

CAPTURE-RECAPTURE ESTIMATES OF HECTOR'S DOLPHIN ABUNDANCE AT BANKS PENINSULA, NEW ZEALAND

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ABSTRACT

Capture-recapture techniques have been extensively used to estimate survival rates of Hector's dolphins at Banks Peninsula, but not abundance. We analyzed nine seasons of photo-identification data using a model-fitting approach in the computer program MARK, and then used MARK's estimates of capture probabilities to calculate the abundance of distinctive individuals. We extrapolated these estimates to include unmarked individuals using five seasons of data on the proportion of identifiable individuals in this population, obtained from "random photography." This capture-recapture approach suggests a 1996 population of about 1,100 (CV = 0.21). This is very similar to the 1997 line-transect estimate of about 900 (CV = 0.28), especially considering that the two techniques do not necessarily measure the same thing. An important advantage of the capture-recapture approach stems from the inherent versatility of photo-ID data. If the sampling design is appropriate, an unbiased abundance estimate can be achieved as a spin-off from work directed at other questions. However, in our view, line-transect estimates are easier to interpret because the sampling design is explicit.

Key words: capture-recapture, Hector's dolphin, *Cephalorhynchus hectori*, abundance.

Hector's dolphins, *Cephalorhynchus hectori*, are small, coastal, dolphins endemic to New Zealand. Studies of mitochondrial DNA indicate that the species is split into at least four genetically separate populations (South Island south, east, west coasts, North Island west coast; Pichler *et al.* 1998, Pichler and Baker 2000), one of which

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(North Island west coast) is now considered a separate subspecies (*C. hectori maui*, Baker *et al.* 2002). Bycatch in gill nets occurs throughout the species' range (Dawson *et al.* 2001), and has resulted in the establishment of two protected areas (at Banks Peninsula, Dawson and Slooten 1993; and off North Island west coast²). Line-transect surveys indicate a South Island population of 7,270 (CV = 0.16; Dawson *et al.* 2004, Slooten *et al.* 2004a), and a North Island population of 111 (CV = 0.44; Slooten *et al.* 2004b).

In 1988 the Banks Peninsula Marine Mammal Sanctuary (BPMMS) was established to protect the local population from entanglement in recreational and commercial gill nets (Dawson and Slooten 1993). Gill-net bycatch continues outside the sanctuary and occasionally, *via* nets set illegally, inside it. It appears that the sanctuary has reduced bycatch, but not to sustainable levels (Slooten *et al.* 2000). Estimates of abundance are required in order to monitor the effectiveness of the sanctuary and to track changes in population size.

Previous abundance estimates of Hector's dolphins at Banks Peninsula have been derived from strip-transect surveys (Dawson and Slooten 1988), and more recently from line-transect surveys undertaken in 1997/1998 and 1998/1999 (Dawson *et al.* 2004). The 1997/98 line-transect abundance estimate computed for the Banks Peninsula Marine Mammal Sanctuary (BPMMS) was 897 (CV = 28.2%); Dawson *et al.* 2004). Photo-identification has been used extensively to study Hector's dolphins at Banks Peninsula since 1984 (*e.g.*, Slooten and Dawson 1988, Slooten *et al.* 1993, Bräger *et al.* 2002). Capture-recapture analyses have been used to estimate survival rates at Banks Peninsula (Slooten *et al.* 1992, Cameron *et al.* 1999), but not abundance.

In most bird and small mammal population studies, for which capture-recapture methods (also termed mark-recapture) were developed, individuals are physically captured and artificially marked. During subsequent samples, the marked individuals that have been recaptured are easily identified. A capture probability is calculated for each marked individual at each sampling occasion to derive a population size estimate (Otis *et al.* 1978, Pollock *et al.* 1990, Lebreton *et al.* 1992). Capture-recapture methods may also be used in studies where individuals are identifiable from natural marks such as color patterns or scars. For example, bobcats (Heilbrun *et al.* 2003), tigers (Karanth and Nichols 1998), and Serengeti cheetahs (Kelly 2001) have all been successfully identified individually using pelt and facial markings. Natural markings have been commonly used to individually identify many cetacean species (see Hammond *et al.* 1990 for a review). In these cases individuals are sighted (and identified) rather than marked and resighted rather than recaptured. The terms are used interchangeably.

