

First evidence that marine protected areas can work for marine mammals

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Summary

1. Marine protected areas (MPAs) have been advocated for the protection of threatened marine mammals, but there is no empirical evidence that they are effective. In 1988, the Banks Peninsula Marine Mammal Sanctuary was established to reduce gillnet mortalities of Hector's dolphin *Cephalorhynchus hectori*, an endangered dolphin species endemic to New Zealand. This study assesses the effectiveness of the MPA in improving the survival rate of Hector's dolphin at Banks Peninsula.
2. Over 21 years, we undertook photo-identification surveys of Hector's dolphins along standardized transects from small outboard-powered boats. From 1986 to 2006, we photographically captured 462 reliably marked individuals. We estimated mean annual survival during the pre-sanctuary and post-sanctuary periods by applying a Bayesian random effects capture-recapture model to the data. Population growth was estimated from population simulations using a stage-structured matrix model.
3. We estimate a 90% probability that survival has improved between the pre-sanctuary and post-sanctuary periods, with estimates of mean survival probability increasing by 5.4% (from 0.863 to 0.917). This improvement in survival corresponds to a 6% increase in mean annual population growth (from 0.939 to 0.995).
4. *Synthesis and applications.* Our study demonstrates improvement in a demographic parameter of an endangered marine mammal species following conservation action. Our results provide evidence that area-based protection measures can be effective for marine mammals. We note that estimating demographic parameters in marine mammals requires many years of data to achieve sufficient precision to detect biologically meaningful change. MPAs should be established with a commitment to long-term monitoring.

Key-words: Bayesian, capture-recapture, demographic, dolphin, gillnet, marine protected area, matrix model, survival

Introduction

The establishment of protected areas is a widely used tool for the preservation of biodiversity. Marine protected areas (MPAs), in which certain fishing methods are restricted or banned, are commonly used to reduce impacts on marine mammals (Hoyt 2005). Quantifying the effects of MPAs is essential for justifying their designation in the first place and evaluating their efficacy as management tools (Kelleher 1999).

However, there is currently little if any empirical evidence that MPAs have been effective for improving demographic parameters in marine mammal populations.

Hector's dolphins *Cephalorhynchus hectori* (van Beneden) are a small, endangered species endemic to the coastal waters of New Zealand. A high level of incidental catch in gillnets set by commercial and amateur fishers led to the creation of the Banks Peninsula Marine Mammal Sanctuary in 1988 (Dawson & Slooten 1993). Within the sanctuary's 1170 km² area (Fig. 1), amateur gillnetting was restricted to specific times and places, and commercial gillnetting was prohibited (Dawson & Slooten 1993). Banks Peninsula has a resident population of

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Fig. 1. Map of New Zealand indicating the location of the Banks Peninsula Marine Mammal Sanctuary.

about 1000 Hector's dolphins (Gormley *et al.* 2005) that show very limited alongshore movement (*c.* 50 km) and high site fidelity (Rayment *et al.* 2009). Adult survival in this population was unsustainably low before the sanctuary's establishment (Slooten, Dawson & Lad 1992), and no significant increase had been detected since designation (Cameron *et al.* 1999; Du Fresne 2005). Furthermore, there are no comparable estimates of bycatch for the region before and after the sanctuary's establishment with which to assess its efficacy.

We hypothesized that reduced gillnetting pressure should result in increased adult survival rate and an associated improvement in population growth. To address whether survival of adult Hector's dolphins has improved following reduction in gillnetting at Banks Peninsula, we applied random effects Bayesian modelling to photographic capture-recapture data gained via photo-ID studies begun in 1985. We then specified a matrix projection model for both the pre- and post-sanctuary periods that combines estimates of survival with available information on other life-history parameters. The matrix model is used to carry out population projections to estimate the population-level effects of the sanctuary's establishment.

