



## Decline in local abundance of bottlenose dolphins (*Tursiops truncatus*) in the Bay of Islands, New Zealand

GABRIELA TEZANOS-PINTO<sup>1,2</sup> and ROCHELLE CONSTANTINE, School of Biological Sciences, The University of Auckland, Private Bag 92019, Auckland, New Zealand; LYNDON BROOKS,<sup>3</sup> Southern Cross University Whale Research Group, Marine Ecology Research Centre, Southern Cross University, Lismore 2480, New South Wales, Australia; JENNIFER A. JACKSON, School of Biological Sciences, The University of Auckland, Private Bag 92019, Auckland, New Zealand and Hatfield Marine Science Center, Oregon State University, 2030, Newport, Oregon 97365, U.S.A.; FABIANA MOURÃO and SARAH WELLS,<sup>4</sup> School of Biological Sciences, The University of Auckland, Private Bag 92019, Auckland, New Zealand; C. SCOTT BAKER, School of Biological Sciences, The University of Auckland, Private Bag 92019, Auckland, New Zealand and Hatfield Marine Science Center, Oregon State University, 2030, Newport, Oregon 97365, U.S.A.

### ABSTRACT

Regional populations of bottlenose dolphins (*Tursiops truncatus*) around New Zealand are genetically isolated from each other and the species was recently classified as *nationally endangered* based on relatively small population sizes and reports of high calf mortality. Here, we estimate the abundance and trends in one of these regional populations, the Bay of Islands, using a photo-identification database collected from 1997 to 1999 and from 2003 to 2006, containing a total of 3,841 records of 317 individual dolphins. Estimates of abundance obtained with the robust design fluctuated widely but showed a significant decline in the number of dolphins present in the bay over time (7.5% annual rate of decline). Temporary emigration was random and fluctuated considerably ( $\gamma = 0.18$ , SE = 0.07 to  $\gamma = 0.84$ , SE = 0.06). Apparent survival was estimated at 0.928 (CI = 0.911–0.942). Seasonal estimates (26 seasons) obtained in POPAN also showed a significant decline in abundance (5.8% annual rate of decline). Despite the decline observed in local abundance, dolphins continue to be found regularly in the Bay of Islands, suggesting that fewer dolphins use the bay on regular basis. Consequently, it seems that a change in habitat use, mortality and possibly low recruitment could underlie the apparent local decline.

<sup>1</sup>Corresponding author (e-mail: gaby@pachamama.co.nz).

<sup>2</sup>Current address: Coastal-Marine Research Group, Institute of Natural and Mathematical Sciences, Massey University, Albany Campus, Auckland, New Zealand.

<sup>3</sup>Current address: British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, England.

<sup>4</sup>Current address: Ecology and Conservation Group, Massey University, Albany Campus, Auckland, New Zealand.

Key words: mark-recapture, abundance estimates, robust design, photo-identification, population decline, survival, MARK, POPAN, marine mammals, *Tursiops truncatus*, bottlenose dolphin.

Bottlenose dolphins (*Tursiops truncatus*) in New Zealand are distributed in three discontinuous and genetically differentiated populations; one inhabiting the northern North Island, a second in the Marlborough Sounds and a third in Fiordland (Constantine 2002, Currey and Rowe 2008, Currey *et al.* 2009a, Merriman *et al.* 2009, Tezanos-Pinto *et al.* 2009). Bottlenose dolphins in the northern North Island are known to occur frequently along 500 km of the northeastern coast, from Doubtless Bay to Tauranga (Constantine 2002). Infrequent sightings have been reported elsewhere, extending the range into the Manukau Harbour on the west coast of the North Island (RC, unpublished data; Fig. 1). The Bay of Islands presents a unique opportunity to study the northern North Island population due to the year-round occurrence of dolphins and the presence of a dolphin-watch tourism industry that provides research platforms and facilitates locating the dolphins.

The Bay of Islands (35.14°S, 174.06°E; Fig. 1) is an open embayment of approximately 244 km<sup>2</sup> containing large estuaries and including varying hydrological conditions ranging from estuarine to oceanic (Booth 1974). The nearest distinct coastal population of bottlenose dolphins is approximately 1,000 km south (Bräger

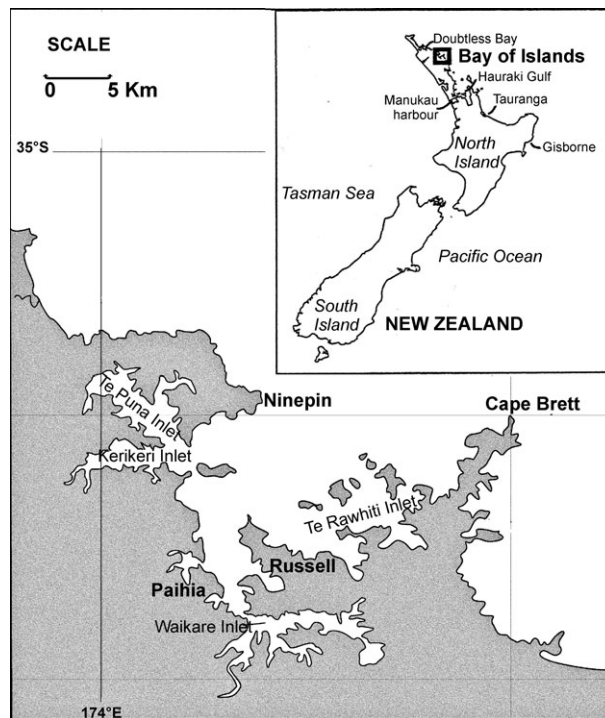


Figure 1. Bay of Islands including the study area (from Ninepin Island to Cape Brett), four inlets and major towns.

and Schneider 1998, Merriman *et al.* 2009) and there is no evidence of genetic interchange between these populations (Tezanos-Pinto *et al.* 2009). In the Bay of Islands, free ranging, non-provisioned bottlenose dolphins have been exposed to dolphin-swim/watch tours since 1991 (Constantine 2001, Constantine *et al.* 2004). Unlike the United States, where regulations prohibit swimming with whales or dolphins, New Zealand allows operators to advertise swimming with dolphins in the wild, subject to the condition that the dolphins are not "harassed." These tours operate under a permitting system that restricts the number and frequency of tour-boats allowing no more than three boats of any type within 300 m of a group of dolphins.<sup>5</sup>

Long-term studies have been conducted in the Bay of Islands, resulting in a photo-identification database that contains 5,577 records of 408 unique individual dolphins sighted in the region at least once from 1993 to 2006 (Ryding 2001, Constantine 2002, Mourão 2006, Tezanos-Pinto 2009). In the Bay of Islands, groups of dolphins range in size from 1 to 60 individuals with a median of 12 dolphins per group (Tezanos-Pinto 2009). Analyses of resighting rates of photo-identified individuals from 1993 to 2006 found that there are no resident dolphins in the Bay of Islands but rather a pattern of varying degrees of habitat use and site fidelity among individuals (frequent users, occasional visitors and transient animals; Constantine 2002, Tezanos-Pinto 2009). At any given time, there is generally only one group of dolphins in the Bay of Islands (Constantine 2002, Tezanos-Pinto 2009), but such groups are seldom stable for more than a few days, showing considerable fission-fusion or simply moving out of the bay to be replaced by others (Mourão 2006). Social affiliations in the Bay of Islands are characterized by two levels of associations including short-term casual acquaintances and long-term companions with intra- and intersexual associations (Mourão 2006).