When using natural marks, it is likely that not all individuals in a population possess marks that enable them to be individually identified. In these cases, capture-recapture analysis produces an estimate of the number of identifiable individuals in the population; no information on the number of unidentifiable individuals is provided. Extrapolation to total population size, therefore, requires information on the proportion of identifiable individuals in the study population (*e.g.*, Jolly 1965, Ballance 1990, Williams *et al.* 1993). We call this proportion "mark rate."

The large number of models available for capture-recapture analysis, as well as a number of estimators for each, results in the difficult question of which are most suitable for the situation at hand (Burnham *et al.* 1995). Use of an inappropriate

² MINISTRY OF FISHERIES. 2003. www.fish.govt.nz/current/press/pr240103.htm. Visited 14 October 2004.

model can lead to a population estimate with an unknown degree of bias and unrealistically small or unacceptably large variance (Burnham and Anderson 1992). In this paper we utilize a long-term photo-ID data set, and estimates of mark rate, to calculate abundance of Hector's dolphin at Banks Peninsula.

METHODS

Field methods have been described previously (see Slooten *et al.* 1992, Bräger *et al.* 2002). Briefly, Hector's dolphins were photographed at Banks Peninsula, between Birdlings Flat in the south and Sumner Head in the north, from 4.5–6-m outboard-powered boats during surveys conducted by S. Dawson, E. Slooten, S. Bräger, and S. Smith (Fig. 1). Along-shore transects were followed until a dolphin or a group of dolphins was encountered, at which point the transect was temporarily stopped to allow all dolphins in the group to be photographed. The transect was then resumed until another individual or group was encountered. Nikon auto-focus cameras (Nikon F4s, N8008s, F90x, and F5) equipped with data-backs imprinting time and date, were used, usually with Nikkor 80–200-mm f2.8 lenses. Images were shot on 100 ISO slide film (Fuji Provia 100) or 400 ISO black and white print film (Kodak TMAX 400). Shutter speeds were kept above 1/500 s at all times and preferably above 1/1000 s. Since 1993, a HP200LX palmtop computer was used to automatically store time, date, GPS fix and search effort information. We restricted the current analysis to data collected between 1989–1997.

High-quality photographs of distinctive individuals were printed and judged usable if the dorsal fin was in focus, completely visible, and perpendicular to the photographer. These criteria ensured that marks would have been seen if present. Each visible dorsal fin was judged to be marked or unmarked and assigned to one of the three categories of mark quality used by Slooten *et al.* (1992: see this paper for examples). Only dolphins with category 1 or 2 marks were used for capture-recapture analysis, as these are permanent marks that are unambiguous and clearly identifiable from high-quality photographs.

Data Analysis

Data were summarized into a matrix of capture histories, in which rows denote the individuals, and columns denote the sampling periods. A "1" denotes that the individual was captured at least once in that sampling period and a "0" denotes that the individual was not captured.

Given the time encompassed by the data set, it was unrealistic to assume that the population was closed to births and deaths, and therefore open population models were used. These models allow the population to be open to births and deaths between sampling periods. Indeed the closure test in the program CAPTURE (Rexstad and Burnham 1991) was highly significant ($P < 0.00001$), strongly rejecting the assumption of a closed population. It should be noted that the closure test is insensitive to behavioral changes in capture probabilities, and may lead to a false rejection of closure.

The basic open population model, commonly termed the Jolly-Seber model, allows both survival and capture probabilities to differ for each sampling period (Pollock *et al.* 1990). Simplifications of the Jolly-Seber model restrict survival and/or capture probabilities to be constant for the entire study period. These models