Materials and methods

FIELD METHODS

Field methods for photo-identification of Hector's dolphins have been described in detail elsewhere (Slooten, Dawson & Lad 1992; Bräger *et al.* 2002). Briefly, standardized along-shore transects around Banks Peninsula were followed in 4–6-m outboard-powered boats. When a dolphin sighting was made, all distinctive dolphins in the group were photographed before continuing the transect. Photographs were judged usable if the dorsal fin was in focus, completely visible and perpendicular to the photographer, thereby ensuring that any identifying marks would be clearly visible if present. Individual

dolphins were judged to be either unmarked or marked and subsequently assigned to one of the three categories of mark quality defined by Slooten, Dawson & Lad (1992: see this paper for examples). Only dorsal fins with permanent, unambiguous marks were used for further analysis, minimizing the possibility of mark changes and subsequent misidentification of individuals on recapture (Du Fresne 2005). A catalogue of identifiable individuals was maintained, along with a data base containing each individual's sighting history. Because of involvement in line-transect surveys (e.g. Dawson *et al.* 2004), no photo-ID fieldwork was conducted in 1998 or 1999.

Data were restricted to captures during November to February inclusive, to maximize the available data whilst attempting to satisfy the assumption of population closure within each sampling period (Pollock *et al.* 1990) for the capture-recapture model (see below). The data were summarized into a capture history for each individual, where $x_{i,t} = 1$ indicates that individual i was observed at least once during sampling period t , and 0 otherwise, where t ranges from 1986 to 2006.

ANALYTICAL METHODS

Statistical model

We used a modified form of the Cormack–Jolly–Seber (CJS) model to estimate annual survival (Cormack 1964; Jolly 1965; Seber 1965). The CJS model allows for imperfect detection, that is, individuals that are alive may be missed during some sampling periods. We implemented the CJS model using a state-space modelling approach that includes a process model that describes the true state (alive or dead) of each individual at each time period, and an observation model that describes whether an individual was captured at each time period, conditional on it being alive.

The alive state of each individual was modelled as a random variate from a Bernoulli distribution, where $A_{i,t} = 1$ indicates individual i is alive at time t , and 0 otherwise:

$$A_{i,t+1} \sim \text{Bern}(\phi_t A_{i,t}), \quad i = 1, \dots, n; t = a_i, \dots, T-1 \quad \text{eqn 1}$$

where ϕ_t is the probability of survival from t to $t+1$, n is the total number of individuals, a_i is the period individual i was first observed, and T is the total number of sampling periods. Survival was modelled on the logit scale allowing for different mean survival before and after the sanctuary was established, with annual variation treated as a random effect:

$$\text{logit}(\phi_t) = \begin{cases} \mu_{\phi_{\text{pre}}} + \varepsilon_{(\phi)_t}, & t = 1, \dots, 4 \\ \mu_{\phi_{\text{post}}} + \varepsilon_{(\phi)_t}, & t = 5, \dots, T-1 \end{cases} \quad \text{eqn 2}$$

where $\mu_{\phi_{\text{pre}}}$ and $\mu_{\phi_{\text{post}}}$ denote the mean survival rate on the logit scale before and after the sanctuary was established, and ε_t is the random effect on survival over time, normally distributed $\varepsilon_{(\phi)_t} \sim N(0, \sigma_{\phi}^2)$, where σ_{ϕ}^2 is the annual process variation in survival.

Heterogeneous capture probabilities were included by using the number of times an individual was observed in a sampling period as a covariate for capture during the next period (Fletcher 1994). The probability of observing each individual was modelled as:

$$x_{i,t} \sim \text{Bern}(A_{i,t} p_{i,t}), \quad i = 1, \dots, n; t = a_i + 1, \dots, T \quad \text{eqn 3}$$

where $p_{i,t}$ is the capture probability of individual i at time t , and:

$$\text{logit}(p_{i,t}) = \alpha_t + \beta_t z_{i,t-1}, \quad i = 1, \dots, n; t = 2, \dots, T \quad \text{eqn 4}$$

where $z_{i,t}$ is the number of times individual i was observed in period t , and α_t and β_t are the regression intercept and slope coefficients,

respectively. These were modelled as normally distributed random effects:

$$\alpha_t = \mu_\alpha + \varepsilon_{(\alpha)t}, \quad t = 2, \dots, T \quad \text{eqn 5}$$

$$\beta_t = \mu_\beta + \varepsilon_{(\beta)t}, \quad t = 2, \dots, T \quad \text{eqn 6}$$

where $\varepsilon_{(\alpha)t}$ and $\varepsilon_{(\beta)t}$ are the random effects on α and β over time, respectively, normally distributed $\varepsilon_{(\alpha)t} \sim N(0, \sigma_\alpha^2)$ and $\varepsilon_{(\beta)t} \sim N(0, \sigma_\beta^2)$.

