Abundance and survival of bottlenose Dolphins in Doubtful Sound and Dusky Sound – 2009 - 2012

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Te Papa Atawhai

Abundance and Survival of bottlenose dolphins in Doubtful Sound and Dusky Sound – 2009-2012

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Abstract

Two populations of bottlenose dolphins in Fiordland, New Zealand, have been the focus of this study. The population in Doubtful Sound has previously been shown to be in decline. The other population, those dolphins within Dusky Sound, are located in a more remote and unmodified region of Fiordland. During a study from 2009-2012, the populations in both Doubtful Sound and Dusky Sound have increased in abundance (Doubtful Sound: 61.4; CV=1.46%; Dusky Sound 122; CV=0.83%). The first reported survival estimates for adult dolphins in Dusky Sound shows a very high survival rate (0.966; 95% CI: 0.944-0.980). Calf survival in Doubtful Sound has improved, with the survival estimate from 2010 onward being 0.622 (95% CI: 0.435-0.830), however, it is still the lowest reported for any wild non-provisioned bottlenose dolphin population. In Dusky Sound, the calf survival rate is 0.722 (95% CI: 0.556-0.844), which is the second lowest survival rate for any wild non-provisioned bottlenose dolphin population.

1. Introduction

The bottlenose dolphin occurs throughout a temperate and tropical range, yet coastal populations often restrict their movements to residence within discrete locations (Leatherwood et al. 1983, Wells & Scott 1999). In recent history some well-documented resident populations have shown declines in population size, most of which have been attributed to anthropogenic impacts (Wells & Scott 1999, Thompson et al. 2000, Currey et al. 2008). These declines have led to management focusing increasingly on protection of key sites (Wilson *et al.* 2004).

Two populations of bottlenose dolphins in Fiordland, New Zealand (44°30', 168°E; 46°10'S, 166°40'E), have been the focus of this study. One population, within Doubtful Sound, has previously been shown to be a declining population exposed to potential impacts from vessels and habitat modification. The other population, inhabiting Dusky Sound and Breaksea Sound (hereafter referred to as Dusky Sound), is located in a more remote and unmodified region of Fiordland.

The bottlenose dolphins of the Doubtful-Thompson Sound complex (referred to as Doubtful Sound) are more accessible for research than the dolphin population of Dusky Sound and for this reason have been studied more extensively. A long-term monitoring project on the dolphins of Doubtful Sound has been ongoing since 1990 (Williams *et al.* 1993). In the years since 1990, research has focused on assessing population size, habitat use, associations, behaviour, and documenting acoustic behaviour. The population shows adaptations to living in a cool water habitat, such as rotund body shape (Chong & Schneider 2001), seasonal calving (Haase & Schneider 2001), and seasonal changes in habitat use (Schneider 1999). Assessing impacts of dolphin-watching and population status have received special attention. Lusseau (2003b) found that dolphins showed various behavioural responses to prolonged interactions with vessels, and that these interactions were potentially more costly for female dolphins. In general, individuals responded to vessel interactions by spending more time underwater but males and females responded differently. The males started avoiding boats as soon as they were present, while females only switched to avoidance by diving once the boat interactions became intrusive (boat interactions violating MMRP regulations; Lusseau 2003b). When vessels were present, dolphins also reduced the time spent socialising by almost half, and resting reduced from 11% to 1% of their behavioural budget. At the same time, the dolphins' time spent travelling increased in duration (Lusseau 2003a). Analysis of dolphin sightings and behavioural states showed that specific areas in Doubtful Sound were especially important for socializing and resting (Lusseau & Higham 2004). Curry *et al.* (2007) analysed photo-identification data spanning a 17-year period, finding that the population had declined by 34-39% over the last 12 years, to 56 (CV=1.0%) individuals in 2007. Coincident with the population decline, the survival of newborn calves decreased from 0.862 (95% CI: 0.685-0.947) prior to 2002, to 0.375 (95% CI: 0.208-0.578) post-2002 (Currey *et al.* 2009). These events prompted the Department of Conservation to produce a discussion paper outlining management options for the bottlenose dolphins of Doubtful Sound, and ultimately, in 2008, establish the Doubtful Sound Code of Management.

The Code of Management created Dolphin Protection Zones (DPZ's), and stricter regulations on how vessels could interact with the dolphins. The DPZ's are a 200m-wide zone from the sides of the fiord, in areas of high dolphin use. Vessels are not permitted to travel within these zones although they are still able to access these areas for reasons such as fishing and diving. Further tour operators cannot seek out dolphin interactions but must leave them up to chance. This code of management is currently voluntary, however all tour operators have signed on to following these guidelines. Currently there is no research into how effective these zones are.

Curry *et al.* (2009) showed that 26-61% of the population decline was driven by a reduction in calf survival. Leslie Matrix models indicated that the population trend was unsustainable (100% of model runs predicted a population decline; Currey *et al.* 2009). Curry *et al.* (2009) suggested that calf survival was at sustainable levels prior to 2001, followed by a decline in calf survival in 2002 to unsustainable levels. Currey *et al.* (2009) also pointed out that this decline coincided with the opening of a second tailrace tunnel for the Manapouri hydroelectric power station. In 1969 the Manapöuri power station came online. In doing so it diverted water from Lake Manapöuri to Deep Cove in Doubtful Sound. This new freshwater input tripled the natural freshwater input into the fiord (Gibbs et al. 2000, Gibbs 2001). It established a permanent low salinity layer within the fiord which dramatically altered the infaunal community, especially in relation to bivalves (Rutger & Wing 2006). This input of freshwater is particularly cold in the spring (Gibbs *et al.* 2000), which is a time of critical importance for calving mothers. The second tailrace tunnel was opened in 2002. It has increased the efficiency of the power station, allowing it to operate above the pre-2002 operational discharge limit of 474 m^3s^{-1} for approximately 16% of the time, but total discharged freshwater has not increased (Cornelisen & Goodwin 2008)[1].

In 2007, research on the dolphin population in Dusky Sound commenced with the express purpose of obtaining a complementary dataset to the monitoring project in Doubtful Sound. Dusky Sound is not as accessible and does not have the same level of tourism or habitat modification as Doubtful Sound. Initial findings suggest a seemingly resident population almost twice the size of the Doubtful Sound population (102: CV=0.9%; Currey *et al.* 2008). Population monitoring has continued in both Doubtful and Dusky Sounds. The aim of this monitoring is to obtain an estimate of adult, sub-adult, and calf survival rates in Dusky Sound to compare with Doubtful Sound.

[1] In 2011 Meridian energy applied for and received resource consent to increase flow to an equivalent total turbine flow not exceeding 550m^3/s.The previous resource consents for the MPS limit the maximum instantaneous discharge from the tailrace of the MPS into Deep Cove to 510m^3/s but in order to avoid breaching this limit the station operated to an operational maximum discharge of 485m^3/s.