Coastal populations of bottlenose dolphins around New Zealand seem to have low abundance. The population using the Bay of Islands (*ca.* 244 km<sup>2</sup>) was estimated at 446 dolphins (CV = 4.2%) over the period 1994–1999 using a closed mark-recapture model (Constantine 2002); whereas the Fiordland (minimum *ca.* 450 km<sup>2</sup>) was estimated at 123 dolphins from 1994 to 2006 (CV = 6.7%, Currey *et al.* 2009a) and the Marlborough Sounds (*ca.* 890 km<sup>2</sup>) was estimated at 211 dolphins from 2003 to 2005 (CI = 195–232, Merriman *et al.* 2009). These low abundances are of concern given that all these populations are targeted by tourism and other potentially invasive human activities (*e.g.*, Constantine 2001, Lusseau 2003a, Constantine *et al.* 2004, Lusseau *et al.* 2006, Merriman 2007, Currey *et al.* 2009b). In the Bay of Islands and Fiordland, where tour operators target dolphins, some detrimental effects on the dolphins' behavior have been observed (Constantine 2001, Lusseau 2003a, Constantine *et al.* 2004, Lusseau 2005). Additionally, in these two populations, relatively high levels of calf mortality are reported (42% in the Bay of Islands and 62.5% in Doubtful Sound (Fiordland); Currey *et al.* 2009b, Tezanos-Pinto 2009). The causes of these deaths are uncertain, but studies conducted in Doubtful Sound attributed the causes of high calf mortality to human disturbance (environmental and behavioral) that included increased water discharge from an hydroelectric power plant and dolphin-related tourism activities (Lusseau 2003a, Currey *et al.* 2009b). Because of the high calf mortality reported, the genetic

<sup>5</sup>Marine Mammal Protection Regulations, 1992. Department of Conservation, Wellington, New Zealand.

isolation between populations and assumed small local population sizes, New Zealand bottlenose dolphins have been recently classified as *nationally endangered* according to the New Zealand Threat Classification System (Baker *et al.* 2010) and the Fiordland population has been classified by the IUCN as *critically endangered* (Currey *et al.* 2009a).

Here, we implement two approaches to estimate the abundance and apparent survival of bottlenose dolphins in the Bay of Islands using capture-recapture records of naturally marked individuals during two periods of consistent research effort and survey methodologies (1997–1999 and 2003–2006): (1) Pollock's Robust Design (RD; Pollock 1982, Kendall *et al.* 1997) with data extracted from the complete data set to fit a robust design sampling structure of closely adjacent secondary samples (*i.e.*, day surveys) within more widely separated primary samples (*i.e.*, sampling survey bouts, hereafter termed "sessions"). These were then used to estimate the number of dolphins present in the Bay of Islands during each session, rates of temporary emigration and apparent survival. For the RD, we did not collapse sighting data by seasons or years to avoid potential violations to the assumption of closure within primary samples (Pollock 1982). (2) The Schwarz and Arnason "super population" parameterization of the Jolly-Seber model (*i.e.*, POPAN; Crosbie and Manly 1981, Schwarz and Arnason 1996) with data pooled by seasons to gain an understanding of the seasonal pattern of survival rates and abundance of animals that visited the area in each season (*i.e.*, users and visitors; Williams *et al.* 2002). This approach also provides an estimate of the "super population," the total number of animals that used the area during the course of the study.

## MATERIALS AND METHODS

### *Field Methods*

The Bay of Islands (35.14°S, 174.06°E; Fig. 1) is an open embayment of approximately 244 km<sup>2</sup>, bordered by Ninepin Island and Cape Brett, containing large estuaries and including varying hydrological conditions ranging from estuarine to oceanic (Booth 1974). Photo-identification photographs of bottlenose dolphins were collected during small-boat surveys or from dolphin-watch vessels during two research periods; 1997–1999 and 2003–2006. Surveys were carried out in reasonable weather conditions (Beaufort scale  $\leq 3$ ). The area was searched extensively, but nonsystematically by an independent research vessel and dolphin-watch vessels (Table 1). Typically, there were several observers maintaining a constant survey for dolphins. Stops were often made to scan the area with the naked eye and using binoculars until a group of dolphins was sighted. Permitted dolphin-watching boats communicated and assisted each other locating the dolphins and would report if more than one group of dolphins were sighted. Depending on the season, the number of permitted dolphin-watch operators ranged from one to six, providing good coverage of the study area. During surveys, boats were driven carefully to minimize disturbance to the dolphins (Constantine *et al.* 2004). For each encounter, basic data were collected, including time, GPS position (using a Garmin 45XL GPS), group size and age-class composition, behavior and individual photo-identification data. Attempts were made to collect photo-identifications of each individual in the group without bias towards distinctively marked dolphins (Würsig and Jefferson 1990).

### Photo-identification

All dorsal fin photographs were classified into four categories of quality (excellent, good, fair, and poor) according to focus, size of the dorsal fin relative to the frame, exposure (contrast between dorsal fin and background) and relative angle to the dolphin. This was consistent with studies conducted on bottlenose dolphins in other regions (Wilson *et al.* 1999, Silva *et al.* 2009). Only excellent and good quality photographs were matched to the Bay of Islands catalog and included in the analyses. Nicks and cuts on the trailing edge of the dorsal fin were the only feature used for identification purposes (Wilson *et al.* 1999). In the bottlenose dolphin such marks allow individual recognition equally from left and right sides (Hammond *et al.* 1990, Würsig and Jefferson 1990).

Photographs of unique individuals were graded according to a scale including three levels of distinctiveness ranging from one (small marks) to three (large marks). Before adding a new individual into the catalog images were checked by three experienced researchers and all photographs were cross-matched to the rest of the catalog. After a match was confirmed (or a new individual identification number was assigned), data were entered into a database.

The Bay of Islands catalog is a curated collection of photographs of individually identified bottlenose dolphins collected since December 1993, in a single reconciled database. The catalog contains the best image of a dorsal fin of a unique individual. The photographic quality of the images used in the catalog and the distinctiveness of nicks used for individual identification were evaluated using the quality scale described above. The quality control review resulted in the exclusion of 40 individuals from the catalog that were included in some previous analyses (Ryding 2001, Constantine 2002, Mourão 2006), leaving a total of 408 individually identified dolphins in the catalog used in this study.

### Mark Ratio

As with other wild populations of dolphins, not all individuals bear sufficient marks for individual recognition. To account for these unmarked dolphins in the local Bay of Islands population, we estimated a mark ratio (Jolly 1965). High quality photographs (only excellent and good quality) were counted including all age-classes to estimate the ratio of individually identifiable dolphins (*i.e.*, marked animals) during 2003–2006. The proportion of marked dolphins ( $P_m$ ) and its variance were estimated (Gormley *et al.* 2005) as follows:

$$\hat{P}_m = \frac{\sum_{i=1}^k \frac{I_i}{T_i}}{k}, \text{ var}(\hat{P}_m) = \left( \sum_{i=1}^k \frac{\hat{P}_{m_i}(1 - \hat{P}_{m_i})}{T_i} \right) / k^2$$

where  $I_i$  is the number of photographs of identifiable (*i.e.*, marked) dolphins,  $T_i$  is the total number of excellent and good quality photographs taken during the  $i$ th sampling day and  $k$  is the total number of sample days for which  $I/T$  was calculated ( $k = 26$ ); for each  $\hat{P}_{m_i} = I_i/T_i$ . Abundance estimates were scaled by the mark-ratio to obtain the total abundance  $\hat{N}_{total}$  (Williams *et al.* 1993) as follows:

$$\hat{N}_{total} = \hat{N}_m / \hat{P}_m$$

where  $\hat{N}_m$  is the abundance of marked dolphins. The variance (var) and standard error (SE) of  $\hat{N}_{total}$  were calculated (Wilson *et al.* 1999) as follows:

$$\text{var}(\hat{N}_{total}) = (\hat{N}_{total})^2 \left( \text{var}(\hat{N}_m) / (\hat{N}_m)^2 + \text{var}(\hat{P}_m) / (\hat{P}_m)^2 \right),$$

$$\text{SE}(\hat{N}_{total}) = \sqrt{\text{var}(\hat{N}_{total})}$$

Log-normal confidence intervals were calculated (Burnham *et al.* 1987) as follows:

$$\hat{N}_{lower} = \hat{N}_{total} / C \text{ and } \hat{N}_{upper} = \hat{N}_{total} \cdot C, \text{ where } C = \exp \left( z_{\alpha/2} \sqrt{\log_e \left[ 1 + (cv(\hat{N}_{total}))^2 \right]} \right)$$

where  $\hat{N}_{lower}$  is the lower bound of the confidence interval,  $\hat{N}_{upper}$  is the upper bound of the confidence interval  $Z_{\alpha/2}$  is the normal deviate,  $\alpha = 0.05$  and  $cv$  is the coefficient of variation.

#### Data Organization

A “sighting” refers to an individual identification photograph obtained during an encounter with a uniquely identified dolphin (ID) and the associated data collected during such an encounter (*e.g.*, date, GPS position, group composition). The complete individual sighting record constitutes the encounter history of a dolphin. Field effort was not originally designed to fit within a RD modeling framework (Pollock 1982, Kendall *et al.* 1997), but the large number of sighting records allowed for extraction of a subset of data with a suitable structure to implement the RD for the periods 1997–1999 and 2003–2006.