The difference between post- and pre-sanctuary survival (on the logit scale) was calculated as $\Delta\mu_\phi = \mu_{\phi\text{post}} - \mu_{\phi\text{pre}}$.

Parameter estimation

The model was fitted in a Bayesian framework using WinBUGS (Spiegelhalter *et al.* 2004). Vague prior distributions were specified for all parameters: logistic (0, 1) for the mean survival parameters ($\mu_{\phi\text{pre}}$ and $\mu_{\phi\text{post}}$), normal (0, 100) for the mean coefficient parameters (μ_α and μ_β) and uniform(0, 100) for all variance parameters (σ_ϕ^2 , σ_α^2 and σ_β^2). The capture probability covariate $z_{i,t}$ was standardized to improve convergence. Three Markov-chains were started from different initial values and run for 10 000 iterations to tune the algorithm. These 'burn-in' samples were discarded and the algorithm run for a further 100 000 samples. Each chain was thinned by taking every fifth value and then combined to give a posterior sample of 60 000 for each model parameter. Convergence was assessed visually (Fig. S1, Supporting information) and by confirming that the Brooks–Gelman–Rubin statistic (Brooks & Gelman 1998) had converged to one (Fig. S2, Supporting information). Goodness-of-fit was assessed using a posterior predictive checking procedure (Link & Barker 2010) for a general CJS model (Appendix S2, Supporting information).

Survival rates on the probability scale, which include both sampling and process variation, were obtained by taking 10 000 samples from the posterior distributions of $\mu_{\phi\text{pre}}$, $\mu_{\phi\text{post}}$ and σ_ϕ :

$$\phi_{\text{pre}} \sim N(\mu_{\phi\text{pre}}, \sigma_\phi^2) \quad \text{eqn 7}$$

$$\phi_{\text{post}} \sim N(\mu_{\phi\text{post}}, \sigma_\phi^2) \quad \text{eqn 8}$$

Our capture-recapture analysis differs from the classical approach in that a single model was specified in which all the parameters are modelled as random effects, that is, the parameters are acknowledged to vary in a random manner with time about some mean, but not in a way that can be explained by covariates and trends (Royle & Link 2002; Schofield, Barker & MacKenzie 2009). This approach is flexible in that it can adequately model constant or time-varying survival without needing to specify different competing models. Furthermore, it naturally separates out the process and sampling variation, enabling us to more easily make inference about parameters of interest such as changes in mean survival. Our code is provided in Appendix S1 (Supporting information).

POPULATION MODEL

A fixed-duration, stage-structured matrix model was specified to carry out population projections (Caswell 2001). We used a stage-structured model with three stages: calf (from birth to age 1), juveniles (age 1 to age of first reproduction) and adults (age of first reproduction to maximum age).

$$A = \begin{pmatrix} 0 & S_J \gamma_J m & S_A (1 - \gamma_A) m \\ S_C \gamma_C & S_J (1 - \gamma_J) & 0 \\ 0 & S_J \gamma_J & S_A (1 - \gamma_A) \end{pmatrix} \quad \text{eqn 9}$$