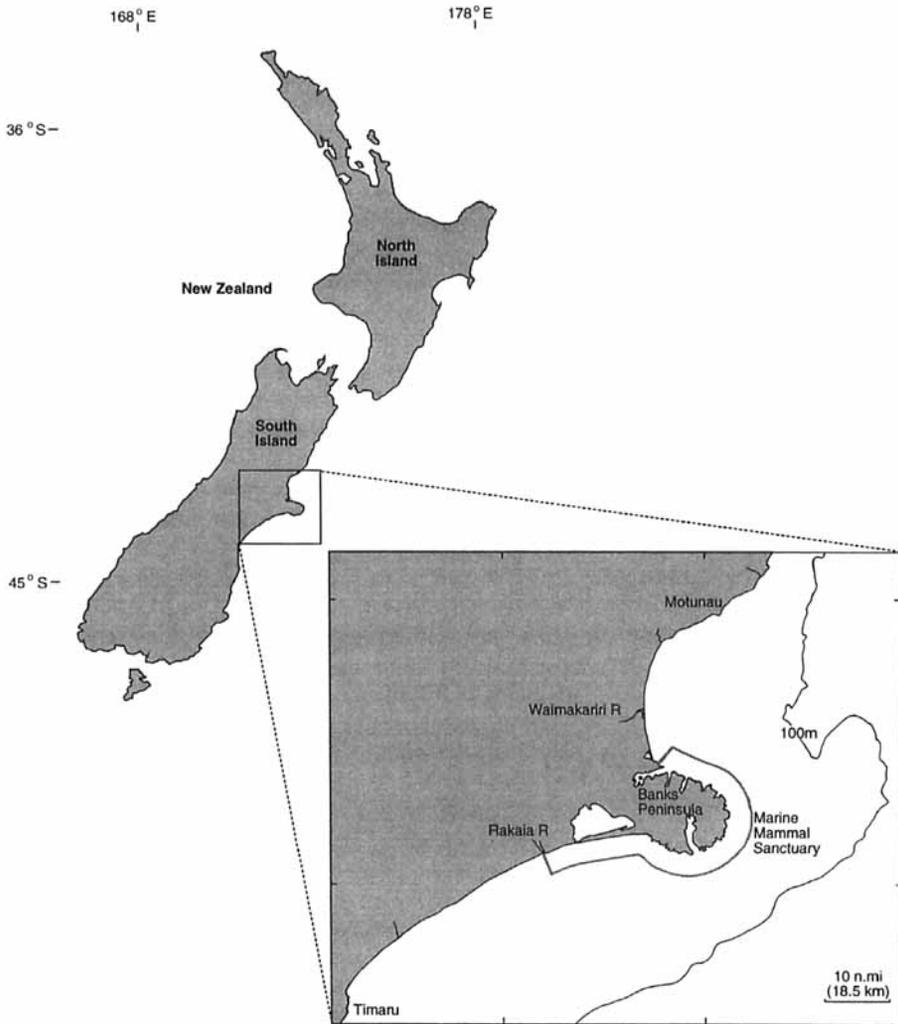


Figure 1. The study area around Banks Peninsula, from Birdlings Flat to Sumner.

are termed Model B (constant survival), Model C (constant capture) and Model D (constant survival and capture) (Jolly 1982). The standard Jolly-Seber model is referred to as Model A. An assumption of this class of models is that all individuals have the same survival and capture probabilities within each sampling period. Heterogeneous capture probabilities can result in an abundance estimate that is negatively biased, although bias decreases if average capture probabilities are relatively high, such as ≥ 0.5 (Pollock *et al.* 1990). A generalization of Model A, termed Model 2, allows the survival probability to change after the first capture (Brownie and Robson 1983). This generalization can be applied to all of the Jolly-Seber class of models to give four models denoted as Models 2, 2_B, 2_C, and 2_D.

Choosing the best model consisted of two main steps. The first step was to assess how well the models fitted the data, that is, how well they explained the variation in the capture history matrix. For this process, goodness-of-fit (GOF) tests in the

program JOLLY (Pollock *et al.* 1990) were used for models A, B, D, and 2 (GOF tests for the other models are not available in the program JOLLY). It should be noted that the GOF tests are not very powerful, but the corollary of this is that any differences detected are likely to be real. JOLLY also performs a Likelihood Ratio Test (LRT) equivalent to the test from Brownie and Robson (1983) that tests for the effect of first capture on survival probabilities.

If a model was deemed to fit the data, the next stage of analysis was to determine whether a simpler model also fitted the data. Generally, bias decreases and variance increases as the number of parameters increases. A model with too few parameters may not be able to adequately model the situation and will likely lead to severe bias, as well as estimates of variances that are unrealistically small (Burnham and Anderson 1992). Conversely, a model with too many parameters will reduce the bias, but at the cost of increased variance for those parameters that are included. In addition, some of the included parameters may be determined to be significant whereas this may not be the case. Our goal was to select a biologically meaningful model with the smallest number of parameters.