2. Methods

2.1 Survey Methods

Daily systematic surveys in Doubtful Sound (45°30' S, 167°00' E) and Dusky Sound (45°45' S; 166°35' E) were conducted from February 2009 to February 2012. Each year there were three field trips to gather demographic data; these were conducted in late spring/early summer, late summer, and in winter. Surveys were undertaken on successive days, weather permitting, and followed pre-determined routes established by Schneider (1999) in Doubtful Sound and Currey *et al.* (2008) in Dusky Sound (Figure 1). Due to the larger area of the Dusky Sound fiord complex, the entire route was covered approximately every two days. The survey craft were primarily 5-6 m aluminium-hulled vessels, powered by 60-75 hp four-stroke outboard engines.

Surveys began as soon as light permitted photography, and the survey route (tracked by Garmin 60CSXGPS every 15 seconds) was followed until a group of dolphins was encountered. Once dolphins were encountered, the group was monitored briefly from a distance (>200 m) to establish their behavioural state prior to engagement. After initial observations, the dolphins were approached in accordance with New Zealand Marine Mammal Protection Regulations (1992). The vessel was moved to approximately 15 m from the dolphins, at which point dorsal fins could be photographed. The group was photographed until approximately four photos of each individual were obtained (i.e. the number of photographs taken were greater than four times the estimate of group size (Würsig & Jefferson 1990), at which point the vessel broke contact and continued the survey route until the route was completed, or light/weather conditions became unworkable (i.e. Beaufort ≥4 or heavy rain).

In this paper, a year is defined as spanning the start of one calving season to the start of the next calving season the following year. The earliest recorded birth has been in October, so a "calf year" spans from the 1st October until 30th September the following year. To be consistent with previous research on the dolphin population in Doubtful Sound, adults are considered >3 years old, sub-adults are one to three years old, and calves are <1 year old (Currey *et al.* 2009). Calves were identified from marks (primarily dorsal fin tooth-rakes), their fin shape, and via persistent association with a particular adult, presumably their mother.

2.2 Field effort

Distance covered during a survey trip is often the standard approach to reporting field effort. However, substantial distances can be accumulated during a dolphin encounter, which may not actually be increasing the area of the fiord searched. To get a measure of actual fiord area searched, the fiord was divided into polygons (using Arc GIS v.10). Polygon size was determined by the assumption that if dolphins were present in a given polygon under established viewing conditions (less than Beaufort 4, no heavy rain), they would be seen. For each day's survey, the sum area of all polygons visited was calculated.

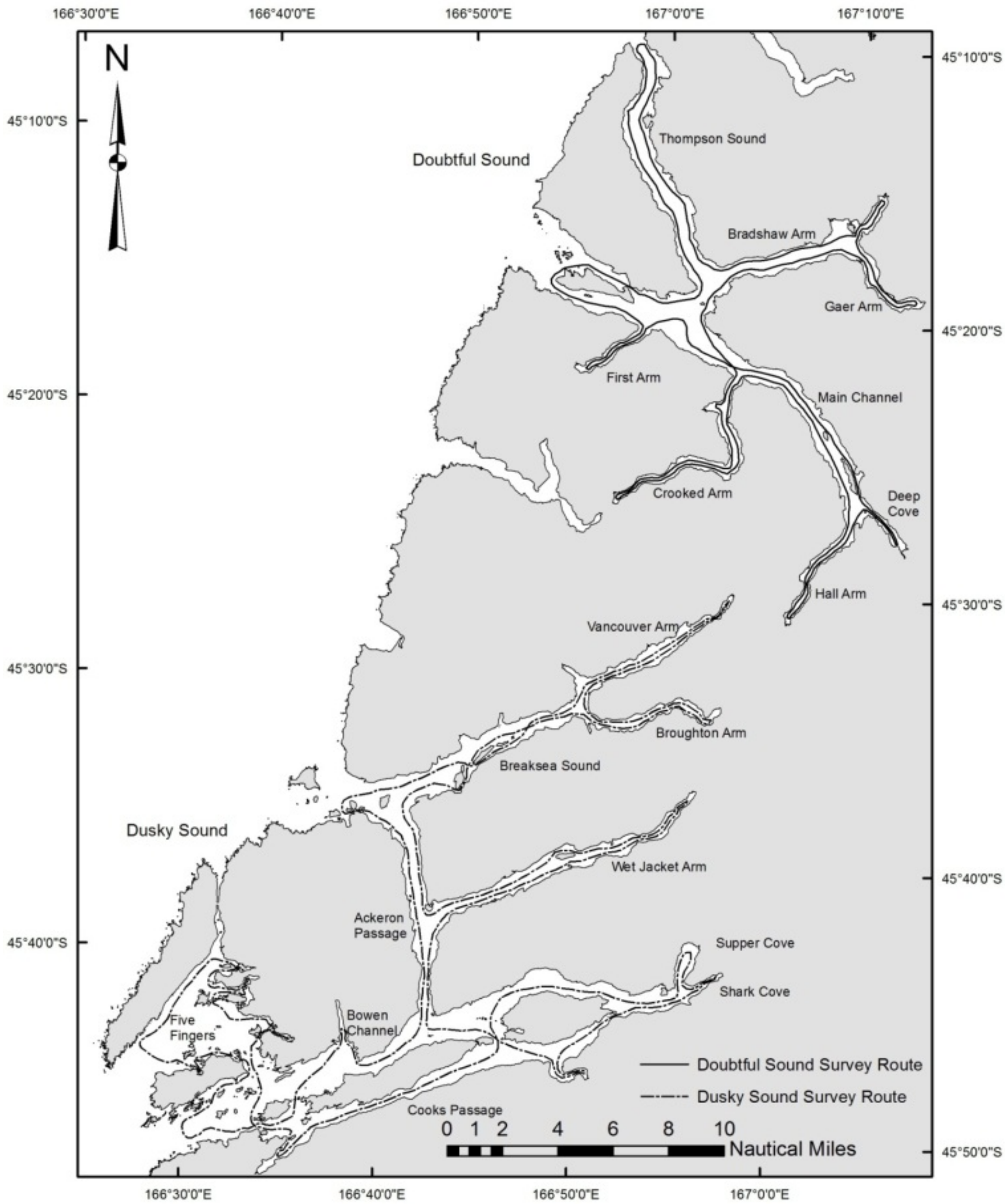

Figure 1. Map of Doubtful Sound and Dusky Sound showing pre-established survey tracks.

2.3 Photo identification

Dorsal fin photo-identification (photo-ID) was first established by Würsig&Würsig (1977), and has become the standard method of identifying dolphins. By regularly updating the photo-ID catalogue to track any changes in marking, dolphins can be identified by the unique, naturally occurring marks on their dorsal fins. Marks fall into two basic categories: nicks and temporary marks. Nicks are holes or tears in the fin. These are permanent injuries; though they may be added to or enlarged, they enable individuals to be identified over decades. Temporary marks (tooth-rakes, scars, pigmentation patterns, and lesions) change more rapidly than nicks. If the period between photo-ID surveys is short enough, temporary marks are a viable tool for identification of un-nicked individuals or to assist in identification of similarly nicked individuals (Wilson et al. 1999, Currey et al. 2007). Photographs were obtained using Nikon DSLR cameras (D2-H, D100, D200, or D90) equipped with AF Nikkor 80-200 mm f2.8 lenses. Efforts were made not to bias photography towards obviously marked animals or any particular individual, enabling an unbiased estimation of the proportion of nicked individuals ("mark rate") in the population. Photos were initially edited by removing any which were not well exposed, not in sharp focus, too distant, or if the fin was not parallel to the frame. Individually identifiable dolphins were then referenced to a photo-ID catalogue that included all known individuals. Sightings made from February 2009 to February 2012 were combined with past researchers' sighting records from 1990 to 2008.