The projection model requires a small number of life-history parameters: stage-specific survival (S_C , S_J and S_A for calves, juveniles and adults, respectively) and fecundity (m), as well as the conditional probability of moving from one stage to the next given survival (γ_C , γ_J and γ_A). The fecundity rate is defined as the average number of female offspring, per mature female, per year, and therefore, the fecundity rate for juveniles and calves is by definition equal to zero. Estimates of the transition parameters γ are not available directly; however, they can be estimated recursively as functions of the other parameters and asymptotic population growth λ (Caswell 2001). The recursive method for estimating the conditional growth parameters is not guaranteed to converge for all combinations of parameter values; however, they did for the range of parameter values we considered. For our model:

$$\gamma_J = \frac{(S\lambda^{-1})^{\alpha-1} - (S\lambda^{-1})^{\alpha-2}}{(S\lambda^{-1})^{\alpha-1} - 1} \quad \text{eqn 10}$$

and

$$\gamma_A = \frac{(S\lambda^{-1})^{\omega-\alpha+1} - (S\lambda^{-1})^{\omega-\alpha}}{(S\lambda^{-1})^{\omega-\alpha+1} - 1} \quad \text{eqn 11}$$

where α and ω are age at first reproduction and maximum age, respectively. Note that $\gamma_C = 1$ by definition (i.e. all surviving calves become juveniles at age one).

Adult survival was estimated from the capture-recapture data using the estimation model described previously ($S_A = \phi$). We also assume juvenile survival was equal to adult survival. Field observations of Hector's dolphins show that like most cetaceans, new-born calves are dependent on their mother for at least the first year of their life. We, therefore, assume that the survival of a calf is dependent on both the survival of that calf, and also of its mother; hence, calf survival is defined as ϕ^2 .

Fecundity ($m = 0.025$) and age at first reproduction ($\alpha = 7.55$) were obtained from Gormley (2009), who used observations of calf–mother pairs, accounting for adult survival, calf and adult detection probabilities, as well as information on age and reproductive status from the teeth and ovaries of dead animals (see also Slooten 1991; Slooten & Lad 1991).

Maximum age (ω) was inferred from the mark-recapture data set using the number of years that individuals are in the catalogue as a minimum estimate. Four individuals have been seen over a span of 20 years corresponding to an age of at least 22 (Hector's dolphins do not enter the catalogue until they are at least 2 years old as 1-year-old juveniles typically do not yet have identifying features). This estimate of maximum age is likely to be low: we did not know the age of the four individuals above when first seen, their age was likely to be greater than two, and they may subsequently survive for some years to come. For the purpose of model simulations, we represent uncertainty in maximum age by a simple triangular distribution, with a mode of 26 and minimum and maximum values of 22 and 30, respectively.

The number of parameters required to specify the matrix reduces to annual survival rate (ϕ), age at first reproduction (α), maximum age (ω) and fecundity (m ; Table 2).

The population projection model was run under two different estimates of survival reflecting the pre-sanctuary and post-sanctuary periods. Fecundity, age at first reproduction and maximum age were assumed to be constant for both scenarios.

Simulations were initialized with a starting population of 500 animals (i.e. approximately, the female population size assuming a sex

ratio of 0.5). A total of 10 000 projections were each run for 50 years. For each iteration, single values for fecundity and age at first reproduction were sampled from their respective posterior distributions, along with a value for maximum age from the triangular distribution specified earlier. Values for μ_ϕ and σ_ϕ were sampled for each iteration, and a value for annual survival rate for each year ϕ_t was sampled from eqns 7 and 8 for the pre- and post-sanctuary periods, respectively. Each year, the matrix projection model was specified and values for the transition parameters derived. The population was projected with demographic stochasticity included on all parameters. The distribution of population growth rate was obtained by:

$$\lambda = \exp\left(\frac{\log(N_T) - \log(N_0)}{T}\right), \quad \text{eqn 12}$$

where N_T is the population size after $T = 50$ years, and N_0 is the initial population size. Population growth is considered to be positive when $\lambda > 1$ and negative otherwise. The proportion of projections where $\lambda > 1$ is interpreted as the probability of positive population growth.

