphins (ranging from 2.7–15.6%; Table 18.1, Leatherwood and Reeves, 1982). This is due in part to different definitions of what is a calf. Most field studies define a calf as being a distinctly smaller individual in close association with another larger animal. Because of our tagging efforts, we have been able to identify mother-calf pairs even after there is little size difference apparent in the field. We have monitored associations between mothers and their calves for up to ten years, whereas in most studies an animal larger than a 2- or 3-year old (ranging from about 165–225cm – Hohn, 1980; unpub. data) would not likely be considered a calf. Of greater relevance to estimation of vital rates, however, are the implications of scoring older calves as young of the year and thus overestimating the annual birth rate.

Immigration
Wells (1986) examined the accumulation of new identifications into the photographic catalogue for the Sarasota population and reported that immigration appeared to be an infrequent event. Wells found an initial rapid increase in the number of identifiable dolphins from 1980 to mid-1982, with very few additions to the catalogue from sources other than birth thereafter. Assuming that the initial rate of increase was an artifact of the initial development of the catalogue and that the period after July 1982 reflected the actual dynamics of the population, Wells estimated the annual immigration rate to be 0.032. This rate was based on the additions to the catalog (during August 1982 – January 1984) of three naturally marked dolphins (Nos. 90, 91 and 107) with dorsal fins distinctive enough to have been readily identifiable previously. During subsequent capture operations, photographs of the twisted peduncle of one of these dolphins (No. 90) were matched with photographs taken in 1980 of an animal with the same twisted peduncle, but an unmarked dorsal fin. Thus, the immigration rate calculated by Wells should be reduced to 0.021. This should be considered a maximum estimate, given the potential difficulties in distinguishing between immigration and undocumented changes in the identifying characteristics of existing community members (Wells, 1986; Scott *et al.*, 1990b).

During 1984–87, nine individuals (non-calves) were added to the catalogue, but no new dolphins were added

during 1986–87. Two of the nine were naturally marked while the others were captured and marked. If we assume that all nine were new immigrants, the weighted mean immigration rate is 0.025 per year ($\pm$ SD 0.0082). This assumption is unlikely to be valid, however and this rate is probably an overestimate, particularly given that there were no additions in 1986–87 and that eight of the nine dolphins were not well-marked previously and could have been present without having been identified. Also, 6 of the 9 were of an appropriate age (less than 7 years old) to have been the offspring of resident mothers who had separated from their calves just prior to the 1984 and 1985 captures. In all cases to date where calves of resident Sarasota females were recognizable prior to separation, the independent offspring remained in the community home range after separation.

Losses from the population
Community members were considered lost from the ranks of the identifiable if their carcasses were recovered by the local stranding network, or if they were not resighted during censuses in at least two consecutive years. In addition to mortality, several other possibilities exist for loss from the population, including permanent emigration, undetected changes in identifying characteristics and separation of non-distinctive calves from well-known mothers. In total, 31 dolphins were considered lost from the Sarasota population during 1980–87. An average maximum mortality rate (known deaths plus disappearances) per year of 0.038 ($\pm$ SD 0.0076; Table 2B) was calculated for animals older than one year for 1980–87.

Mortality
A mean annual minimum mortality rate of 0.010 ($\pm$ SD 0.0039; Table 2B) was calculated for the period 1980–87 based on six known or presumed deaths to animals older than one year. These mortalities included four recovered carcasses and two adults observed with extensive skin diseases who disappeared and presumably died. Additionally, seven young of the year disappeared and likely died, yielding a mean mortality rate in the first year of 0.189 ($\pm$ SD 0.0644). The actual mortality rates were probably higher than those reported here; some carcasses recovered by the stranding network were too decomposed to permit identification and some deaths probably did not result in beachcast carcasses. Thus, the true mortality rate for dolphins older than one year probably lies between 0.010 and 0.038.