Individual photo-identification data from bottlenose dolphins in the Bay of Islands collected during 1997–1999 and 2003–2006 were structured into two data sets: (1) sessions for RD and (2) seasons for POPAN.

For (1) A subset of the data set 1997–1999 and 2003–2006 was selected into a hierarchical structure (primary samples or sessions, secondary samples within primary samples) to allow implementation of the RD, gain an understanding of the number of dolphins present in the Bay of Islands in each session, and estimate rates of survival and temporary emigration between sessions. Sighting data were selected in closely adjacent clusters of days with discrete breaks between clusters, to implement the selection of secondary samples (*i.e.*, sampling days) and primary samples (sessions). Secondary periods were composed of near-consecutive day-surveys with a minimum of two and a maximum of nine day-surveys (median four day-surveys), and primary samples were separated by a minimum of 22 d (0.06 decimal years) and a maximum of 1,127 d (3.1 decimal years) between their mid dates (median 80 d or 0.22 decimal years). For the RD, we did not collapse sighting data by seasons or years to avoid violation of the assumption of closure within primary samples (Pollock 1982).

Table 1. Summary of photo-identification (photo-ID) effort conducted in the Bay of Islands using similar methodologies during 1997–1999 and 2003–2006 including surveys from an independent research vessel (IRV) and tour boats (TB).

	1997	1998	1999	2003	2004	2005	2006
Photo-ID surveys	59	88	99	47	91	51	16
Surveys IRV	25	16	60	10	13	44	10
Surveys TB	34	72	39	37	78	7	6
Hours on survey	189	318	395	194	367	320	89.1
Groups encountered	47	79	72	57	103	83	22
Total ID dolphins	182	166	162	110	117	85	69
Total sightings	531	726	454	390	860	639	241
Total sightings	1,711			2,130			
Total ID dolphins	256			159			
Total groups encountered	198			265			

For (2) the data sets for 1997–1999 and 2003–2006 were pooled by austral seasons for analysis in POPAN to estimate survival, abundance and any trends over time of animals by season, and to estimate the total number that used the area during the course of the study (the “super population”).

### Statistical Analysis

Pollock’s Robust Design models were fitted to the data set structured into sessions (data set 1) and POPAN models were fitted to the seasonal data (data set 2). All models were fitted using program MARK (Vs 5.1).

### Robust Design Model

The data were organized in a hierarchical sampling structure of primary samples (sessions) and secondary samples (daily surveys within sessions). The intervals between sessions were specified in decimal years between their mid dates to obtain consistent, per annum estimates of survival. For each session we estimated the capture probability ( $p$ ) and abundance ( $N$ ) of dolphins in the bay. From the intervals between sessions, we estimated the apparent survival probability ( $\phi$ ), the probability that an animal is outside the study area in a sampling occasion given that it was inside the study area in the previous occasion ( $\gamma''$ ), and the probability that an animal is outside the study area in a sampling occasion given that it was outside the study area in the previous occasion ( $\gamma'$ ; Kendall *et al.* 1995, 1997). Models were considered with temporal variation in capture probabilities between ( $s$  = sessions or primary samples), within ( $t$  = daily surveys within a session, secondary samples) and both between and within primary periods ( $s^*t$ ). Recapture probabilities were constrained to equal capture probabilities on each occasion for all models because there was no evidence of a behavioral effect (refer to Table 2). We initially used the “closed models” option in MARK to fit models without heterogeneity in capture probability and subsequently evaluated heterogeneity using the “closed captures with heterogeneity” option with two mixtures (unidentified groups of animals with different capture probabilities, Pledger 2000). For models assuming no heterogeneity we fitted models with no temporary emigration (*i.e.*,  $\gamma'' = \gamma' = 0$ ), random (*i.e.*,  $\gamma'' = \gamma'$ ) and Markovian tempo-



Table 2. Data sets employed for mark-recapture estimates including type of pooling, start, end of period, number of occasions and number of unique individual dolphins captured (ID captured). Table 2a. Summary data for the Robust Design (RD). The CAPTURE model selection criterion (MSC, as implemented in MARK) was used to evaluate the best closed model. Table 2b. Summary data for POPAN as implemented in MARK including the number of unique dolphins captured (ID captured) and the number of unique dolphins captured excluding the first capture occasion (ID no first capture).

Year	Session	Start date	End date	Occasions	ID Captured	MSC
<i>a.</i> Summary table for the RD data set structured into sessions.						
1997	1	22 February	27 February	5	29	$M_r$
	2	15 April	23 April	5	21	$M_r$
	3	6 July	20 July	4	45	$M_o$
1998	4	3 October	13 October	4	59	$M_o$
	5	11 January	15 January	4	33	$M_o$
	6	4 March	17 March	5	75	$M_r$
	7	3 May	10 May	6	27	$M_o$
	8	11 September	25 September	5	42	$M_o$
1999	9	1 December	13 December	4	29	$M_o$
	10	4 January	18 January	5	29	$M_r$
	11	8 March	20 March	7	64	$M_r$
	12	18 June	30 June	6	24	$M_o$
2003	13	18 August	25 August	4	32	$M_{rb}$
	14	9 December	23 December	3	45	$M_{rb}$
	15	16 January	21 January	4	55	$M_o$
	16	26 April	28 April	3	32	$M_o$
	17	10 July	12 July	3	11	$M_o$
2004	18	2 December	6 December	5	65	$M_o$
	19	7 June	9 June	3	15	$M_{rb}$
	20	14 October	20 October	5	57	$M_{rb}$
2005	21	15 November	21 November	5	53	$M_{rb}$
	22	7 December	12 December	6	58	$M_r$
	23	24 February	26 February	3	33	$M_{rb}$
	24	5 April	9 April	5	15	$M_{rb}$
	25	13 September	24 September	10	55	$M_r$
2006	26	9 November	20 November	6	65	$M_r$
	27	9 February	13 February	4	48	$M_r$
	28	21 March	24 March	4	45	$M_r$

Year	Season	Start date	End date	Occasions	ID captured (ID no. first capture)	
<i>b.</i> Summary table for the seasonal POPAN data set.						
1997	1	Summer	6 January 1997	28 February 1997	17	73 (0)
	2	Autumn	2 March 1997	25 May 1997	18	86 (34)
	3	Winter	7 June 1997	17 August 1997	7	60 (39)
	4	Spring	1 September 1997	20 November 1997	11	96 (62)
1997–1998	5	Summer	15 December 1997	28 February 1998	14	91 (74)
1998	6	Autumn	1 March 1998	30 May 1998	25	136 (118)
	7	Winter	4 June 1998	22 August 1998	14	61 (61)
1998–1999	8	Spring	11 September 1998	10 October 1998	7	45 (43)
	9	Summer	1 December 1998	18 February 1999	14	68 (60)
1999	10	Autumn	8 March 1999	3 May 1999	11	86 (72)
	11	Winter	1 June 1999	25 August 1999	18	81 (76)
	12	Spring	17 October 1999	25 November 1999	6	39 (37)
1999–2000	13	Summer	9 December 1999	23 December 1999	3	45 (34)
2002–2003	14	Summer	15 January 2003	22 January 2003	10	39 (34)

(Continued)



Table 2. (Continued)

Year	Season	Start date	End date	Occasions	ID captured (ID no. first capture)	
2003	15	Autumn	26 April 2003	28 April 2003	3	32 (26)
	16	Winter	3 June 2003	12 July 2003	9	31 (28)
	17	Spring	25 September 2003	30 November 2003	8	26 (22)
2003–2004	18	Summer	1 December 2003	6 December 2003	6	66 (54)
2004	19	Winter	7 June 2004	30 August 2004	8	26 (24)
	20	Spring	22 September 2004	21 November 2004	24	93 (71)
2004–2005	21	Summer	7 December 2004	26 February 2005	12	72 (69)
2005	22	Autumn	5 April 2005	9 April 2005	5	15 (15)
	23	Winter	10 June 2005	28 July 2005	8	18 (18)
	24	Spring	20 September 2005	20 November 2005	24	75 (74)
2005–2006	25	Summer	8 February 2006	13 February 2006	6	49 (48)
2006	26	Autumn	21 March 2006	1 May 2006	7	64 (63)

rary emigration (*i.e.*,  $\gamma'' \neq \gamma'$ ) (Huggins 1991, Kendall *et al.* 1997). We assumed no temporary emigration for our assessment of models with heterogeneity to limit the number of parameters estimated. To provide parameter identifiability for the Markovian models, we either constrained survival ( $\phi$ ) to be constant or added a constraint (session  $k =$  session  $k - 1$ ) resulting in the last two parameters in the time series set to equal (Kendall *et al.* 1997).