2.4 Abundance estimation

2.4.1 Doubtful Sound

In previous monitoring trips, both capture–recapture and census methods for abundance estimation have provided very similar estimates (Currey *et al.* 2007). While the high mark rate of the population and the high re-sighting rates may make the capture-recapture seem redundant, it has the advantages of not relying on encountering every individual every time, and providing an estimate of the precision of abundance estimates (Currey *et al.* 2007). Both the census and capture-recapture estimates have been calculated. For consistency with prior studies, capture-recapture estimates have been calculated using 2 different methods: (1) assuming that we could identify all individuals, (2) using only nicked individuals and scaling the estimate by the mark. Capture-recapture results have been calculated for the whole population, and to enable comparisons with previous abundance estimates the 2009-2011 estimates were recalculated to exclude all individuals under three years of age. These estimates were combined with previously reported estimates (Williams et al. 1993, Schneider 1999, Haase 2000, Currey et al. 2007).

The capture-recapture abundance estimate calculations have been made in accordance with prior dolphin studies in Fiordland (Williams *et al.* 1993) using the Chapman modification of the Lincoln-Petersen estimator (Chapman 1951). Log-normal confidence intervals were calculated, as these better reflect the uncertainty in abundance estimates (Buckland *et al.* 1993). Abundance estimates were calculated using the winter and spring trips. The winter trip was considered the "capture" trip and the spring was the "recapture" trip. Two trips in different seasons were used for the following reasons: (1) this is a resident population with exceptionally high resighting rates (Currey *et al.* 2009) so there is little danger of violating the closed population assumption, (2) this approach gives a population estimate for the end of the year but prior to the calves being born in the following calving season, so new individuals are not entering the population between the capture and recapture periods, and (3) for constancy with prior research which also used a two trips capture-recapture period (Currey et al. 2007, Currey et al. 2008).

2.4.2 Dusky Sound

Capture-recapture abundance estimates for Dusky Sound were calculated as for Doubtful Sound. However, only the adult estimate has been calculated in 2011. Prior to 2011 differentiating between adults and sub-adults was not possible. Only until known calves of the year had been followed for three years did we know that all other older individuals must be adults.

2.5 Capture – Recapture analysis for survival and recapture rate

2.5.1 Doubtful Sound

Capture-recapture analysis for survival of adult bottlenose dolphins was conducted using a dataset from 1990 until February 2012. For calves the analysis included data from the start of the 1994/1995 calving season until February 2012, by which time it was known if the calves born in the 2010/2011 calving season had survived until one year old.

Apparent survival (φ) and recapture probability (p) were modelled in Program Mark (White & Burnham 1999) using the Cormack–Jolly–Seber (CJS) capture-recapture method (Cormack 1964, Jolly 1965, Seber 1965). The CJS model assumes a closed population. Models were implemented for naturally marked bottlenose dolphin adults and calves sighted in Doubtful Sound. Mortality and permanent emigration are confounded in capture-recapture estimates of φ. However, in Doubtful Sound, census counts consistently match capture-recapture estimates, suggesting that immigration and/or emigration are exceedingly rare (Currey *et al.* 2007). Apparent annual adult survival (φ_a) was defined as the probability of an adult dolphin surviving from one year (t), to the next (t+1) and remaining in the study location, given that it was alive in the first year (t). Further, apparent first-year calf survival (φ_c) was defined as the probability of a dolphin calf surviving to age one (t+1), given its mother gave birth (t) and the mother was sighted 12 months later (t+1) using a modified CJS capture-recapture approach (see Currey *et al.* 2009, for further details on this method). The same modified CJS capture-recapture approach was used for sub-adults (φ_{sa}); 1-2 year olds (φ_{sa1}) were modelled separately from 2-3 year olds (φ_{sa2}).

2.5.2 Capture – Recapture Models

Models were constructed to assess whether there was evidence for time-based variation in φ over the course of the study (for φ_a , φ_c, φ_{sa1} and φ_{sa2}); however, models were not constructed for evidence of gender-based variation as results from Currey *et al.*(2009) showed that no effect of gender was the most parsimonious model. Currey *et al.* (2009) employed models corresponding to four hypotheses concerning the demographic source of the population decline:

(a) a single estimate of φ spanning the study period (φ (.))

(b) yearly estimates of φ across the study period (φ (t_{Year}))

(c) two estimates of φ corresponding to the periods before and after 2002 (φ (t_{Period}), referred to in this chapter as $\varphi(t_{2002})$,

(d) monotonic decreases in φ using a cumulative logit link function to reflect a decrease in φ in any year or across multiple years with the exception of 2002 (φ (t_{CLogit}), referred to in this chapter as $\varphi(t_{\mathrm{CLogit2002}})$. The year 2002 was excluded as it was the basis for model (c), to include it again would not have differentiated it from the previous model.

Increasing the dataset by three years and including sub-adults expanded the range of models with the hypotheses:

(e) a periodic shift in survival in a year other than 2002 ($\varphi(t_{year?})$)

(f) two periodic shifts ($\varphi(t_{period1\&period2})$

(g) monotonic decrease in φ using a cumulative logit link function to reflect a decrease in φ in any year or across multiple years (φ ($t_{CLdecrease}$)

(h) monotonic increase in φ using a cumulative logit link function to reflect an increase in φ in any year or across multiple years (φ ($t_{CLincrease}$).

Where single or double periodic shift models are incorporated into the final model list then the cumulative logit models will not incorporate those years so both models remain independent. For each of these models, *p* was considered as either constant across years (*p*(.)), or variable across years ($p(t_{Year})$). Model goodness-of-fit was assessed using the bootstrap simulation procedures provided in Program Mark (White & Burnham 1999). Candidate models were compared using an information-theoretical assessment of model parsimony, the best model being that with the highest AIC_c weight (Akaike 1973, Burnham & Anderson 2002). To assist in choosing between models, evidence ratios were calculated by dividing the AIC weight of the most parsimonious model by the AIC weight of each of the less parsimonious models (Anderson 2008). Further, model-averaged estimates of φ were produced to reflect the AIC_c weight of the candidate models (Burnham & Anderson 2002).

2.5.3 Dusky Sound

Survival and recapture estimates of bottlenose dolphins in Dusky Sound were calculated as for Doubtful Sound, with a few exceptions: (1) Sub-adult ($φ_{sa}$)estimates were not calculated, as there were too few mortality events in the sub-adults to calculate reliable estimates. (2) Because there were only four years of survival data, capture–recapture models were limited to φ (.), φ (t_{Year}), φ ($t_{CLincrease}$), and φ ($t_{CLdecrease}$). These models were calculated for both adult ($φ_a$) and calf ($φ_c$) survival.