Different age and sex classes appear to suffer different rates of mortality within the Sarasota population. Of 19 known or presumed deaths recorded during 1976–88, 7 (36.8%) were young of the year, 2 (10.5%) were approximately two-year-old males, 7 (36.8%) were subadults or young adults (<13 years old) and 3 (15.8%) were adults (1 male, 1 female, 1 unknown). Of the 7 subadults and young adults, 5 (83.3%) were males. Thus, young of the year and subadult males appear to suffer the highest rates of mortality. Hersh (1987) reported that young of the year comprised 11.2% of all stranded dolphins in the Indian and Banana River system. It is unclear how this value compares with the rate for the Sarasota population, however, because our lost young of the year were scored based on their disappearances rather than on recovery of their carcasses. Hersh also reported that males comprised 68.2% of the yearling carcasses, but she found that the sex ratios were not skewed for older age classes.

Emigration and other losses
We could not distinguish emigration from other undetermined losses unless the emigrant was identified outside its original community's home range. We have not yet confirmed any permanent emigrations from the Sarasota area during the 1980s, either from surveys by us or other researchers in neighboring areas or from reports by the boating public. A complete lack of emigration would be highly unusual for a large mammal. The recent resightings of an adult male (No. 136) after not being sighted for eight years suggest that at least a small number of community members may shift their core areas outside the community home range for extended periods of time. If all losses other than confirmed or presumed mortalities were considered to be emigration, then the mean annual maximum emigration rate would be approximately 0.029 ($\pm$ SD 0.0066; Table 2B). In all probability, however, the actual mortality rate is higher than 0.010 and thus the maximum emigration rate would be overestimated. Additional losses may result from changes in the identifiability of some dolphins from undocumented changes in dorsal fin markings, or when calves lacking individually-distinctive markings become independent from their marked mothers. In time and as we continue our expanded census coverage into Tampa Bay during 1989–92, we may be able to confirm occurrences of these apparently unusual emigration events.

Annual survival rate
DeMaster and Drevenak (1988) calculated annual survival rates (ASR) for three species of captive cetaceans, including bottlenose dolphins. They calculated the number of animal-days that an individual survived and converted these values to annual rates. We made similar calculations for the Sarasota population for comparison with the data from captives.

We used two methods for calculating ASR. In the first method, we simply subtracted the maximum mortality rates (Table 2B) from 1.0. In the second, we estimated the number of days survived by each individual for each year. Whereas precise values for days survived were available to DeMaster and Drevenak for captives, it was difficult to pinpoint the exact date of death in the wild unless a fresh carcass was recovered. In the case where dolphins disappeared, we assumed the date of death to be that of the last sighting of the dolphin, although this likely biased the estimate downwards slightly. We stratified our sample into two age classes: young of the year and older dolphins.

The two methods produced similar results (Table 2B). Using the method described by DeMaster and Drevenak (1988), we obtained a mean ASR for young of the year of 0.803 ($\pm$ SD 0.0703) during 1980-87. DeMaster and Drevenak calculated a lower ASR for captive calves of 0.61. For older dolphins, we obtained a mean ASR of 0.961 ($\pm$ SD 0.0079) during 1980–87. DeMaster and Drevenak reported a lower ASR for captives of 0.93.

PHOTOGRAPHIC VS FIELD IDENTIFICATION

Our extensive use of photography, even of seemingly well-marked animals, has proved valuable over the years. Real-time identifications 'by eye' alone do not provide the degree of certainty about identifications that is necessary for the kinds of analyses we present here. Our ability to identify by eye the resident Sarasota dolphins was tested by examining a sample of 43 schools observed during 1986 and

1987 for which we had at least four identifiable photographs per recognizable dolphin, indicating that all identifiable dolphins were captured in the photo record (with a 95% probability level; Würsig, 1978; Ballance, 1990). We spent an average of 19.3 min (± SD 11.2 mins) with each school. On average, 89.3% (± SD 21.8%) of the dolphins present were correctly identified in real time. This is likely a best-case situation for identifying animals in the field because of the long-time familiarity of the researchers with the dolphins and because virtually all the dolphins were well-marked due to the regular capture operations. In addition to providing a more complete and accurate record of dolphins present than is possible simply by eye, the photographic records allowed us to follow changes in identifying characteristics through time and in a number of cases allowed us to distinguish between individuals with nearly identical markings.