#### POPAN Model

A super population approach was applied in POPAN, as implemented in MARK, to estimate the seasonal abundance and apparent survival rates of bottlenose dolphins along the northern North Island that use the Bay of Islands and the total number of animals that used the area during the course of the study. The approach is based on a reparameterization of the Jolly-Seber (JS) model with an additional parameter  $N_{\text{super}}$  that denotes the size of the super population. The intervals between seasons were specified in decimal years between their mid dates to obtain consistent, per annum estimates of apparent survival and other parameters. The model estimates the apparent survival probability ( $\phi$ ) and probability of entry ( $\beta$ ) between seasons, the capture probability ( $p$ ), and abundance ( $N$ ) of dolphins for each season, and the total number of dolphins that used the bay through 1997–1999 and 2003–2006 ( $N_{\text{super}}$ ). Models were considered with constant ( $\cdot$ ) and temporal variation ( $t$ ) in capture probabilities between seasons. We added a constraint to the first two and the last two capture probabilities to provide parameter identifiability for all models (Cooch and White 2011).

#### Goodness of Fit Tests and Model Selection

The RD does not have a goodness of fit test, however because this method is a combination of open and closed models, traditional tests for open and closed models can be applied. Consequently, each session was tested for closure using CloseTest (Stanley and Burnham 1999) and analyzed in CAPTURE (as implemented in MARK; White and Burnham 1999) to examine potential effects of behavioral response and heterogeneity. Data were pooled into sessions and analyzed in a Cormack-Jolly-Seber (CJS) framework in order to estimate the variance inflation factor ( $\hat{c}$ ) and to carry out goodness of fit tests. Median  $\hat{c}$  was estimated in MARK (White and Burnham 1999, Cooch and

White 2011). Where median  $\hat{c} > 1$  (indicative of overdispersion in the data) we incorporated  $\hat{c}$  into a QAIC<sub>c</sub> statistic and used this instead of AIC<sub>c</sub> in model selection (Quasi-likelihood Akaike Information Criterion; Burnham and Anderson 2002).

Goodness of fit tests (TEST 2 and TEST 3) were run in U-CARE V 2.2 (Choquet *et al.* 2005) to evaluate potential violations of assumptions for both data sets. A significant result in TEST 2 indicates that capture probabilities differ among individuals (heterogeneity). TEST 2 can be further partitioned into TEST 2.CT, which examines whether there is a behavioral response to the first capture (trap-avoidance statistic  $z > 0$ , trap-happy statistic  $z < 0$ ) and TEST 2.CL, which examines whether there is variation in the time between re-encounters for captured and not captured (but known to be alive) individuals. A significant result in TEST 2.CL indicates that the trap effect lasts for more than one interval. TEST 3 evaluates the assumption that all individually identifiable dolphins have the same probability of survival between sampling occasions. TEST 3 is partitioned into two additional tests: TEST 3.SR incorporates a statistic for transience, with a significant result ( $z > 0$ ;  $P < 0.05$ ) suggesting a transience effect (*i.e.*, dolphins sighted only once during the course of the study more often than expected), whereas TEST 3.SM examines whether there is an effect of capture on survival (Choquet *et al.* 2005).

## RESULTS

### *Survey Effort and Data Sets*

A total of 246 field surveys were conducted during 1997–1999, including 145 surveys conducted from tour boats and 101 from an independent research vessel (1.44 tour boats to 1 research vessel). During 2003–2006, a total of 205 field surveys were conducted, including 128 conducted from tour boats and 77 from an independent research vessel (1.66 tour boats to research vessel).

The 1997–1999 data set contained a total of 1,711 sightings records of 198 groups, representing 256 individual dolphins observed during 246 surveys. The 2003–2006 data set contained a total of 2,130 sightings records of 265 groups, representing 159 individual dolphins observed during 205 surveys. Overall, the two data sets (1997–1999 and 2003–2006) included a total of 3,841 sighting records of 317 unique individual dolphins.

The data sets used for our analyses included: (1) 28 sessions for the RD resulting in a total of 2,017 sighting records of 290 unique individual dolphins from a total of 133 survey days (Table 2a) and (2) 26 seasonal data for 1997–1999 and 2003–2006 for POPAN totaling 1,574 sighting records of 317 unique individuals. There were only two records during autumn 2004 and this season was excluded from the analyses (Table 2b).

### *Mark Ratio*

The mark ratio was estimated from a total of 2,293 high-quality photographs collected from 26 surveys during 2003–2006. Of these, 1,640 photographs represented identifiable individuals (*I*). From this, the mark ratio ( $P_m$ ) was estimated at 0.720 (SE = 0.11).

### Goodness of Fit Tests

Results from CloseTest indicated that all our primary sessions for the RD were closed (data not shown). The model selection procedure from CAPTURE selected 11 models with equal catchability for all dolphins at all times ( $M_0$ ), 10 models with catchability varying by time ( $M_t$ ), 7 models with catchability varying both by time and among dolphins (heterogeneity) ( $M_{tb}$ ), and none with behavioral responses to first capture (trap-happiness, trap-shyness; Table 2a).

Goodness of fit tests conducted in U-CARE for both sets of data (by sessions and seasons) indicated significant overdispersion (RD by sessions GLOBAL TEST 2 + 3:  $P < 0.0001$ ,  $\chi^2 = 295$ ,  $df = 104$ ,  $\hat{c} = 2.84$ ; POPAN by seasons GLOBAL TEST 2 + 3:  $P < 0.0001$ ,  $\chi^2 = 320$ ,  $df = 127$ ,  $\hat{c} = 2.52$ ). There was evidence of a “trap-happy” effect in both data sets (Table 3) and the effect lasted for more than one interval (significant result of TEST 2.CL). There was no evidence of an effect of capture on survival (nonsignificant Test 3.SM, Table 3). Both data sets showed an excess of individuals sighted only once (*i.e.*, effect of transience; Test 3.SR). To account for this, we excluded the first encounter of every individual from the seasonal data set and reran the goodness of fit tests and the models in POPAN (Pradel *et al.* 1997). For this data set, results from the transience test (Test 3.SR) were not significant (Table 3). For the RD analyses we did not remove sightings because we were interested in obtaining estimates of the total number of dolphins present in the bay from session to session despite the dolphins’ pattern of habitat use.

### Robust Design Analyses

The RD data set by sessions resulted in an estimated median  $\hat{c} = 2.57$  (SE = 0.102); model selection therefore used QAIC<sub>c</sub> calculated with this value. We first attempted to simplify the capture probability structure but models with fully time-varying captures ( $s^{*t}$ ) were strongly favored. We then tested models with dependence in capture probabilities  $p(s^{*t})$  and constant survival probability  $\phi$  (.) (models 1, 2, 7, 9–12). The likelihood ratio test (LRT) rejected models with no temporary emigration (models 6, 7, 10) when tested against models with random

Table 3. Results from Goodness of Fit tests run in U-CARE for the two different mark-recapture data sets (sessions and seasons) of bottlenose dolphins collected during 1997–1999 and 2003–2006, including the results of the global test (Test 2 + 3).

		Test 3.SR	Test 3.SM	Test 2.CT	Test 2.CL	Global test
RD data by sessions	P-value	0.0001	0.61	0.002	0.05	0.0001
	Statistic	5.85		-4		
	df	16	23	25	40	104
	$\chi^2$	70.47	20.6	81.2	122.5	295
POPAN data by seasons	P-value	0.0001	0.07	0.0001	0.05	0.0001
	Statistic	5.4		-9.3		
	df	16	22	23	41	107
	$\chi^2$	53.75	32.8	129.6	81.7	316.2
POPAN data by seasons no first capture	P-value	0.18	0.07	0.0001	0.05	0.001
	Statistic	1.34		-6.4		
	df	13	20	22	26	81
	$\chi^2$	8.3	37.05	79.9	59.5	184.5

Table 4. Model selection for 1997–1999 and 2003–2006 sighting data of bottlenose dolphins in the Bay of Islands. Model results are for Robust Design (RD) data structured into sessions (top), and POPAN data pooled by seasons without the first capture of each individual (bottom).