We calculated the sensitivity of λ to each of the projection model parameters, that is, the relative change in λ for a small absolute change in any parameter θ (Caswell 2001):

$$s(\theta) = \frac{\partial \lambda}{\partial \theta}. \quad \text{eqn 13}$$

Uncertainty in λ was decomposed into contributions because of uncertainty in each of the estimates of the projection model parameters to estimate the amount of variation in λ explained by the variance associated with each parameter. This was carried out for each parameter in the projection model using the sensitivity and variance of that parameter and then scaled to sum to 1:

$$\text{var}(\lambda_{\theta_i}) = \frac{s(\theta_i)^2 \text{var}(\theta_i)}{\sum_j s(\theta_j)^2 \text{var}(\theta_j)} \quad \text{eqn 14}$$

Because we are interested in the variation because of uncertainty in our parameter estimates (sampling variation), we excluded environmental stochasticity (process variation) in survival and used the inverse-logit of $\mu_{\phi_{\text{pre}}}$ and $\mu_{\phi_{\text{post}}}$.

Results

ESTIMATES OF SURVIVAL

During 1986–2006, a total of 462 reliably marked individuals were photographically captured during the summer periods (i.e. between November and February inclusive; Table 1). Direct estimates and functions of model parameters are given in Table 2. The posterior densities of $\mu_{\phi_{\text{pre}}}$ and $\mu_{\phi_{\text{post}}}$ indicate a difference in mean survival between the pre- and post-sanctuary periods (Fig. 2). From the posterior density of $\Delta\mu_\phi$, there is a 90% probability that survival has improved between the pre- and post-sanctuary periods. This difference translates to a mean increase in annual survival of 5.4% since the establishment of the sanctuary (from 0.863 to 0.917).

The estimates of annual survival are characterized by annual variability in the mean values, indicative of environmental stochasticity, and considerable levels of uncertainty, as indicated by the 95% credible intervals (Fig. 3). The estimates of annual survival show the improvements in survival in greater

Table 1. The total number of individuals captured (i.e. photographed) each summer, and the number of those that were recaptured (i.e. were first captured in an earlier time period). Note that no field work was carried out in 1998 or 1999

| Year | Total | Recaptures |
|------|-------|------------|
| 1986 | 62 | NA |
| 1987 | 58 | 35 |
| 1988 | 85 | 51 |
| 1989 | 23 | 16 |
| 1990 | 9 | 5 |
| 1991 | 46 | 29 |
| 1992 | 42 | 28 |
| 1993 | 48 | 34 |
| 1994 | 48 | 39 |
| 1995 | 54 | 39 |
| 1996 | 33 | 25 |
| 1997 | 18 | 18 |
| 1998 | – | – |
| 1999 | – | – |
| 2000 | 36 | 6 |
| 2001 | 76 | 35 |
| 2002 | 84 | 50 |
| 2003 | 77 | 48 |
| 2004 | 72 | 48 |
| 2005 | 163 | 98 |
| 2006 | 124 | 92 |

Table 2. Estimates for the seven model parameters from the full random effects model (above the dashed line), derived parameters: difference in mean survival on the logit scale $\Delta\mu_\phi = \mu_{\phi_{\text{post}}} - \mu_{\phi_{\text{pre}}}$, overall survival probabilities ϕ_{pre} and ϕ_{post} where sampling and process variation are included, and reproductive parameters age at first reproduction (α) and fecundity (m ; from Gormley 2009), and maximum age (ω) from triangular distribution with a mode of 26 and minimum and maximum of 22 and 30, respectively

| Parameter | Mean | SD | 2.5% | 97.5% |
|----------------------------|-------|-------|--------|-------|
| $\mu_{\phi_{\text{pre}}}$ | 1.991 | 0.380 | 1.286 | 2.842 |
| $\mu_{\phi_{\text{post}}}$ | 2.547 | 0.280 | 2.145 | 3.264 |
| σ_ϕ | 0.474 | 0.340 | 0.089 | 1.340 |
| μ_α | 1.490 | 0.331 | 0.856 | 2.156 |
| σ_α | 0.871 | 0.233 | 0.498 | 1.413 |
| μ_β | 5.356 | 0.686 | 4.055 | 6.755 |
| σ_β | 1.192 | 0.697 | 0.090 | 2.729 |
| $\Delta\mu_\phi$ | 0.557 | 0.473 | –0.351 | 1.583 |
| ϕ_{pre} | 0.863 | 0.084 | 0.647 | 0.971 |
| ϕ_{post} | 0.917 | 0.050 | 0.802 | 0.984 |
| α | 7.55 | 0.423 | 6.71 | 8.41 |
| ω | 26.00 | 1.63 | 22.88 | 29.10 |
| m | 0.205 | 0.050 | 0.129 | 0.324 |

detail, with all but one (1991) of the point estimates of annual survival from the post-sanctuary period greater than those from the pre-sanctuary period (Fig. 3).