MARK-RECAPTURE ESTIMATES

The high proportion of known individuals in this population allowed us to examine some characteristics of mark-recapture estimates for dolphin populations. In the central and southern sections of the area (i.e., Anna Maria Sound, Sarasota and Palma Sola Bays and the passes and shores along the Gulf), 77 dolphins (of which 15 were calves) were known in July 1986. Calves were not included in the mark-recapture calculations because of the lack of independence in sightings of the calves and their mothers. In addition, two of the remaining 62 dolphins had very similar marks at that time (Nos. 146 and 149) and could not always be distinguished. For this reason, their sightings were excluded from the analyses. During 12 days of surveys (3–14 July 1986), only two unmarked dolphins were seen. If each of these sightings were of a different individual, then the population for the purposes of this analysis contained 62 dolphins.

Comparison of different estimators

With the population size known, we could then compare the accuracy of different estimators of population size ($\hat{N}$). We calculated both Petersen and Schnabel estimates for the 12-day survey period mentioned above. We used the Chapman modification of the Petersen estimator (Chapman, 1951):

$$\hat{N}_i = \frac{(M_i + 1)\, (n_i + 1)}{m_i + 1} - 1$$

where M_i = the number of different dolphins sighted prior to sampling period i, n_i = the number of different dolphins sighted in sampling period i and m_i = the number of dolphins sighted both before and during sampling period i. We assumed that there were no dolphins marked prior to the surveys and that the dolphins were all individually identifiable and were 'marked' at their first sighting. A maximum of one sighting per individual per sampling period was counted. A different population estimate was calculated for each pair of consecutive days and the series of estimates was averaged. Unweighted and weighted averages were both calculated, the number of marked dolphins present (M_i) being used as the weighting factor. (The standard error of the estimate, which is often used as a weighting factor, could not be used because the high proportion of marked dolphins in the population sometimes yielded recapture rates of one and standard errors of zero.)

The form of the Schnabel estimator used was:

$$[1-(r/\hat{N})] = \sum_{i=1}^{s}[1-(n_i/\hat{N})]$$

where r = the number of marked dolphins in the population, $\hat{N}$ = the population size, s = the number of sampling periods, and n_i = the number of dolphins sighted in sampling period i (Seber, 1982: Equation 4.4). A single population estimate was produced by solving iteratively for $\hat{N}$. A 1000-replication bootstrap method was used to estimate the variance and percentile confidence limits (see review by Efron and Tibshirani, 1986).

Each method underestimated the known population size of 62 dolphins (Table 4). The weighted average Petersen estimate of 53 was slightly less biased than the unweighted average of 51, but the series of estimates converged at the end of the survey period to 55, the number of different marked dolphins sighted during the period. The Schnabel estimate of 56 was less biased than the average Petersen estimates. The underestimates produced by these methods are likely due to heterogeneity in sighting probabilities (see below). This effect was particularly evident in the Petersen estimates made early in the 12-day period when there was a lower proportion of 'marked' dolphins in the population. This biased the weighted-average estimate downwards and gave the false appearance of an increasing trend in population size over the period of the surveys.

Table 4

Comparison of Petersen and Schnabel estimators. The Petersen estimates were computed for each pair of consecutive survey days; these estimates were then averaged.

Day i	1	2	3	4	5	6	7	8	9	10	11	12
Petersen Estimator												
M_i	0	19	25	32	33	39	44	49	51	55	55	55
n_i	19	12	17	8	6	15	29	16	17	8	20	16
m_i	0	6	10	7	0	10	24	14	13	8	20	16
N_i	-	36	42	36	-	57	53	56	66	55	55	55

Unweighted Average N=51.0   SE = 1.6; 95%CI = (48.7, 55.3)
Weighted Average   N=53.0   SE = 1.3; 95%CI = (51.5, 56.7)

Schnabel Estimator
[where r = 55]   N=56.1   SE = 1.2; 95% CI = (53.6, 58.2)