In order to choose a suitable model, the data were analyzed using the program MARK (White and Burnham 1999). We used Akaike's Information Criterion (AIC) corrected for small sample bias (AIC_C; Hurvich and Tsai 1989) to choose among possible models. The selection procedure consists of computing the AIC_C score for each model that is being considered, and selecting the one with the smallest score. Effectively this provides a compromise between fit and complexity, *i.e.*, is a measure of model fit penalized by the number of parameters.

Once a model was chosen, estimates of abundance were derived. Program MARK produces estimates of survival and capture probabilities, not of abundance for the "recaptures only" data-type. Nevertheless, abundance estimates and variances may be obtained by:

$$\hat{N}_j = \frac{n_j}{\hat{p}_j} \quad (1)$$

$$\text{var}(\hat{N}_j) = \left(\frac{n_j}{\hat{p}_j} \right)^2 \left(\frac{\text{var}(\hat{p}_j)}{\hat{p}_j^2} \right) \quad (2)$$

where n_j is the number of captured individuals and \hat{p}_j is the estimated capture probability in period j (Seber 1982, Loery *et al.* 1997).

Estimating Mark Rate

The abundance estimate given by eq. (1) relates only to identifiable individuals and must be scaled by mark rate in order to obtain an estimate of the total population size. As long as photographs are taken randomly (*i.e.*, without any bias towards naturally marked or unmarked individuals) the proportion of photographs showing naturally marked animals should be an unbiased measure of the proportion of identifiable individuals in the population (*i.e.*, the mark rate). To estimate mark rate, we randomly shot about 20 rolls of 36-exposure film of dorsal fin photos in each of five consecutive years (1992–1996). To reduce variation, all photographs were taken by the same photographer (S.M.D.) with the same camera/lens combination (Nikon F4S with Nikkor AF80–200ED f2.8 lens) from a 6.6-m rigid-hulled inflatable (with a 90-hp outboard motor) driven by the same driver (E.S.). On each encounter, the aim was to take three times as many photographs as the dolphins'

group size to standardize effort and increase the chance of "capturing" every group member (Würsig 1978, Würsig and Jefferson 1990). The survey design and assessment of photographs was the same as described earlier. The random photography work was undertaken independently from the capture-recapture surveys.

Although the random photography for mark-rate analysis was performed during 1992–1996, we assume that the mark-rate is constant over the entire study period. This assumption is made because it is unlikely that the mark-rate will change dramatically from year to year. The variance is assumed to be largely measurement error. Hence, only one estimate of mark-rate and variance is produced by:

$$\hat{Q} = \frac{\sum_{i=1}^k \frac{I_i}{T_i}}{5} \quad (3)$$

$$\text{var}(\hat{Q}) = \left(\sum_{i=1}^k \frac{Q_i(1-Q_i)}{T_i} \right) / k^2 \quad (4)$$

where I_i is the number of photographs of individuals with grade 1 and grade 2 marks, k is the total number of "random photography" periods and T_i is the total number of photographs taken during the i th "random photography" period. Note that there were $k = 5$ "random photography" periods and that for each $Q_i = I_i/T_i$.

Total Population Size

The abundance estimate given by eq. (1) is then scaled by the mark-rate given by eq. (3) to give an estimate of total abundance. The estimate of the total abundance and its variance is thus given by:

$$\hat{N}_j^* = \frac{\hat{N}_j}{\hat{Q}} \quad (5)$$

$$\text{var}(\hat{N}_j^*) = \left(\frac{\hat{N}_j}{\hat{Q}} \right)^2 \left(\frac{\text{var}(\hat{N}_j)}{\hat{N}_j^2} + \frac{\text{var}(\hat{Q})}{\hat{Q}^2} \right) \quad (6)$$

To incorporate the relative contributions of the capture-recapture variance (eq. 2) and the mark-rate variance (eq. 4) into the overall variance (eq. 6), the coefficient of variation (CV) of \hat{N}_j^* can be expressed in terms of the CV of \hat{N}_j and \hat{Q} :

$$\text{CV}(\hat{N}_j^*) = \sqrt{\text{CV}(\hat{N}_j) + \text{CV}(\hat{Q})} \quad (7)$$