The random effects modelling approach allowed capture probabilities to vary with time and also allowed us to describe the positive relationship between the number of captures in a period of an individual and the probability of its capture in the following period ($\mu_\beta = 5.356$, 95% CI = 4.055, 6.755).

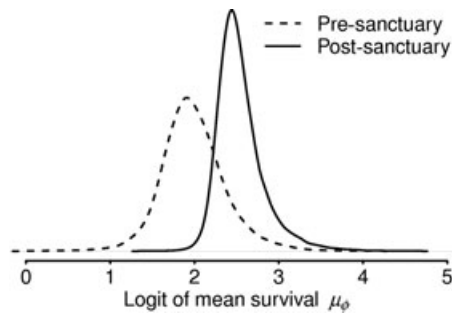


Fig. 2. Posterior density for the mean survival rate on the logit scale before and after creation of the Banks Peninsula Marine Mammal Sanctuary ($\mu_{\phi_{pre}}$ and $\mu_{\phi_{post}}$).

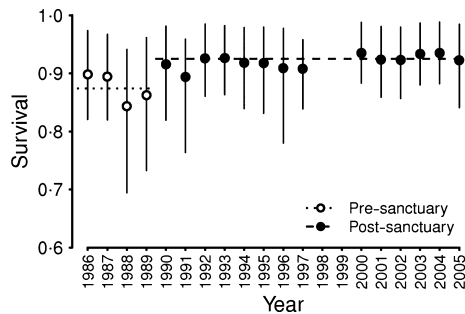


Fig. 3. Predicted values of annual survival with means and 95% credible intervals shown. The dotted and dashed lines indicate the inverse-logit of the posterior means for $\mu_{\phi_{pre}}$ and $\mu_{\phi_{post}}$, respectively.

POPULATION PROJECTIONS

The mean estimated annual population growth rate from the stage-structured matrix model (λ) was 0.939 (95% CI = 0.779, 1.025) and 0.995 (95% CI = 0.927, 1.048) for the pre- and post-sanctuary periods, respectively (Fig. 4). Using the proportion of projections with $\lambda > 1$ as a measure of positive growth, there was a much greater chance of positive population growth in the post-sanctuary period (41%) compared to the pre-sanctuary period (7%). Under the pre-sanctuary survival scenario, 16% of population projections declined to extinction within the 50-year projection interval, compared to only 0.6% under post-sanctuary survival.

The uncertainty in the estimate of population growth is because of the uncertainty in the estimates of the projection model parameters (Fig. 5). In the pre-sanctuary scenario, most of the uncertainty about λ is because of uncertainty in the estimate of fecundity (0.501), followed by survival (0.447, the sum of contributions from S_A and S_J ; Table 3). In the post-sanctuary scenario, most of the uncertainty about λ is because of uncertainty in the estimate of fecundity (0.795) with a smaller contribution from survival (Table 3), because of an improved precision in the estimate of mean post-sanctuary survival ($\mu_{\phi_{post}}$; Table 2). In both scenarios, the contributions to the variance of λ from age at first reproduction (α) and maximum age (ω) are very small despite relatively high levels of uncertainty in the estimates of those parameters (Table 2). This result is because of the comparatively small sensitivity of annual population growth to changes in those parameters (Table 3).