	Model	QAICc	Delta QAICc	AICc weight	ML	NP	Qdev
<b>Robust design models: data by sessions</b>							
1	$\Phi(.) \gamma(.) p_G^*(t) c(=p) N_G$	1,611.220	0	0.98431	1	188	2,628.09
2	$\Phi(.) \gamma''(.) \gamma'(.s) p_G^*(t) c(=p) N_G$	1,619.500	8.280	0.01567	0.0159	214	2,572.07
3	$\Phi_G) \gamma'(.s) p_G^*(t) c(=p) N_G$	1,633.310	22.090	0.00002	0	214	2,585.88
4	$\Phi_G) \gamma''(.s, k = k - 1) \gamma'(.s, k = k - 1) p_G^*(t) c(=p) N_G$	1,652.886	41.666	0	0	238	2,544.42
5	$\Phi_G) \gamma'(.s) p_G^*(t) c(=p) N_G$	1,653.047	41.828	0	0	188	2,669.92
6	$\Phi_G) \gamma = \gamma' = 0 p_G^*(t) c(=p) N_G$	1,653.495	42.276	0	0	188	2,670.37
7	$\Phi_G) \gamma = \gamma' = 0 p_G^*(t) c(=p) N_G$	1,694.391	83.172	0	0	188	2,711.26
8	$\Phi_G) \gamma'(.s) p_G^*(t) c(=p) N_G$	1,807.908	196.688	0	0	321	2,474.92
9	$\Phi_G) \gamma''(.s) \gamma'(.s) p_G^*(t) c(=p) N_G$	1,827.550	216.331	0	0	323	2,488.88
10	$\Phi_G) \gamma = \gamma' = 0 p_G^*(t) c(=p) N_G$	1,832.137	220.917	0	0	322	2,496.31
11	$\Phi_G) \gamma'(.s) p_G^*(t) c(=p) N_G$	1,854.837	243.617	0	0	322	2,519.01
12	$\Phi_G) \gamma''(.s) \gamma'(.s) p_G^*(t) c(=p) N_G$	2,412.043	800.823	0	0	531	2,397.77
<b>Seasonal POPN data; no first capture</b>							
1	$\Phi(.) p(t, p_1 = p_2, p_k = p_k - 1) B(.) N$	1,455.734	0	0.998	1	27	465.19
2	$\Phi(.) p(t, p_1 = p_2, p_k = p_k - 1) B(.) N$	1,469.111	13.379	0.001	0	51	427.39
3	$\Phi(t) p(t, p_1 = p_2, p_k = p_k - 1) B(.) N$	1,480.653	24.919	0	0	51	438.93
4	$\Phi(t) p(t, p_1 = p_2, p_k = p_k - 1) B(.) N$	1,495.659	39.925	0	0	75	400.68

Abbreviations: apparent survival ( $\phi$ ), capture ( $p$ ), recapture ( $p'$ ) and temporary emigration ( $\gamma$ ) probabilities, Qdev = deviance. For the RD:  $s$  = sessions or primary samples,  $t$  = daily surveys within a session and  $s^*$  = variation between and within primary periods. For POPAN:  $t$  = seasons. The lowest QAICc value represents the model that has the most support from the data. NP denotes the number of parameters. Notation:  $\gamma' = \gamma' = 0$ : no temporary emigration;  $\gamma''(x) = \gamma'(x)$ : random temporary emigration model;  $\gamma'(x) \gamma'(x)$ : Markovian temporary emigration model;  $(p)$  mixture proportion;  $(.)$  constant parameter;  $p(x) = c(x) =$  no behavioral effect (following Kendall *et al.* 1997).

( $\chi^2 = 83.2$ ,  $df = 28$ ,  $P < 0.0001$ ) and Markovian ( $\chi^2 = 139.2$ ,  $df = 54$ ,  $P < 0.0001$ ) temporary emigration. QAICc indicated that models with random temporary emigration (models 1, 3, 5, 8, 11) received more support from the data than models with Markovian emigration (models 2, 4, 9, 12; Table 4). Models incorporating heterogeneity (models 8–12) did not receive much support from the data and results from the LRT were not significant (model 1 *vs.* model 8, LRT:  $\chi^2 = 153.2$ ,  $df = 133$ ,  $P < 0.116$ ), indicating no advantage for heterogeneity models.

The best fitting model assumed constant survival, random temporary emigration varying by sessions and fully time-varying capture probabilities (model 1). This model attracted 98.4% of the QAICc weight in the model set. Capture probabilities were highly variable within and between sessions ranging from 0.11 to 0.91 (data not shown). Estimates of abundance varied considerably from a high of 240 dolphins (95% CI = 99–581) in October 1997 to a low of 21 (95% CI = 14–31) in October 2004 and September 2005 (95% CI = 15–28), reflecting fluctuating numbers of dolphins present in the area from session to session (Fig. 2). Values of temporary emigration varied considerably and had low precision. The random emigration model estimated a minimum probability of 0.182 (95% CI = 0.08–0.37) and a maximum probability of 0.820 (95% CI = 0.71–0.94) for an individual to move out ( $\gamma'$ ) or remain outside of the study area ( $\gamma''$ ). The model estimated a constant apparent survival rate of 0.928 (SE = 0.008; 95% CI = 0.911–0.942). Abundance estimates by sessions varied widely but showed a 7.5% rate of annual decline. A linear regression fitted to the natural log (ln) of the RD estimates of abundance by sessions resulted in a significant decline (SE = 0.609  $P < 0.011$ ).

### POPAN Analyses

The POPAN models for the seasonal data set without the first capture were adjusted for an estimated median  $\hat{c} = 2.53$  (SE = 0.13). The best fitting model for this data set incorporated constant survival, time-varying capture probability (with a

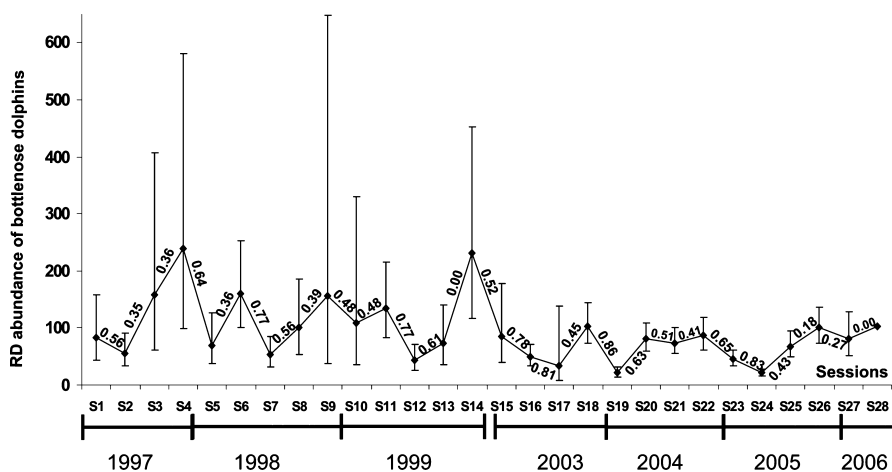


Figure 2. Robust design estimates of bottlenose dolphins (marked and unmarked) found in the Bay of Islands during survey sessions from 1997–1999 and 2003–2006, including 95% confidence intervals and estimates of temporary emigration.

constraint) and constant probability of entry (model 1, Table 4). This model carried 99.9% of the QAICc weight. Capture probabilities ranged from a high of 0.86 (SE = 0.05) during autumn 1998 to 0.16 (SE = 0.06) during summer 2004–2005. Seasonal estimates of abundance excluding the first capture of each individual, varied from a

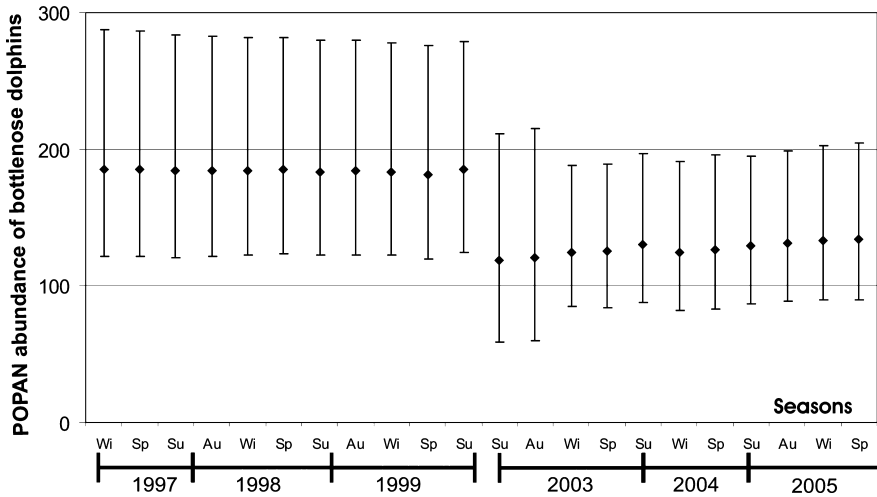


Figure 3. Seasonal abundance estimates of bottlenose dolphins (marked and unmarked) in the Bay of Islands from 1997–1999 and 2003–2006 obtained with POPAN (excluding transients) including 95% confidence intervals. Abbreviations: Su = summer, Au = autumn, Wi = winter, Sp = spring.