3. Results

3.1 Field effort

From February 2009 until February 2012, 106 days were spent searching for dolphins in Doubtful Sound. Dolphins were found on 100 of these days (94.3%). In Dusky Sound during the same time period, 102 days were spent searching for dolphins. Dolphins were found on 96 of these days (94.1%).

The area surveyed in both fiords from 2009 to 2011 increased significantly from previous years (Doubtful: Kruskal-Wallis test: H (1, N= 238) =28.328 p =.000; Dusky: Kruskal-Wallis test: H (1, N= 107) =6.229 p =.0126; Figure 2). This can most likely be attributed to an alternate research project, which had a goal of obtaining temperature and salinity data throughout the fiord complexes, in addition to the typical search for dolphins. Other researchers also tended to spend more time with the dolphins groups in order to make other observations, such as sound recordings and behavioural observations.

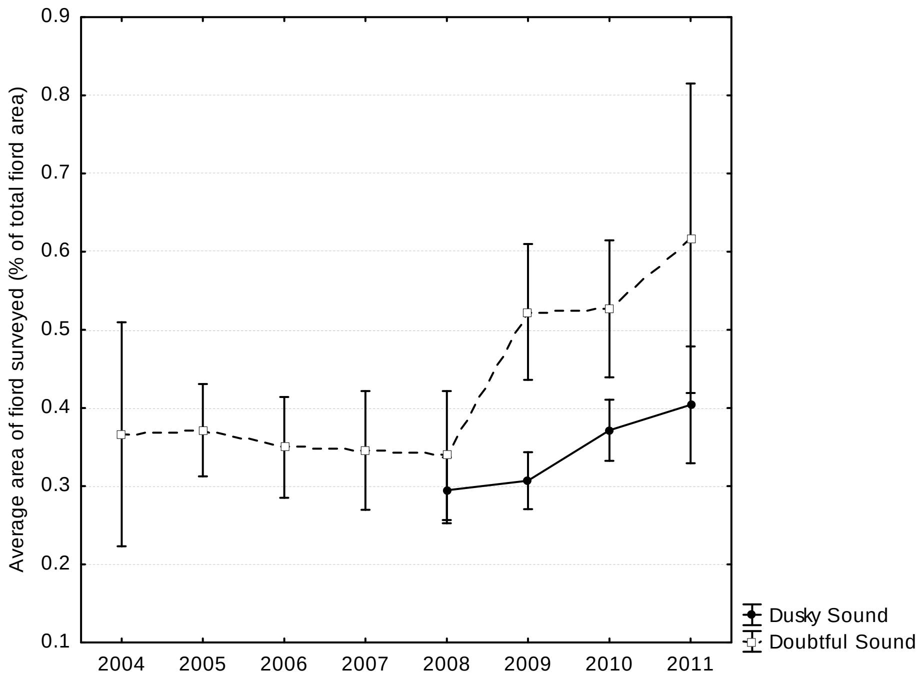

Figure 2.Average area of the fiord visited (as a percentage of the total fiord area) per day in Doubtful and Dusky Sound from 2004 to 2011.

3.2 Discovery

In Doubtful Sound from February 2009 to February 2012, there were no sightings of unknown individuals. Zero unknown individuals (other than new calves) have been sighted in Doubtful Sound since December 2004. Due to the lower sampling effort in 2004, there is also some debate as to whether these "new" individuals were simply previously identified individuals whose markings had changed substantially. In Dusky Sound, no new individual has been sighted since the first trip of this study in 2009.

3.3 Population Demographics and abundance estimation

3.3.1 Doubtful Sound

In Doubtful Sound, there are currently 61 resident bottlenose dolphins (calves born during the summer of 2011/2012 have not been included in this population count). Table 1 shows how the population has fluctuated since the last population estimation (Currey & Rowe 2008). The calves under three years of age that were missing are assumed to have died, as it is generally accepted that calves stay in close association with their mothers for three to six years (Read *et al.* 1993), and the mothers of these missing calves were regularly sighted.

Every capture-recapture estimate, which assumed all dolphins were identifiable, resulted in an abundance estimate which was identical to the census. As all dolphins were identified in either the "capture" or "recapture" period, the associated coefficient of variation (CV) was zero for every trip. The capture-recapture estimates for "nicked" individuals had very similar results to the other two methods. It is likely that the slight differences in "nicked" estimates were the result of the photography not being truly random between "nicked" and "non-nicked" individuals, rather than an actual difference in the population size. Recalculated results (only individuals >3 years old) from 2009-2011 suggest that the dolphin population has had a slight increasing trend over the last three years (Figure 7.3).

Table 1: Fluctuations in the dolphin population of Doubtful Sound from the summer of 2008/2009 until the summer of 2011/2012. Population census is for all individuals. The 'Calves' column is the number of calves born in the year and the number which died that year. 'Sub-adult' and 'adult' columns are the number of individuals which died or emigrated from the fiord during that year.

Year	Pop. Census	Adult census	Calves	Sub-adults	Adults	"Nicked" C-R estimate
2008	52	44	+5/-2	-2		51.5 (CV=2.06%)
2009	51	45	+1/-1		-1	50.5(CV=0.96%)
2010	56	49	+8/-3			55.8 (CV=1.05%)
2011	61	48	+8/-2		-1	61.4(CV=1.46%)

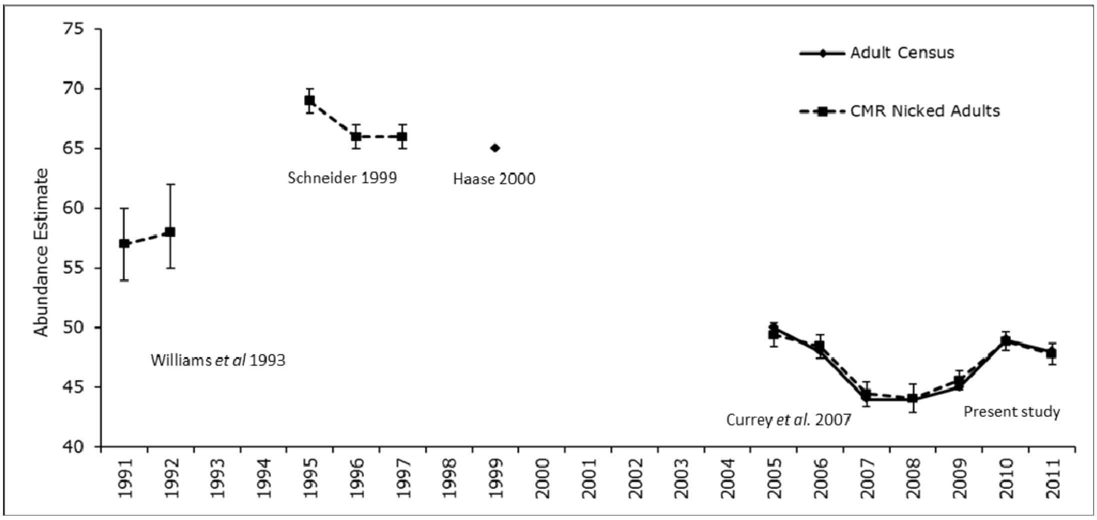

Figure 7.3. Annual end-of-year abundance estimates for adult bottlenose dolphins in Doubtful Sound, calculated using census and capture-recapture methods (with 95% log-normal CI). Data from the present study are compared with estimates from Williams *et al.* (1993), Schneider (1999), Haase (2000), and Currey *et al.* (2007).