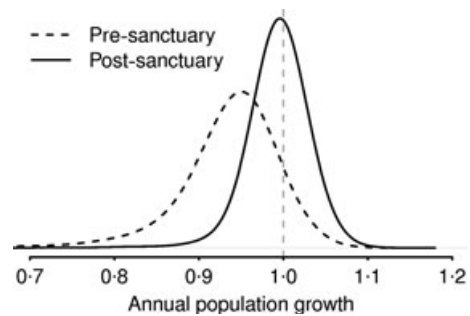


Fig. 4. Posterior distribution for theoretical population growth λ before and after creation of the Banks Peninsula Marine Mammal Sanctuary.

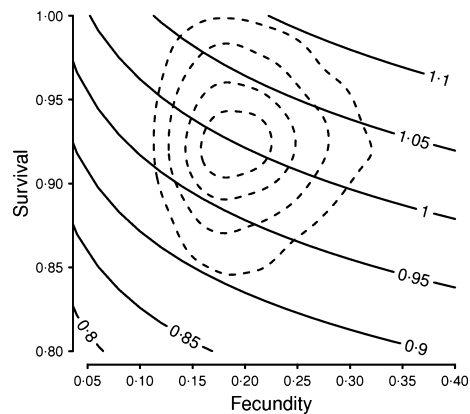


Fig. 5. Plot of asymptotic population growth λ against fecundity vs. survival conditional on mean values of age at first reproduction ($\alpha = 7.55$) and maximum age (26). Solid lines represent theoretical values of λ from the matrix model for the range of values for fecundity and survival on the x-axis and y-axis, respectively. Dashed black contour lines show the 25%, 50%, 75% and 95% percentiles for λ that result from sampling the distributions of fecundity and survival.

Table 3. Sensitivities and the amount of variation in λ explained by uncertainty in estimates of the parameters of the matrix projection model for the pre- and post-sanctuary cases

| Parameter | Pre-sanctuary | | Post-sanctuary | |
|-----------|---------------|----------------------------------|----------------|----------------------------------|
| | Sensitivity | Contribution to var(λ) | Sensitivity | Contribution to var(λ) |
| S_A | 0.608 | 0.282 | 0.589 | 0.085 |
| S_J | 0.465 | 0.165 | 0.571 | 0.080 |
| m | 0.278 | 0.501 | 0.338 | 0.795 |
| α | -0.003 | 0.005 | -0.007 | 0.024 |
| ω | 0.003 | 0.047 | 0.002 | 0.016 |

Discussion

Marine protected areas are now widely recognized as an effective management option for a variety of taxa (Halpern 2003). However, despite their increasing popularity, we found no published studies empirically examining the efficacy of MPAs for marine mammals. The increase in annual survival after the establishment of the Banks Peninsula Marine Mammal Sanc-

tuary suggests that the Sanctuary's restrictions on gillnetting have reduced the bycatch of Hector's dolphins. Furthermore, an increase in survival of this magnitude is biologically significant, with a corresponding increase in population growth of 6%.

To examine the impact of the sanctuary, we studied survival rate and projected population growth rather than direct estimates of abundance. Survival is typically estimated with less bias and greater precision than abundance (Pollock *et al.* 1990) and so is often a more sensitive measure of population change. Furthermore, direct measurement of dolphin abundance is difficult, and estimates usually have considerable uncertainty. This is especially so as populations become rare (Taylor & Gerrodette 1993), hence the ability to detect population changes from trends in abundance is usually poor (Taylor *et al.* 2007).

The post-sanctuary survival rate estimate of 0.917 is substantially higher than the pre-sanctuary rate (0.054 increase), but appears to be still too low to allow population recovery. The mean estimate of annual population growth from the population projections with post-sanctuary survival corresponds to a decrease of 0.5% per year, with only 41% of the simulations resulting in a population increase. This conclusion is consistent with other recent research showing that the Banks Peninsula Marine Mammal Sanctuary is too small to afford effective protection to the Hector's dolphin population (Slooten, Rayment & Dawson 2006; Rayment *et al.* 2009; Rayment, Dawson & Slooten 2010a,b; Slooten & Dawson 2010).