Burnham *et al.* (1987) recommend that log-normal confidence intervals be constructed for abundance estimates, as standard confidence intervals often result in a lower limit below zero, a situation that is not realistic. Log-normal confidence intervals give a lower limit of $\hat{N}_L^* = \hat{N}^* / r$, and an upper limit of $\hat{N}_U^* = \hat{N}^* \times r$. For 95% confidence intervals, r is given by:

$$r = \exp \left[1.96 \sqrt{\ln(1 + \text{CV}(\hat{N}^*)^2)} \right] \quad (8)$$

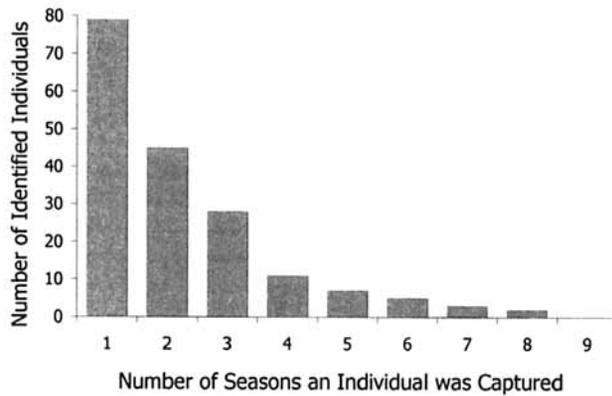


Figure 2. Distribution of the number of seasons individuals have been captured.

RESULTS

Between 1989 and 1997, we identified 180 individuals from distinct nicks and notches on their dorsal fins. Resighting rates were relatively low, with 79 individuals seen in only one sampling period, and only 17 individuals seen in more than 4 sampling periods (Fig. 2). The number of individuals “captured” in a sampling period averaged 44.3 (range: 18–79) (Fig. 3). The discovery curve shows an increasing number of identifiable individuals over the study period (Fig. 3).

Goodness-of-fit (GOF) tests in JOLLY indicated non-significant values for Model B (constant survival, time dependent capture) and Model 2 (time dependent survival and capture with temporary trap response on survival) (Table 1). A Likelihood Ratio Test (LRT) was also performed in JOLLY to test whether the survival rate of newly captured animals is the same as the survival rate of previously captured animals, effectively testing between Model A (the Jolly-Seber model: time dependent survival and capture) and Model 2. This test was just significant rejecting the simpler Model A over the more general Model 2 ($P = 0.049$), suggesting a possible “trap response” to capture. These results indicate that Model 2 and Model B are appropriate models.

Because of the limited number of models available in JOLLY, and the possibility of a temporary trap-response on survival, the AIC_C procedure in MARK was used to

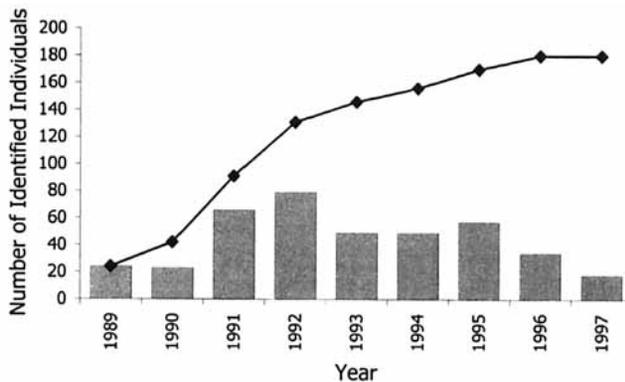


Figure 3. Number of individuals captured during each sampling period and discovery curve for Hector's dolphins at Banks Peninsula.

Table 1. Goodness-of-fit tests for the models in JOLLY.

Test	χ^2	df	P
GOF Model A	27.99	15	0.022
GOF Model B	30.84	21	0.076
GOF Model D	54.43	28	0.002
GOF Model 2	10.73	8	0.218
LRT Model A vs. 2	12.64	6	0.049

find a more parsimonious model. The best model found assumed time-dependent capture probabilities and constant survival probabilities, with a temporary effect of first capture on survival (Table 2). This model, termed Model 2_B, calculates that the survival probability for an individual after its first capture is 0.725 (CV = 0.07), whereas after the second and subsequent capture, the survival rate increases to 0.888 (CV = 0.04). These values correspond to new individuals having a 73% chance of surviving, remaining in the study area, and being photographically reidentified at the next capture period, with this probability rising to 89% for those individuals that have been previously identified.