Heterogeneity of sighting probabilities

Heterogeneity in the probabilities of sighting and identifying individuals is a common violation of the assumption of equal 'catchability.' Heterogeneity will cause the population estimates to be biased downwards (e.g., Hammond, 1986). As shown in Table 5, sighting probabilities are not the same for different age and sex classes in this population. Adult males were resighted less frequently than females and the sighting probability decreased as the males matured. In two extreme cases, males that were frequently seen in 1970–71 and 1975–76, were rarely seen in 1980–88 (No. 112 – 3 sightings; No. 136 – 2 sightings). The lower sighting probabilities of the males are due to their greater tendencies to travel outside the community home range, to occur in less-easily sighted small groups and to inhabit areas within the home range which were difficult to survey completely (e.g., the more open waters of Sarasota Bay).

Table 5

Mean sightings per day for each age-sex class in 1980-1984
(from Wells, 1986).

	Mean (SD)	Number of dolphins
Adult females	0.33 (0.12)	23
Subadult males (<8y and <245cm)	0.33 (0.11)	5
Transitional males (8-10y and 245-9cm)	0.18 (0.04)	3
Adult males (>10y and >249cm)	0.15 (0.09)	7

One way that the bias due to unequal identification probabilities can be reduced, however, is to increase the sampling effort so that animals with lower sighting probabilities would be more likely to be sampled. This method requires that (1) marked dolphins are counted at most once during each sampling period regardless of the number of times they are actually sighted and (2) unmarked dolphins are also counted at most once during each sampling period, i.e., once they are sighted during the surveys, they become marked. This latter assumption implies that all individuals can be identified uniquely.

We compared the performance of Petersen and Schnabel estimators as we varied both the number and length of the sampling periods. Both estimators produced less biased results as the number of 1-day sampling periods increased from 2 to 12 days (Fig. 2). As the number of days surveyed increased, the number of dolphins marked also increased. By having a larger number of marked dolphins in the population, the estimated variances decreased.
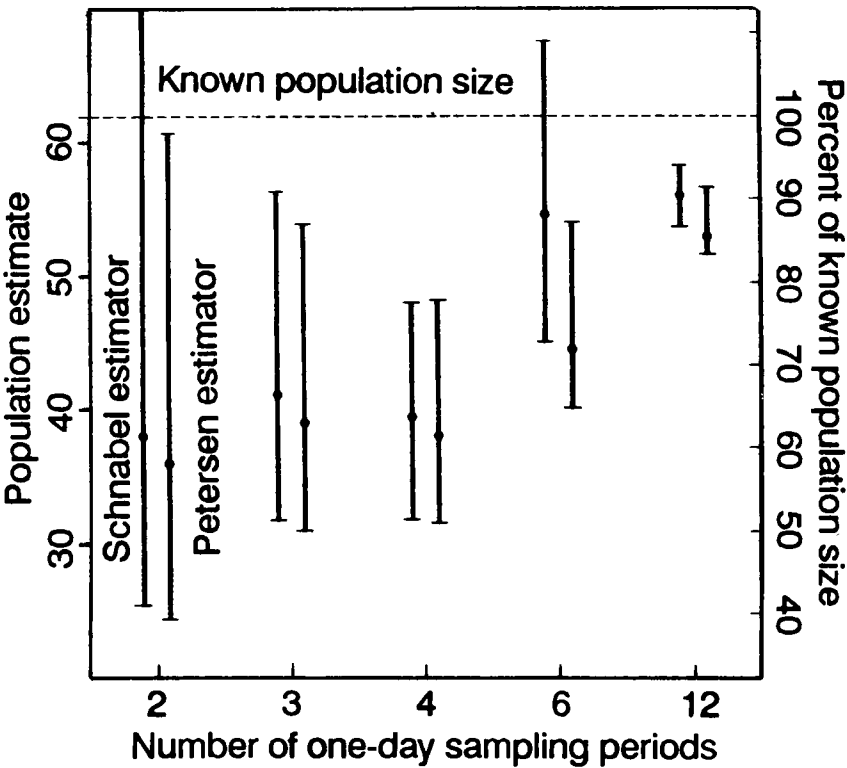
Fig. 2. Population estimates and 95% confidence intervals obtained from samples in which the number of one-day sampling units varied. The population size was known, consisting of 62 dolphins.