Some variation in the estimate of population growth from the population model (Fig. 5) results from uncertainty associated with estimating the life-history parameters. Estimates of survival from capture-recapture can be negatively biased because of captured individuals being, on average, older than the population (Manly 1970), especially when using permanent natural marks that are acquired via injury. Lower survival in older individuals is present in marine mammals in general (Barlow & Boveng 1991), but is undocumented in any small cetacean. However, for populations with relatively high annual survival rates, high rates of senescence may only result in negative bias in the order of 0.5% (Fletcher & Efford 2009). Furthermore, as field and photo-ID protocols have remained constant over the study's duration, it does not seem likely that potential biases in the survival rate estimates would affect the validity of the pre-/post-sanctuary comparison. Future planned work on improving estimates of life-history parameters will aid in quantifying population growth and will provide better insight into the effectiveness of the sanctuary.

The projection model we have specified incorporates good biological understanding and is supported by strong data to support the parameters (Williams, Nichols & Conroy 2002). A more complex model (i.e. including density dependence, age- and/or sex-specific survival, age-specific fecundity) could have been specified; however, there are insufficient data to support the additional parameters. Density dependence was not included as the aim of the projection model was not to predict population size at a future date, but rather to compare estimates of theoretical population growth from two different time

periods as a result of changes in survival. From our current data, there is no indication of reproductive senescence. This is typical of other small cetaceans (e.g. Franciscana dolphins *Pontoporia blainvillei*, Danilewicz 2003; Secchi 2006). Studies of bottlenose dolphins *Tursiops truncatus* indicate that juvenile survival is lower than adult survival; however, DuFresne (2004) found some evidence that juvenile survival of Hector's dolphins is slightly higher than adult survival.

In May 2008, New Zealand's Minister of Fisheries announced a suite of measures to provide additional protection for Hector's dolphin, including banning commercial and recreational gillnetting along the majority of the South Island's east coast out to 4 n.mi. offshore (Ministry of Fisheries 2008). On the same date, the acting Minister of Conservation announced the intention to extend the sanctuary to 12 n.mi. offshore (Department of Conservation 2008). Acoustic seismic surveys are now regulated within this extended sanctuary area, but there are no restrictions on fishing beyond 4 n.mi. offshore. Thus, the Ministry of Fisheries' changes have resulted in additional restrictions on gillnetting to the north and south of the existing sanctuary, but no difference to the offshore extent of the gillnet prohibition in the sanctuary. It is essential that these management changes be evaluated to determine the effect on survival of Hector's dolphins. Such an evaluation will only be possible through the continuation of the photo-ID project at Banks Peninsula. Our work emphasizes the value of long-term data sets for assessing the efficacy of MPAs.

Finally, we note that whilst the simplest explanation that matches our data is that the sanctuary resulted in the increase in survival, other explanations cannot be eliminated. In an experimental design context, our study is a before-after design without controls or replicates. A long-term study, such as this one, requires a very substantial commitment in time and funding, and duplication of it, in an area without gillnet restrictions, would have been unrealistic. Likewise, replication of sanctuary areas was proposed to managers in 1988, but was considered to be politically unattainable.

Conclusion

Estimating demographic parameters in marine mammals is challenging, often requiring many years of data to achieve sufficient precision to detect biologically meaningful change. We believe that this study is the first to demonstrate improvement in a demographic parameter of a marine mammal species following conservation action. Our study, therefore, provides evidence that area-based protection measures can be effective for marine mammals. Furthermore, by placing the change in survival in the context of other vital rates, we are able to show that the resulting level of population growth may be insufficient to adequately protect the population.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Output from WinBUGS showing three chains for pre- and post-sanctuary survival (indicated by $\mu_{\phi\text{pre}}$ and $\mu_{\phi\text{post}}$) and model deviance, indicating adequate mixing.

Fig. S2. Output from WinBUGS showing the Brooks–Gelman–Rubin (BGR) diagnostic plots for pre- and post-sanctuary survival (indicated by $\mu_{\phi\text{pre}}$ and $\mu_{\phi\text{post}}$).

Appendix S1. WinBUGS code used to fit the capture-recapture model to data from field surveys.

Appendix S2. Goodness-of-fit for capture-recapture model.

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