3.3.2 Dusky Sound

In Dusky Sound, the census for the whole population closely matches the "Nicked" capture-recapture estimate suggesting that all or close to all the dolphins present within the fiord during the survey are being sighted (Table 2). From 2007 to 2012 there have been four trips where two to five individuals are missing for that trip and are present on the next trip. This could mean the individuals are leaving the fiord complex or the larger size of the fiord means not encountering or photographing individuals is more likely. As the discovery curve has stabilized, it is likely that even if dolphins are leaving the fiord complex, the full population of dolphins that utilizes Dusky Sound has been accounted for.

Table 2: Fluctuations in the dolphin population of Dusky Sound from the summer of 2007/2008 until the summer of 2011/2012. Population census is for all individuals. Calves column is the number of calves born in the year and the number that died that year (*alive but not yet one year old). The Adult census column only includes a census for 2011 as prior to that not enough survey years had been done to determine all individuals who were adults.

Year	Pop. Census	Adult census	Calves	"Nicked" C-R estimate
2008	102		+12/-5	102.0 (CV=0.9%)
2009	114		+6	106.5(CV=1.32%)
2010	113		+10/-1	111.8 (CV=0.61%)
2011	124	96	+14/-4(3*)	122(CV=0.83%)

3.4 Capture – Recapture Models of Survival and Recapture

3.4.1 Doubtful Sound

Adult Survival

From 1990 to 2011, 88 adult bottlenose dolphins with dorsal fin nicks were sighted. Bootstrap goodness of fit (GOF) analysis indicated that the most parameter-saturated model (φ_a (t_{Year})p_a (t_{Year})) fit the data. The probability of observing a model deviance as large as the estimated deviance for the most parameter-saturated model was 0.499 based on 1000 iterations. No adjustment for over-dispersion was therefore needed (White & Burnham 1999).

The most parsimonious model (φ_a (t_{2007})p_a (.);AIC_c weight = 0.544) showed a periodic shift in survival in 2007 (Table 3). Currey et al (2009) found the time-invariant model (φ_a (.)p_a (.)) to be the most parsimonious model. With the additional years of data (2008-2011), the time-invariant model was now the third best, 29.8 times less likely than the new most parsimonious model. The most parsimonious model parameter estimates for survival showed an average survival rate prior to 2007 of 0.943 (95% CI: 0.925-0.958). After 2007, this survival rate rose to 0.988 (95% CI: 0.956-0.997). Prior to 2002, the model-averaged parameter estimates for adult survival averaged 0.942 (95% CI: (0.935-0.950). Post-2002 the average adult survival rate was 0.968 (95% CI: 0.961-0.975).

Table 3. Model ranking of Cormack–Jolly–Seber capture–recapture models estimating apparent annual survival (φ_a) and recapture probability (p_a) for adult bottlenose dolphins observed in Doubtful Sound from 1990 to 2011. ER (evidence ratio) is the relative likelihood of the model compared with the most parsimonious model.

Model	AIC_c	ΔAIC_c	AIC_cwt	Likelihood	Parameters	Deviance	ER
φ_a (t_{2007}) p_a(.)	437.92	0.00	0.5437	1.00	3	164.51	
φ_a ($t_{CLIncrease}$) p_a(.)	438.40	0.47	0.4292	0.79	4	162.96	1.2
φ_a (.)p_a (.)	444.71	6.79	0.0183	0.03	2	173.31	29.7
φ_a (t_{Year})p_a (.)	447.96	10.04	0.0036	0.01	21	137.50	151.0
φ_a (t_{2007}) p_a(t_{Year})	448.79	10.87	0.0024	0.00	23	129.88	226.5
φ_a ($t_{CLIncrease}$) p_a(t_{Year})	449.16	11.24	0.0020	0.00	22	132.37	271.9
φ_a (t_{Year})p_a (t_{Year})	451.25	13.33	0.0007	0.00	21	140.79	776.7
φ_a (.)p_a (t_{Year})	453.40	15.48	0.0002	0.00	39	104.30	2718.5

1-2 year old survival

For the 1-2 year olds the most parsimonious model was time-invariant for both φ_{sa1} and p_{sa1} (Table 4). This model was 8.7 times more likely than a model showing a monotonic increase in φ_{sa1} using a cumulative logit link function to reflect an increase in φ_{sa1} in any year or across multiple years (φ_{sa1} ($t_{CLincrease}$)). From 1996 to 2011, the model-averaged parameter estimates showed survival to be 0.878 (95% CI: 0.847-0.948).

Table 4. Model ranking of Cormack–Jolly–Seber capture–recapture models estimating apparent annual survival (φ_{sa1}) and recapture probability (p_{sa1}) for adult bottlenose dolphins observed in Doubtful Sound from 1996 to 2011. ER (evidence ratio) is the relative likelihood of the model compared with the most parsimonious model.

Models	AIC_c	ΔAIC_c	AIC_cwt	Likelihood	Parameters	Deviance	ER
φ_{sa1} (.)p_{sa1} (.)	34.18	0.00	0.8157	1.00	2	7.07	
φ_{sa1} ($t_{CLincrease}$) p_{sa1}(.)	38.50	4.32	0.0942	0.12	5	5.23	8.7
φ_{sa1} ($t_{CLdecrease}$) p_{sa1}(.)	38.59	4.41	0.0901	0.11	5	5.32	9.1
φ_{sa1} (t_{Year})p_{sa1} (.)	56.88	22.70	0.0000	0.00	16	0.00	
φ_{sa1} (.)p_{sa1} (t_{Year})	59.98	25.80	0.0000	0.00	15	5.32	
φ_{sa1} ($t_{CLincrease}$) p_{sa1}(t_{Year})	62.11	27.93	0.0000	0.00	16	5.23	
φ_{sa1} ($t_{CLdecrease}$) p_{sa1}(t_{Year})	63.94	29.76	0.0000	0.00	16	7.07	
φ_{sa1} (t_{Year})p_{sa1}(t_{Year})	94.46	60.28	0.0000	0.00	32	0.00	

2-3 year old survival

For 2-3 year old sub-adults the most parsimonious model was for a shift in survival rate occurring in 2003 (AIC_c weight =0.49, table 5). However, this parameter model was only 1.5 times as likely as the survival invariant model, and 2.8 times as likely as the monotonic decrease model. The model adjusted parameter estimates prior to 2003 average 0.922 (95% CI: 0.667-0.986). After 2003 the estimate drops to 0.798 (95% CI: 0.534-0.932).