We also examined the effect of changing the length of the sampling period from 1 to 6 days, while holding the number of survey days constant (for example, twelve 1-day surveys could be compared with two 6-day surveys). The estimates became less biased when the sampling periods were longer and the estimates from the 6-day samples were the only ones whose confidence limits included the true population size (Fig. 3).
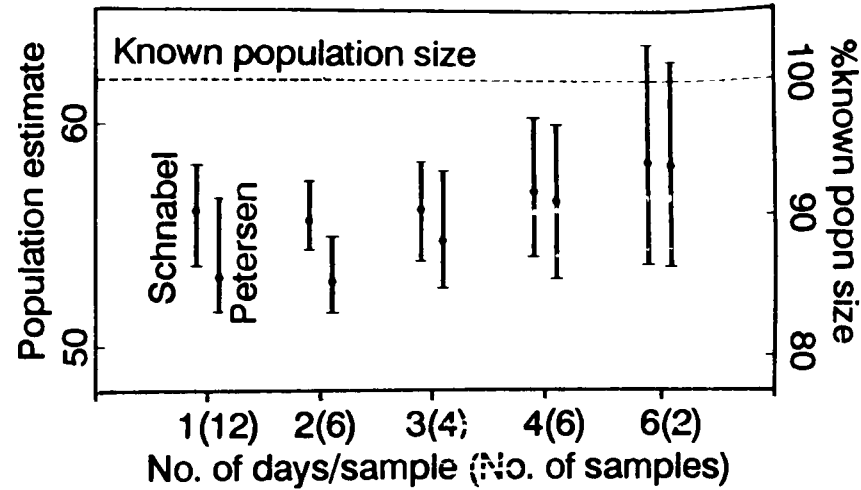
Fig. 3. Population estimates and 95% confidence intervals obtained from samples in which the number of days that comprised a sampling unit varied. The number of these sampling units also varied in order that the total number of days surveyed remained constant.

CONCLUSIONS

Our long-term studies of a well-known resident bottlenose dolphin population have allowed us to begin to compile baseline time series data on population parameters. In addition, this natural laboratory has provided opportunities to empirically test field measurement techniques and some of the more commonly used abundance estimation techniques.

The Schnabel estimator of population size proved to be less biased than the average Petersen estimators. The Petersen estimates produced for each individual sampling period converged toward the Schnabel estimates as the number of sampling periods increased, but this also gave the false appearance of an increasing trend in population size. Both estimators, however, were subject to downward bias caused by heterogeneity. This bias could be reduced by increasing the sampling time and increasing the number of marked animals in the population.

The variances of the estimates can be underestimated if the sighting of one individual is not independent from that of another. We eliminated the calves from this analysis because of the probability of sighting and identifying a calf was not independent from that of its mother. This exclusion, however, removes only the most obvious violation of the assumption of independence of sightings. For social dolphins in general and for this population in particular, associations among individuals are not random and many individuals are sighted consistently together (Wells et al., 1980; 1987). The non-independent probabilities of recognizing individuals would not affect the population estimates, but would have the effect of underestimating the variances (P. Hammond and S. Buckland, pers. comms). Thus, the confidence limits reported here are minimum estimates of the true limits.

Because the precision of the estimate is an important factor in determining the level of change in the population, it underlines the importance of identifying reliably a large percentage of the population. This has implications for the survey designs for examining trends in population sizes, because, as demonstrated by Gerrodette (1987), the number of surveys required to detect a trend will be strongly influenced by the precision of the estimates.

The use of non-lethal techniques such as individual identification and capture-release efforts has provided one of the first data bases of its kind for studies of the dynamics of a resident population of dolphins. The collection of similar kinds of data from other dolphin populations will

allow more in-depth interpretation of the preliminary data presented here. We hope that such time-series data bases can be applied in time to assessing the status of resident dolphin populations and thus towards the use of these animals as biological indicators of the health of inshore ecosystems.

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