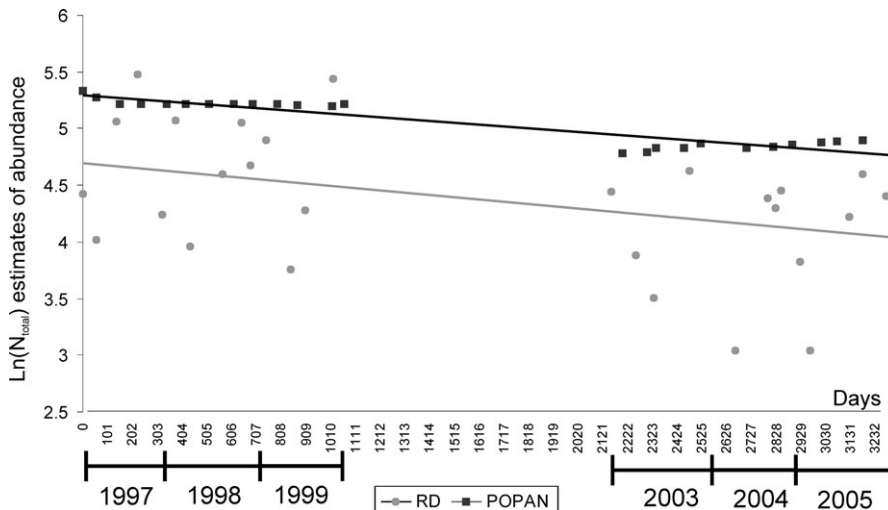


Figure 4. Natural log ( $\ln$ ) of abundance estimates of bottlenose dolphins (marked and unmarked) in the Bay of Islands obtained with POPAN (seasons) and Robust design (RD by sessions) during 1997–1999 and 2003–2006.

high of 185 dolphins in autumn-winter 1997 (CI = 122–285) to a low of 119 dolphins (CI = 79–182) during summer 2002–2003 (Fig. 3). The probability of entry ( $\beta$ ) was estimated to be constant at 0.019 (SE = 0.002, CI = 0.0015–0.025). The probability of apparent survival excluding transient dolphins was 0.85 (SE = 0.019). Abundance estimates by seasons varied but showed a 5.8% rate of annual decline. A linear regression fitted to the natural log (ln) of the estimates of abundance resulted in a significant decline ( $r^2 = 0.87$ , SE = 0.186,  $P < 0.001$ ; Fig. 4).

The Bay of Islands super population including transient animals ( $n = 84$ ) through 1997–1999 and 2003–2006 was estimated at 348 marked dolphins (SE = 6.47, 95% CI = 336–361). Correcting this value for the unmarked proportion of the population (28%) the total super population ( $N_{\text{super}}$ ), was estimated at 483 dolphins (SE = 74.7, 95% CI = 358–653).

## DISCUSSION

### *Estimates of Abundance*

We have estimated the number of dolphins present in the Bay of Islands across nearly 10 yr of surveys using both the RD model for those using the bay across sessions and with the POPAN open population models across seasons. We found consistent and significant declines in abundance between 1997 and 2006 for both models (see below).

The estimates of abundance by session from the RD varied considerably but showed a significant 7.5% annual rate of decline from a high of 240 dolphins (95% CI = 99–581) in October 1997 to a low of 21 (95% CI = 14–31) in October 2004 and September 2005 (95% CI = 15–28). The estimates of temporary emigration were highly variable and sometimes large. Such large fluctuations in abundance and temporary emigration rates indicate highly variable use of the area through time. POPAN estimates by season were consistent within periods but differed between periods showing a 5.8% annual rate of decline in the number of dolphins that visited the bay more than once during each season.

Estimates of abundance of bottlenose dolphins in the Bay of Islands were variable per session and season, suggesting differing patterns of habitat use among individuals. The Bay of Islands is only a part of the range of a larger population of bottlenose dolphins. The super population estimates from POPAN suggested that 483 (SE = 74.7, 95% CI = 358–653) dolphins used the area at least once, during the course of the study (1997–2006). This estimate includes those animals that may have died or permanently emigrated.

Behavioral response to capture was observed between sessions and seasons but not within sessions. The behavioral response identified was “trap-happy,” which could result from individuals displaying a preferential response to the research boat or from preferential habitat use by a small subset of the population (Constantine 2002, Tezanos-Pinto 2009). Dolphin groups stay in the bay over varying periods of time (e.g., during a session); however group membership fluctuates considerably given the fission-fusion nature of their associations including dolphins’ preferred and avoided companions (Mourão 2006). This resulted in some individuals being encountered more often than others. We suggest that it was the group structure that was detected in the goodness of fit test as overdispersion (nonindependence of capture probabilities) and preferential use of the habitat by some dolphins. Unmodeled trap-happiness



biases estimates of abundance downwards causing underestimation of this parameter, and this effect may be present in our results.

### *Apparent Survival Rates*

Apparent annual survival rates between sessions obtained with the RD (0.928, SE = 0.008) were higher than the values estimated with POPAN by seasons (0.850, SE = 0.019, data set POPAN by seasons without first capture). In POPAN, permanent emigration is confounded with apparent survival (*i.e.*, death + emigration) and temporary emigration (not estimable in POPAN) can affect capture probability with a knock-on effect on survival probability. The RD estimate of survival takes temporary emigration into account, resulting in a higher and perhaps, less biased estimate. The RD estimate of apparent survival is comparable with the range reported for other bottlenose dolphin populations, such as Sarasota Bay, Florida (0.962, SD = 0.0076, Wells and Scott 1990) and Doubtful Sound, New Zealand (0.937, CI = 0.917–0.953, Currey *et al.* 2009b), or dolphins in captivity (0.93, CI = 0.92–0.94, DeMaster and Drevenak 1988). RD estimates of survival over time did not show a trend; however, confidence intervals were large (data not shown). Analyses conducted here do not exclude the possibility that increased mortality might have caused the decline in abundance in the local Bay of Islands bottlenose dolphin population. Evidence of mortality however, is scarce and relies on beach-cast carcasses, observation of predation events or reports of bycaught dolphins. Analysis of the New Zealand stranding database<sup>6</sup> did not suggest an increase in mortality events throughout the course of the study (Tezanos-Pinto 2009). Similarly, reports of by-catch and predation events on bottlenose dolphins are rare and infrequent (Constantine 2002, Tezanos-Pinto 2009). This information suggests multiple causes of bottlenose dolphin mortality, but is not sufficiently detailed to allow accurate estimates of true mortality.

### *Decline in Local Abundance in the Bay of Islands*

While there was a considerable variation in the abundance estimates, especially from the RD model, both approaches showed a declining trend. However, the encounter ratio (*i.e.*, the number of days with dolphin encounters over the total number of days surveyed) increased from 0.69 in 1997–1999 to 0.87 in 2003–2006 (Tezanos-Pinto 2009) suggesting that fewer dolphins were sighted more frequently. Recent research conducted in the area indicates that dolphins are still sighted in the Bay of Islands on a regular basis (encounter ratio = 0.80; Hartel 2010).

We consider two nonexclusive scenarios to explain the decline in local abundance in the Bay of Islands: (1) A “true” population decline in the larger northern North Island population as a result of increased mortality and/or lowered recruitment through reproduction or (2) an “apparent” decline in the local abundance caused by a shift in habitat use (*i.e.*, increased emigration, less frequent use of the bay).