Over the five "random photography" periods between 1992 and 1996, a total of 2,921 photographs were taken of which 305 contained individuals with category 1 or 2 marks. The overall mark-rate was estimated to be 0.1046 (SE = 0.0057) (Table 3). This mark rate was applied to all years.

The estimates derived from Model B and Model 2_B were scaled by the mark rate to produce an estimate of the total population of Hector's dolphins at Banks Peninsula (Fig. 4, 5). Abundance estimates for 1996 from Model 2_B and Model B were 1,119 (CV = 0.21) and 1,007 (CV = 0.21) respectively. These are shown with the line-transect estimate from 1997 (Dawson *et al.* 2004), in Table 4. The average capture probability was 0.44 (CV = 0.16) for Model 2_B and 0.43 (CV = 0.16) for Model B. For both Model 2_B and Model B, the average relative contribution to the variance of the overall abundance estimate was 89% from the capture-recapture variance, and 11% from the mark-rate variance.

DISCUSSION

The estimates derived from Model 2_B and Model B are very similar. This is expected, since Model 2_B is only a slight generalization of Model B. The difference between the two models is the effect of first capture on survival that is present in

Table 2. AIC_C scores for the various models from MARK, ordered by AIC_C.

Model	Capture probability	Survival probability	Temporary trap response on survival	AIC _C	Parameters	-2* log likelihood
2 _B	Time	Constant	Yes	919.836	10	899.2414
B	Time	Constant	No	923.243	9	904.7578
C	Constant	Time	No	928.049	9	909.5638
2 _C	Constant	Time	Yes	931.419	16	897.9245
2 _D	Constant	Constant	Yes	933.221	3	927.1573
A	Time	Time	No	933.234	15	901.9189
D	Constant	Constant	No	933.254	2	929.2223
2	Time	Time	Yes	934.793	22	887.9662

Table 3. Summary of data from "random photography" period used to calculate mark-rate. T is the total number of photographs taken, I is the number of those with identifiable individuals, and Q is the resulting mark rate (eq. 3).

Period	T	I	Q	SE (Q)
1992	526	63	0.1200	0.0142
1993	601	76	0.1265	0.0136
1994	585	59	0.1009	0.0125
1995	588	40	0.0680	0.0104
1996	621	67	0.1084	0.0124
Average			0.1046	0.0057

Model 2_B. As was shown by the LRT, this effect of capture was barely significant ($P = 0.049$). Selection of the overall best model in this situation is somewhat subjective. The results agree well with the line-transect estimate (Table 4).

Although temporary response on apparent survival is common for capture-resighting studies in which animals are physically handled (Brownie and Robson 1983), it seems highly unlikely in photo-identification studies of marine mammals. The most likely explanation is that the apparent trap-response on survival is an edge effect (Otis *et al.* 1978) caused by those individuals having home ranges which overlap only partly with the geographic extent of the photo-ID surveys.

Having used both line-transect (L-T) and capture-recapture (C-R) techniques to estimate abundance of the same population allows comment on their respective merits. There is no evidence that either of the two approaches is significantly biased. The C-R estimate has higher precision (smaller CV), though it represents many more sampling days.

We would argue that L-T estimates are easier to interpret, because they apply to the area sampled by the transect lines. This is not true of the C-R estimate, which, because it is made over a much longer period, includes animals that stray only occasionally into the sampling area. Hence C-R estimates (even of resident animals) typically apply to a larger area than was sampled. Insight into how much greater that area is can be gained from studies of home range/movement. Also, L-T methods measure the population that is "present" in the study area at the time of the survey. C-R methods

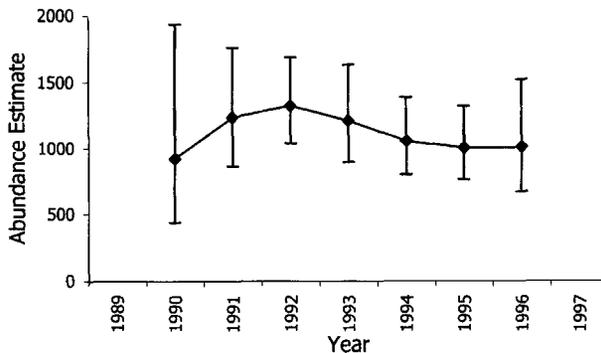


Figure 4. Abundance estimates from Model B (constant survival), scaled by mark rate, shown with log-normal 95% confidence intervals. (Abundance estimates are not available for the first or last sampling period for this model.)