Table 5. Model ranking of Cormack–Jolly–Seber capture–recapture models estimating apparent annual survival (φ_{sa2}) and recapture probability (p_{sa2}) for adult bottlenose dolphins observed in Doubtful Sound from 1996 to 2011. ER (evidence ratio) is the relative likelihood of the model compared with the most parsimonious model.

Models	AIC_c	ΔAIC_c	AIC_cwt	Likelihood	Parameters	Deviance	ER
φ_{sa2} (t_{2003}) p_{sa2}(.)	32.58	0.00	0.4909	1.00	3	8.67	
φ_{sa2} (.)p_{sa2} (.)	33.35	0.77	0.3338	0.68	2	11.49	1.5
φ_{sa2} ($t_{Cldecrease}$) p_{sa2}(.)	34.64	2.06	0.1753	0.36	4	8.67	2.8
φ_{sa2} (t_{Year}) p_{sa2}(.)	51.93	19.35	0.0000	0.00	16	0.00	
φ_{sa2} (t_{2003}) p_{sa2}(t_{Year})	62.87	30.29	0.0000	0.00	17	8.67	
φ_{sa2} (.) p_{sa2}(t_{Year})	63.42	30.84	0.0000	0.00	16	11.49	
φ_{sa2} ($t_{Cldecrease}$) p_{sa2}(t_{Year})	65.16	32.58	0.0000	0.00	18	8.67	
φ_{sa2} (t_{Year}) p_{sa2}(t_{Year})	80.42	47.84	0.0000	0.00	28	0.00	

Calf survival

The most parsimonious model for calves was one showing three periods of differing calf survival (Table 6). One period was prior to 2002, one period from 2002 to 2009, and the final period was from 2010 onward. This model was 2.1 times more likely than a model showing only two periods of differing calf survival (before and after 2002). The model adjusted parameter estimates prior to 2002 average 0.856 (95% CI: 0.800-0.911), from 2002 to 2009 the average was 0.434 (95% CI: 0.360-0.508), and from 2010-2011 the average was 0.622 (95% CI: 0.435-0.830, Figure 4). The post 2002 model adjusted estimate would be 0.500 (95% CI: 0.359-0.641).

Table 6. Model ranking of Cormack–Jolly–Seber capture–recapture models estimating apparent annual survival (φ_c) and recapture probability (p_c) for bottlenose dolphins calves, observed in Doubtful Sound from 1994 to 2011. ER (evidence ratio) is the relative likelihood of the model compared with the most parsimonious model.

Models	AIC_c	ΔAIC_c	AIC_cwt	Likelihood	Parameters	Deviance	ER
φ_c ($t_{2002\&2010}$) p_c(.)	91.62	0.00	0.6237	1.00	4	20.12	
φ_c (t_{2002}) p_c (.)	93.09	1.48	0.2981	0.48	3	23.64	2.1
φ_c ($t_{Cldecrease}$) p_c(.)	96.36	4.74	0.0583	0.09	5	22.82	10.7
φ_c (t_{Year})p_c (.)	98.88	7.26	0.0165	0.03	17	0.00	37.8
φ_c (.)p_c (.)	102.04	10.42	0.0034	0.01	2	34.61	183.4
φ_c ($t_{2002\&2010}$) p_c(t_{Year})	123.37	31.75	0.0000	0.00	19	20.12	
φ_c (t_{2002}) p_c(t_{Year})	124.69	33.08	0.0000	0.00	18	23.64	
φ_c ($t_{Cldecrease}$) p_c(t_{Year})	128.26	36.64	0.0000	0.00	20	22.82	
φ_c (t_{Year}) p_c(t_{Year})	132.70	41.08	0.0000	0.00	32	0.00	
φ_c (.)p_c(t_{Year})	133.49	41.87	0.0000	0.00	17	34.61	

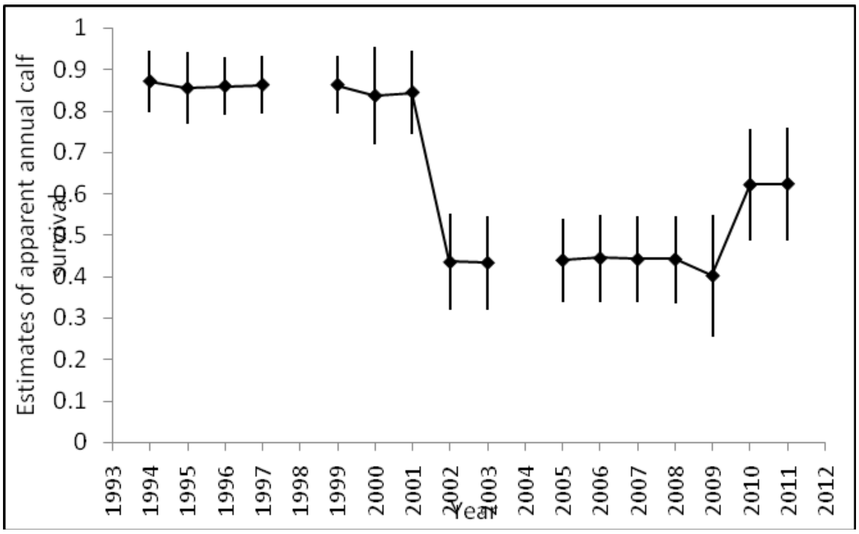

Figure 4.Model-averaged estimates of apparent annual survival (φ_c) for bottlenose dolphin calves observed in Doubtful Sound from 1994 to 2011. Estimates were derived using Cormack–Jolly–Seber capture–recapture models (Table 3.5). Error bars are unconditional standard errors that account for both parameter and model uncertainty. There were no observations made in 1998 and 2004.

3.4.2 Dusky Sound

Adult survival

From 2007 to 2011, 97 adult bottlenose dolphins with nicked dorsal fins were sighted in Dusky Sound. Bootstrap GOF analysis indicated that the most parameter-saturated model (φ_a (t_{Year})p_a (t_{Year})), fit the data. The probability of observing a model deviance as large as the estimated deviance for the most parameter saturated model was 0.757 based on 1000 iterations. No adjustment for over-dispersion was therefore needed (White and Burnham, 1999).

The most parsimonious model was time-invariant for both survival and recapture rates (Table 7). This model was only 1.6 times as likely as the model with the next highest weight which showed a monotonic decrease in survival any year or across multiple years. The time-invariant model was also only two times more likely than the third most parsimonious model which showed time dependent survival. The adult survival estimate for the chosen model (φ_a ()p_a (.)) was 0.966 (95% CI: 0.944-0.980). The model-averaged survival ranged from 0.959 (95% CI: 0.908-0.983) to 0.982 (95% CI: 0.880-0.998). The survival rate CV averaged 2.03%.

Table 7. Model ranking of Cormack–Jolly–Seber capture–recapture models estimating apparent annual survival (φ_a) and recapture probability (p_a) for adult bottlenose dolphins observed in Dusky Sound from 2007 to 2011. ER (evidence ratio) is the relative likelihood of the model compared with the most parsimonious model.