*Scenario 1: A true population decline in the larger northern North Island population resulting from increased mortality and/or lowered recruitment through reproduction*—The survival

<sup>6</sup>Unpublished data from the New Zealand Marine Mammal Stranding Database, Museum of New Zealand Te Papa Tongarewa and the Department of Conservation. Database available upon request from [www.doc.govt.nz](http://www.doc.govt.nz), Aquatic and Threats Unit, Marine Conservation Team, PO Box 10-420, New Zealand. Version: April 2009.

rate estimate obtained here with the RD lies within the lower boundaries of estimates published for this species in other populations (Wells and Scott 1990, Currey *et al.* 2009b). Analysis of a stranding database did not suggest an increase in mortality events throughout the course of the study (Tezanos-Pinto 2009). However, 14 known dolphins classified as “frequent users” (or core users) during 1997–1999 in the Bay of Islands were entirely absent in the area during 2002–2006; five of these dolphins have died (Tezanos-Pinto 2009). Analysis of photo-identification data sets suggested that these frequent users were also absent in the Hauraki Gulf (240 km south), indicating that they permanently emigrated or died.

In Doubtful Sound, a reduction in calf survival is reported to have caused a decline in bottlenose dolphin abundance. The decline was attributed to anthropogenic disturbance (environmental and behavioral) that included increased water discharge from a hydroelectric power plant and dolphin-related tourism activities (Lusseau 2003a, b; Currey *et al.* 2009b). In the Bay of Islands, 42% of bottlenose dolphin calves die before reaching one year of age (Tezanos-Pinto 2009). This value is considerably higher than those reported in other bottlenose dolphin populations using similar methods to estimate calf mortality, such as Sarasota Bay (first year mortality = 19%, Wells and Scott 1990), Shark Bay, Western Australia (first year mortality of calves born to non-provisioned females = 24%; Mann *et al.* 2000) and are equivalent to that for bottlenose dolphins kept in captivity (first year mortality = 39%, DeMaster and Drevenak 1988).

In Shark Bay, female bottlenose dolphins (*Tursiops* spp.) showed a negative correlation between cumulative dolphin-watching boat exposure, their reproductive success and their ability to raise offspring to weaning age (Bejder 2005). In the Bay of Islands, bottlenose dolphins changed their behavior in response to dolphin swim/watch tours over a relatively short period of time, increasing their avoidance of swimmers and spending less time resting (Constantine 2001, Constantine *et al.* 2004). Whether these behavioral changes have had any effect on recruitment in the Bay of Islands is currently unknown. However, the causes of low recruitment (*i.e.*, high calf mortality) observed in the Bay of Islands are of concern and require further investigation (Tezanos-Pinto 2009).

*Scenario 2: The decline in local abundance observed in the Bay of Islands is a consequence of dolphins changing their pattern of use of the area (i.e., an apparent decline in the regional population)*—Comparison of individual identification catalogs between the Bay of Islands and the Hauraki Gulf (240 km south) showed that 65% ( $n = 136$ , Tezanos-Pinto 2011) of dolphins sighted in the Hauraki Gulf were observed in the Bay of Islands during 2000–2006 suggesting that a large number of dolphins range widely along this coastline. Analysis of resighting rates and residency patterns of bottlenose dolphins in the Bay of Islands suggested a change in use of the area over time, with fewer dolphins sighted more frequently (Tezanos-Pinto 2009). A recent study indicates that there has been a change in habitat use within the bay between 1996 and 2010 (Hartel 2010). Foraging locations appeared to have changed over time and this spatial change may be due to potential shifts in prey type, prey distribution or foraging strategies. If the quantity or quality of prey has changed inside or outside the Bay of Islands, this may influence the distribution of dolphins along the northern North Island. Sightings of bottlenose dolphins in other regions however, are currently sporadic and no formal study has been conducted to properly address this question.

Apparent declines in bottlenose dolphin abundance due to shifts in habitat have been reported in other populations around the world. Potential causes identified to date consist of environmental (*e.g.*, prey availability inside and outside the study site,

changes in SST) or anthropogenic factors that resulted in shifts in home range (*e.g.*, Wells and Scott 1990, Bejder *et al.* 2006, Lusseau *et al.* 2006). Vessel traffic displaced bottlenose dolphins during periods of heavy traffic in Milford Sound, New Zealand (Lusseau 2005) and Clearwater, Florida (Allen and Read 2000). In Shark Bay the relative abundance of a bottlenose dolphin population declined 14.9% when the number of dolphin-watching tour boats increased from one to two, as some dolphins in the population shifted their home range to avoid the tour boats (Bejder *et al.* 2006).

Environmental factors are known to affect bottlenose dolphin distribution, for example fluctuations in SST due to the warm-water incursion of El Niño event of 1982–1983 in California (Wells *et al.* 1990). Along the coast of California, 5%–12% of the resident population of coastal bottlenose dolphins undertook a 670 km migration to the north, shifting their home range (Wells *et al.* 1990). This migration seemed to be in response to patchy, unstable and scarcely distributed prey within the open waters of the California coast (Defran and Weller 1999). In the present study, it seems that dolphins shifted their home-range or used it differently but apparently underwent no general increase in mortality (*i.e.*, true population decline) that would have affected the larger population. In the Moray Firth, bottlenose dolphins underwent a shift in home range that resulted in an overall range expansion (Wilson *et al.* 2004). Along the northern North Island however, no study has been conducted to analyze the effect of environmental variables on bottlenose dolphin distribution, or that of their prey.

With the available records from the Bay of Islands, it is not possible to conclude with certainty, whether the observed decline in abundance is due to a shift in habitat use, low recruitment due to reduced calf survival, episodic adult mortality, or some combination of the three factors. Continued monitoring of the Bay of Islands could help distinguish between these scenarios, especially if there is a reversal of the shift in habitat use (*e.g.*, the dolphins previously sighted in the Bay of Islands return). However, larger scale surveys of dolphins around the north eastern North Island are also needed to better understand the demographic parameters and habitat use of the regional population, especially the potential for shifts in local habitat use.

#### ACKNOWLEDGMENTS

Fieldwork research was conducted under permits to CSB, RC, and GTP from the New Zealand Department of Conservation (DOC). Funding for this project was provided by the Northland Marine Mammal Trust, Department of Conservation, Northland (GTP and RC); PBRF Funding from the School of Biological Sciences, University of Auckland (GTP); Marsden Fund of the Royal Society of New Zealand (CSB); Society for Marine Mammalogy, Emily B. Shane Award (RC); the Whale and Dolphin Conservation Society (RC); Cetacean Society International (GTP and RC); New Zealand Lotteries Grant Board (CSB and RC); University of Auckland Postgraduate Research Grants (GTP and RC). Support was provided by Department of Conservation staff especially J. Berghan, N. Henry, A. Fleming, R. Pierce, T. Beauchamp, and E. Reufels. We thank the tour operators (crew and management) in the Bay of Islands for their support and assistance (Carino, Fullers-Great Sights and Dolphin Discoveries). We thank Anton van Helden (Museum of New Zealand Te Papa Tongarewa) and Steve Smith (DOC) for providing access to the stranding database. We thank all the volunteers who participated in the collection of field data, our colleagues at the Molecular Ecology and Evolution lab (University of Auckland), Dr. K. Stockin and colleagues at the Coastal-Marine Research Group (Massey University) and Rob Mattlin for reviewing an early version of the manuscript. We

thank Phil Hammond and three anonymous reviewers for the time spent reviewing our manuscript and for the constructive comments that considerably improved the quality of this work.