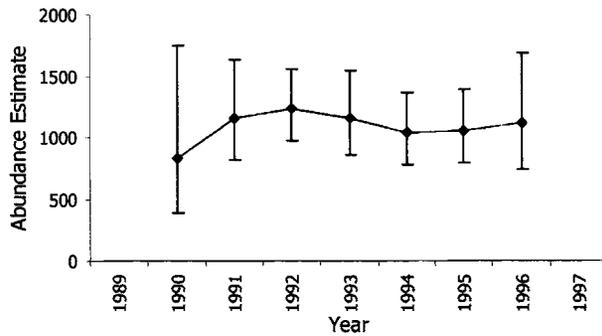


Figure 5. Abundance estimates from Model Z_B , scaled by mark rate, shown with log-normal 95% confidence intervals. (Abundance estimates are not available for the first or last sampling period for this model.)

measure the overall population that “uses” the area, whether or not all individuals are present at any one time (Childerhouse *et al.* 1995, Calambokidis and Barlow 2004).

An advantage of L-T surveys is that the sampling design is explicit, and it is easier to develop designs that cover an area randomly or equally. In contrast, C-R sampling is always “closing mode,” that is, when a group is encountered the boat stops to photograph the individuals. During that sampling other individuals may be seen, and they will be targeted in turn. Thus the sighting effort in C-R surveys is neither random nor equal (see also Calambokidis and Barlow 2004). This is likely to contribute to sighting heterogeneity.

It could be also said that L-T surveys use every observation, while C-R surveys of species that are not 100% marked do not. In addition, L-T surveys take less time, because animals only need to be seen once. The above points largely favor L-T surveys. C-R approaches, however, have two very important advantages. The first is that the photo-ID data used in C-R estimates of abundance, especially if gathered over a long period, can provide a wealth of other information including home range, movement, survival rate, calving interval, longevity and associations (see Hammond *et al.* 1990, for examples). Indeed, with care, a C-R analysis of abundance could be a spin-off from photo-ID research directed at other questions. The second important advantage is that photo-ID is best suited to small, relatively inexpensive vessels. L-T surveys, because they need a stable platform for measuring distances to sightings, typically require larger, more expensive survey platforms (Dawson *et al.*, 2004).

There is no indication that population size has increased noticeably since the Banks Peninsula Marine Mammal Sanctuary was created. Likewise, there is no indication that survival rates have improved (Cameron *et al.* 1999, DuFresne 2004). This makes sense in the light of evidence for continued dolphin bycatch in gill nets immediately north, south and offshore of the sanctuary boundaries.^{3,4} Taken together, data from observer programs to estimate bycatch, population surveys and

³ BAIRD, S. J., and E. BRADFORD. 2000. Estimation of Hector's dolphins bycatch from inshore fisheries, 1997/98 fishing year. Published client report on contract 3024, funded by Conservation Services Levy. Department of Conservation, Wellington. 28 pp. <http://www.csl.org.nz>

⁴ STARR, P. 2000. Comments on “Estimation of the total by-catch of Hector's dolphins (*Cephalorhynchus hectori*) from the inshore trawl and set net fisheries off the East Coast of the South Island in the 1997–98 fishing year.” Unpublished paper presented to Conservation Services Levy Working Group. Department of Conservation, Wellington, New Zealand. 4 pp.

Table 4. Population estimates from line transect survey and capture-recapture. The line transect results are from Dawson *et al.* (2004).

Method	<i>n</i>	CV	Lower 95% CI	Upper 95% CI
Line transect 1997/98	897	0.28	522	1543
Model 2 _B 1996	1,119	0.21	744	1682
Model B 1996	1,007	0.21	667	1519

capture-recapture analyses to estimate abundance and survival indicate that the Banks Peninsula Marine Mammal Sanctuary is not large enough to be effective. Extending the north, south and offshore boundaries would protect a larger portion of the local population, and is needed for the population to recover to non-threatened status.

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