Model	AIC_c	ΔAIC_c	AIC_cwt	Likelihood	Parameters	Deviance	ER
φ_a (.)p_a (.)	126.31	0.00	0.3791	1.00	2	12.34	
φ_a ($t_{CLdecrease}$) p_a(.)	127.21	0.90	0.2415	0.64	3	7.12	1.6
φ_a (t_{Year})p_a (.)	127.66	1.35	0.1928	0.51	6	5.51	2.0
φ_a ($t_{CLincrease}$) p_a(.)	128.34	2.03	0.1374	0.36	3	12.34	2.8
φ_a ($t_{CLdecrease}$) p_a(t_{Year})	131.26	4.95	0.0319	0.08	7	7.04	11.9
φ_a ($t_{CLincrease}$) p_a(t_{Year})	133.80	7.49	0.0090	0.02	7	11.65	42.1
φ_a (.)p_a (t_{Year})	134.03	7.72	0.0080	0.02	6	11.88	47.4
φ_a (t_{Year})p_a (t_{Year})	140.24	13.93	0.0004	0.00	12	5.51	94.8

Calf survival

The most parsimonious model was time-invariant for both survival and recapture rates (Table 8). This model was 3.2 times more likely than a model showing time dependent survival rates. Calf survival estimates for the time-invariant model were 0.722 (95% CI: 0.556-0.844). Model-averaged yearly estimates of survival fluctuated between 0.670 (95% CI: 0.400-0.861) and 0.794 (95% CI: 0.947).

Table 8. Model ranking of Cormack–Jolly–Seber capture–recapture models estimating apparent annual survival (φ_a) and recapture probability (p_a) for bottlenose dolphins calves observed in Dusky Sound from 2007 to 2011. ER (evidence ratio) is the relative likelihood of the model compared with the most parsimonious model.

Model	AIC_c	ΔAIC_c	AIC_cwt	Likelihood	Parameters	Deviance	ER
φ_a (.)p_a (.)	46.71	0.00	0.6087	1.00	2	6.75	
φ_a (t_{Year})p_a (.)	49.01	2.30	0.1926	0.32	6	0.00	3.2
φ_a ($t_{CLincrease}$) p_a(.)	49.43	2.72	0.1560	0.26	4	5.08	3.9
φ_a ($t_{CLincrease}$) p_a(t_{Year})	52.61	5.91	0.0317	0.05	7	1.18	19.2
φ_a (.)p_a (t_{Year})	54.77	8.06	0.0108	0.02	6	5.76	56.4
φ_a (t_{Year})p_a (t_{Year})	64.74	18.04	0.0001	0.00	12	0.00	6087.0
φ_a ($t_{CLdecrease}$) p_a(.)	67.49	20.78	0.0000	0.00	4	23.13	
φ_a ($t_{CLdecrease}$) p_a(t_{Year})	69.32	22.61	0.0000	0.00	7	17.88	

4. Discussion

The capture-recapture abundance estimates for adult bottlenose dolphins in Doubtful Sound show a decline between 1999 and 2008 from around 65 individuals to fewer than 50 (Schneider 1999, Currey et al. 2007). From 2008 to 2011, a total of nine new individuals were added to the bottlenose dolphin population, all as the result of births within the current population. The adult/sub-adult (i.e. individuals >3 years old) part of the population has increased by four. The last two years have been above average for both the number of births and the calf survival rate.

In Dusky Sound, population estimates have shown an increase from estimates made in the summer of 2007/2008 (Currey *et al.* 2008). No new adult or sub-adult individuals have been sighted since the first trip in 2009. However, there have been more instances of individuals being missed during a population survey trip, when compared to Doubtful Sound. The individuals missed are often the most heavily scarred males. When sighted these individuals are often solitary or in small groups of two to four individuals. Males with heavy scarring are considered older individuals that are often more solitary (Schneider 1999). Given the size of the Dusky Sound complex, it is possible that these individuals are present within the fiord, but are simply not sighted. The other possibility is that these missing individuals are outside the fiord. There has never been a sighting of a known dolphin from Dusky Sound in Doubtful Sound. There have been very few surveys of the fiords to the south of Dusky Sound so it is possible the dolphins travel further south. Dolphins are occasionally sighted in the fiords south of Dusky Sound, but only one day of photo-ID survey effort has occurred there. None of the dolphins in those photos matched Dusky Sound dolphins, and there are not members of any other population that is currently catalogued.

When comparing different models of survival, evidence ratios help make interpretations more rigorous (Anderson 2008). Evidence ratios should not be used as automatic cut offs to say a model is implausible because there may be unknown variables in a model's favour (Anderson 2008). In general once a model is 1:50 against the more preferred model it should be ruled out as being plausible (Anderson 2008). Since Currey *et al.*(2009), the best model for adult survival in Doubtful Sound has changed from a time-invariant model (0.9374, 95% CI: 0.9170–0.9530), to one showing a shift in survival in 2007 (pre-2007: 0.943, 95% CI: 0.925-0.958, post-2007: 0.988, 95% CI: 0.956-0.997). Evidence ratios suggest that the weight for the most parsimonious model is basically the same as a model showing increasing survival over the years, and at 30 times less likely the time-invariant model cannot be ruled out. While the most parsimonious model shows an increase in survival in 2007, the confidence intervals suggest that this increase would not be significant. That said, the current adult survival rate of 0.988 is the second highest reported survival rate for any bottlenose dolphin population (Hersh et al. 1990, Small & Demaster 1995, Sanders-Reed et al. 1999, Wells 2000, Gaspar 2003, Stolen & Barlow 2003, Fortuna 2007). The only higher rate was 0.994 which was calculated for a population in Sado, Portugal from 1986 until 1990 (Gaspar 2003). It should be noted that calculating adult survival using this method will produce best-case estimates as survival is not curved by age. This is probably not an issue in large population estimates but with small populations if there are a lack of older individuals in the population, the survival rate will shift accordingly.

Four years of data in Dusky Sound is quite short for making survival estimates. The precision of any survival estimate increases as the capture probability increases (Pollock *et al.* 1990). The annual recapture rate estimate is exceptionally high in Dusky Sound (0.998; 95%CI: 0.991-1.00). The precision of survival estimates increases as the number of samples increase (Pollock *et al.* 1990), and the population in Dusky Sound is twice as high as in Doubtful Sound. High recapture rates also cause CI estimates to stabilize very quickly, and for the survival estimates in Doubtful Sound this was the case after only a few years (Rayment *et al.* 2010). Therefore, while there are only four years of capture-recapture data for Dusky Sound, there is enough to present preliminary survival estimates. In Dusky Sound, an adult survival rate of 0.966 (95% CI: 0.944-0.980; CV=0.92%) is similar to what Wells and Scott (1990) reported for the dolphins resident to Sarasota, FL. Although the post-2007 rate in Doubtful Sound is 0.988 (95% CI: 0.956-0.997), suggesting it is higher than in Dusky Sound, the confidence intervals overlap suggesting this would not be a significant difference. Even if the adult survival rate is high in Doubtful Sound it does not necessarily mean that tourism vessels(see Lusseau 2003b, a, 2004, 2006, Lusseau et al. 2006) or the freshwater input from the Manapöuri tailrace are not having negative effects on the survival of the adult dolphin population in Doubtful Sound. Instead, the lower survival rate in Dusky Sound could indicate additional factors in Dusky Sound which act to lower the adult survival rate. However, given the exceptionally high adult survival rate in Doubtful Sound, the anthropogenic impacts probably are not having much of an impact on the adult dolphins. Also, with the population in Doubtful Sound being relatively small (48 adults), a small number of surviving adults since 2007 can have a relatively large effect on the overall survival rate.