#### LITERATURE CITED

- Allen, M. C., and A. J. Read. 2000. Habitat selection of foraging bottlenose dolphins in relation to boat density near Clearwater, Florida. *Marine Mammal Science* 16:815–824.
- Baker, C. S., B. L. Chilvers, R. Constantine, *et al.* 2010. Conservation status of New Zealand marine mammals (suborders Cetacea and Pinnipedia). *New Zealand Journal of Marine and Freshwater Research* 44:101–115.
- Bejder, L. 2005. Linking short and long-term effects of nature-based tourism on cetaceans. Ph.D. thesis, Dalhousie University, Halifax, Canada. 158 pp.
- Bejder, L., A. Samuels, H. Whitehead, *et al.* 2006. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conservation Biology* 20:1791–1798.
- Booth, J. D. 1974. Observations on the hydrology of the Bay of Islands, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 8:671–689.
- Bräger, S., and K. Schneider. 1998. Near-shore distribution and abundance of dolphins along the west coast of the South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 32:105–112.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference. Springer-Verlag, New York, NY.
- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis of fish survival experiments based on release–recapture data. American Fisheries Society Monograph, Bethesda, MD.
- Choquet, R., A. M. Reboulet, J. D. Lebreton, O. Gimenez and R. Pradel. 2005. U-CARE 2.2 (Utilities–CApture–REcapture) User’s Manual. CEFE, Montpellier, France.
- Constantine, R. 2001. Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism. *Marine Mammal Science* 17:689–702.
- Constantine, R. 2002. The behavioural ecology of the bottlenose dolphins (*Tursiops truncatus*) of Northeastern New Zealand: A population exposed to tourism. Ph.D. thesis, The University of Auckland, Auckland, New Zealand. 195 pp.
- Constantine, R., D. Brunton and T. Dennis. 2004. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. *Biological Conservation* 117:299–307.
- Cooch, E., and B. N. White. 2011. Program MARK. “A gentle introduction”. Colorado State University, Fort Collins, CO.
- Crosbie, S. F., and B. F. J. Manly. 1981. Parsimonious modelling of capture-mark-recapture studies. *Biometrics* 41:385–398.
- Currey, R., and L. Rowe. 2008. Abundance and population structure of bottlenose dolphins in Doubtful and Dusky Sounds. Population monitoring in Summer 2007/2008. Report submitted to the Department of Conservation, Southland Conservancy Invercargill, New Zealand. 33 pp. Available at <http://www.doc.govt.nz/documents/conservation/native-animals/marine-mammals/abundance-population-structure-bottlenose-dolphins-doubtful-dusky-sounds.pdf>.
- Currey, R., S. M. Dawson and E. Slooten. 2009a. An approach for regional threat assessment under IUCN Red List criteria that is robust to uncertainty: The Fiordland bottlenose dolphins are critically endangered. *Biological Conservation* 142:1570–1579.
- Currey, R., S. M. Dawson, E. Slooten, *et al.* 2009b. Survival rates of declining bottlenose dolphins in Doubtful Sound, New Zealand: An information theoretic approach to assessing the role of human impacts. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19:658–670.

- Defran, R. H., and D.W. Weller. 1999. Occurrence, distribution, site fidelity and school size of bottlenose dolphins (*Tursiops truncatus*) off San Diego, California. *Marine Mammal Science* 15:366–380.
- DeMaster, D. O., and J. K. Drevenak. 1988. Survivorship patterns in three species of captive cetaceans. *Marine Mammal Science* 4:297–311.
- Gormley, A. M., S. M. Dawson, E. Slooten and S. Bräger. 2005. Capture-recapture of Hector's dolphin abundance at Banks Peninsula, New Zealand. *Marine Mammal Science* 21:204–216.
- Hammond, P. S., S. A. Mizroch and G. P. Donovan. 1990. Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters. Report of the International Whaling Commission (Special Issue 12). iv + 440 pp.
- Hartel, L. 2010. Habitat use by bottlenose dolphins (*Tursiops truncatus*) in the Bay of Islands, New Zealand. M.Sc. thesis, The University of Auckland, Auckland, New Zealand. 101 pp.
- Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47:725–732.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both birth and immigration, a stochastic model. *Biometrika* 52:225–247.
- Kendall, W. L., K. H. Pollock and C. Brownie. 1995. A likelihood based approach to capture recapture estimation of demographic parameters under the robust design. *Biometrics* 81:293–459.
- Kendall, W. L., J. D. Nichols and J. E. Hines. 1997. Estimating temporary emigration using capture recapture data with Pollock's robust design. *Ecology* 78:563–578.
- Lusseau, D. 2003a. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. *Conservation Biology* 17:1785–1793.
- Lusseau, D. 2003b. Male and female bottlenose dolphins *Tursiops* spp. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. *Marine Ecology Progress Series* 257:267–274.
- Lusseau, D. 2005. The residency pattern of bottlenose dolphins (*Tursiops* spp.) in Milford Sound, New Zealand, is related to boat traffic. *Marine Ecology Progress Series* 295:265–272.
- Lusseau, D., E. Slooten and R. Currey. 2006. Unsustainable dolphin-watching tourism in Fiordland, New Zealand. Report SC/58/WW6 submitted to the International Whaling Commission.
- Mann, J., R. Connor, L. M. Barre and M. R. Heithaus. 2000. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): Life history, habitat, provisioning, and group-size effects. *Behavioral Ecology* 11:210–219.
- Merriman, M. G. 2007. Abundance and behavioural ecology of bottlenose dolphins (*Tursiops truncatus*) in the Marlborough Sound, New Zealand. M.Sc. thesis, Massey University, Palmerston North, New Zealand. 151 pp.
- Merriman, M. G., T. Markowitz, A. D. Harlin-Cognato and K. Stockin. 2009. Bottlenose dolphin (*Tursiops truncatus*) abundance, site fidelity, and group dynamics in the Marlborough Sound, New Zealand. *Aquatic Mammals* 35:511–522.
- Mourão, F. 2006. Patterns of association among bottlenose dolphins in the Bay of Islands, New Zealand. M.Sc. thesis, The University of Auckland, Auckland, New Zealand. 118 pp.
- Pledger, S. 2000. Unified maximum likelihood estimates for closed capture-recapture models with heterogeneity. *Biometrics* 434–442.
- Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:752–757.
- Pradel, R., J. E. Hines, J. D. Lebreton and J. D. Nichols. 1997. Estimating survival rate and proportion of transients using capture-recapture data from open populations. *Biometrics* 53:88–1999.

- Ryding, A. 2001. Computational methods used for the photo-identification of bottlenose dolphins in the Bay of Islands. M.Sc. thesis, The University of Auckland, Auckland, New Zealand. 99 pp.
- Schwarz, C. J., and A. N. Arnanson. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics* 52:860–873.
- Silva, M. A., S. Magalhães, R. Prieto, R. Serrão Santos and P. S. Hammond. 2009. Estimating survival and abundance in a bottlenose dolphin population taking into account transience and temporary emigration. *Marine Ecology Progress Series* 392: 263–276.
- Stanley, T. R., and K. P. Burnham. 1999. A closure test for time-specific capture-recapture data. *Environmental and Ecological Statistics* 6:197–209.
- Tezanos-Pinto, G. 2009. Population structure, abundance and reproductive parameters of bottlenose dolphins (*Tursiops truncatus*) in the Bay of Islands (Northland, New Zealand). Ph.D. thesis. The University of Auckland, Auckland, New Zealand. 243 pp.
- Tezanos-Pinto, G. 2011. Photo-identification and re-sighting rates of bottlenose dolphins (*Tursiops truncatus*) in the Hauraki Gulf and abundance along the north-eastern coast of the North Island. Report for the Department of Conservation (Bay of Islands), 26 pp. (Available from the author; e-mail: gaby@pachamama.co.nz).
- Tezanos-Pinto, G., C. S. Baker, K. Russell, *et al.* 2009. A worldwide perspective on the population structure and genetic diversity of bottlenose dolphins (*Tursiops truncatus*) in New Zealand. *Journal of Heredity* 100:11–24.
- Wells, R. S., and M. D. Scott. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. Report of the International Whaling Commission (Special Issue 12):407–416.
- Wells, R. S., L. J. Hansen, A. Baldrige, T. P. Dohl, D. L. Kelly and R. H. DeFran. 1990. Northward extension of the range of bottlenose dolphins along the California Coast. Pages 421–431 in S. Leatherwood and R. R. Reeves, eds. *The bottlenose dolphin*. Academic Press, San Diego, CA.
- White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:120–139.
- Williams, J. A., S. M. Dawson and E. Slooten. 1993. The abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. *Canadian Journal of Zoology* 71:2080–2088.
- Williams, B. K., J. D. Nichols and M. J. Conroy. 2002. *Analysis and management of animal populations*. Academic press, San Diego, CA.
- Wilson, B., P. S. Hammond and P. M. Thompson. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecological Applications* 9:288–300.
- Wilson, B., R. J. Reid, K. Grellier, P. M. Thompson and P. S. Hammond. 2004. Considering the temporal when managing the spatial: a population range expansion impacts protected areas-based management for bottlenose dolphins. *Animal Conservation* 7:331–338.
- Würsig, B., and T. A. Jefferson. 1990. Methods of photo-identification for small cetaceans. Report of the International Whaling Commission (Special Issue 12):43–52.

Received: 25 March 2011  
Accepted: 29 September 2012