This study was the first to estimate survival rate in 1-2 year old sub-adults in Doubtful Sound. While the confidence intervals are probably not significantly different, estimates suggested that the survival rate for 2-3 year olds was less than for 1-2 year olds. In Currey *et al.*(2009) the assumption was made that survival rate for one-three year olds could be a forced linear relationship between the calf survival rate and the adult survival rate. This has been shown to not be the case. Most studies looking at the survival of bottlenose dolphins have observed that survival of 1-2 year olds is higher than for calves of the same year (Small & Demaster 1995, Mann et al. 2000, Stolen & Barlow 2003, Fortuna 2007). Few have reported two to three year survival rates (Mann et al. 2000, Stolen & Barlow 2003, Fortuna 2007). Of those that have, both Mann et al (2000) and Fortuna (2007) calculated a decline in survival in the third year. Weaning often occurs around three years of age in bottlenose dolphins (Mann *et al.* 2000). As weaning approaches, the young spend increasing periods of time away from their mothers (Shane 1990, Mann et al. 2000). This increased separation has been suggested to increase the chances of mortality due to predatory attacks by sharks (Scott et al. 1990, Herzing 1997), injury caused by other dolphins (Mann *et al.* 2000), or from boat strikes (Wells & Scott 1990). After weaning the young may not be sufficiently equipped to forage properly (Mann *et al.* 2000). Currently, population surveys have not been ongoing for long enough in Dusky Sound to calculate an estimate for one to three year survival. It would be very informative to continue research there to determine whether rates are similar to those found in Doubtful Sound.

Updated survival rates for calves of the year in Doubtful Sound, show that there has been increased survival in 2010 and 2011. This increase is reflected in the most parsimonious model being one showing three periods of differing calf survival. One period was prior to 2002, one period from 2002 to 2009, and the final period was from 2010 onwards. While the current survival rate (post-2010: 0.622, 95% CI: 0.435-0.830) is considerably higher than the previously reported survival rate (0.3750 (95% CI: 0.2080–0.5782; Currey *et al.* 2009), it is still lower than any other reported survival rate for a wild, non-provisioned population of bottlenose dolphins (Herzing 1997, Mann et al. 2000, Wells 2000, Stolen & Barlow 2003, Kogi et al. 2004, Fortuna 2007). In Dusky Sound the calf survival rate was been estimated as 0.722 (95% CI: 0.556-0.844). Although this is higher than the current rate in Doubtful Sound, it is still not as high as the pre-2002 rate in Doubtful Sound. It also ranks lower than any other reported survival rate for a wild, non-provisioned population of bottlenose dolphins. The next closest calf survival rate was 0.771 (95% CI: 0.625-0.872; Fortuna 2007) in the Adriatic Sea where the bottlenose dolphins have known levels of pollutants, especially PCB's (Corsolini *et al.* 1995), in concentrations higher than those found in animals showing reproductive failure and physiological impairment (Corsolini *et al.* 1995). Stolen and Barlow (2003) found relatively low calf survival and postulated that the burden of contaminants passed down from the mother as well as other health related stresses may put the young dolphins at greater risk of disease and death. While no work in relation to pollutants has been carried out on the dolphins in Fiordland, trace metal studies in *Mytilus edulis* (Blue mussel) has shown higher levels of Cadmium in Doubtful Sound than either the Otago Peninsula or Banks Peninsular (Linwood 1993).

Calf survival rate was lower in both Doubtful Sound and in Dusky Sound than in all other areas where detailed studies have been conducted (Mann et al. 2000, Wells 2000, Stolen & Barlow 2003, Kogi et al. 2004, Fortuna 2007). The bottlenose dolphins of Fiordland are at the southern limit of the species' worldwide range, and show seasonal movements and seasonal calving (Schneider 1999) in response to water temperature. Because the adults show high levels of survival in both Dusky Sound and Doubtful Sound it is unlikely that water temperature is directly affecting adult survival. However, there is evidence to suggest that cold water temperatures can directly affect the survival of neonates. Mann *et al.* (2000) also suggested that food availability for lactating females could play a role in calf survival.

Although calf survival is low in both Doubtful Sound and Dusky Sound, why it is substantially lower in Doubtful Sound could be due to two anthropogenic factors playing a role: tourism vessels and the Manapöuri tailrace. Impacts of commercial tour boat activities on the dolphins' behaviour have been demonstrated (Lusseau 2003a). From 1994 to 2002, the commercial tour boat industry in Doubtful Sound increased from three to nine vessels and two kayak companies (Lusseau 2002). The largest proportion of trips were in the summer and the number of summer trips increased 40% from 2000 to 2002 (Lusseau 2002). Female bottlenose dolphins have a higher biological cost associated with boat interactions than males and this could manifest itself in decreased calf survival rates or increased stillbirths (Lusseau 2003b). Pregnant or lactating females are therefore at the highest risk during the summer months when there are more dolphin-boat interactions. Secondly, the Manapöuri tailrace input maintains a permanent low salinity layer (LSL) within the fiord while large rainfall events can cause temporary but dramatic deepening of the LSL (Gibbs 2001). While the location of dolphins within the fiord has not been directly affected by the flow rate of the tailrace or the salinity regime within the fiord (see Chapter 3), the tailrace may influence other factors such as prey availability.

In Doubtful Sound there has been a significant increase in the calf survival rate from in 2010 and 2011. Possible reasons for this improvement include: establishment of the dolphin code of management, increased temporary movement out of the fiord, and more pelagic food seen within the fiord. In response to the work published on the effects of tourism (Lusseau 2003b, a, 2004, Lusseau & Higham 2004) and the reported decline in the dolphin population (Currey *et al.* 2007), in 2008 the Department of Conservation established dolphin protection zones in areas of high dolphin presence. Although there are no data on the effectiveness of these measures, it is assumed that the number of dolphin-tour boat interactions has declined. The total number of regular vessels offering sight-seeing tours has also declined from nine vessels and two kayak companies in 2002 (Lusseau 2002), to six vessels and two kayak companies, in 2012 (DOC, unpublished data). Also, dolphins are believed to be leaving the fiord on a semi-regular basis; the first observation of this was in 2009 and it seems to be increasing in frequency. The reason for this departure is unknown, however similar range expansion has been seen in another dolphin population at Moray Firth, Scotland (Wilson *et al.* 2004). In that population, the expansion was considered to be in response to changes in prey distribution (Wilson *et al.* 2004).

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