



Assessing the design and power of capture–recapture studies to estimate demographic parameters for the Endangered Oceania humpback whale population

E. L. Carroll^{1,*}, L. Brooks², C. S. Baker^{3,4}, D. Burns^{2,5}, C. Garrigue^{6,7},
N. Hauser⁸, J. A. Jackson⁹, M. M. Poole¹⁰, R. M. Fewster¹¹

¹School of Biology, University of St Andrews, Fife, St Andrews KY16 8LB, Scotland, UK

²Marine Ecology Research Centre, Southern Cross University, PO Box 157 Lismore, New South Wales, 2480 Australia

³School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

⁴Hatfield Marine Science Center, Oregon State University, 2030 SE Marine Science Drive, Newport, Oregon 97365, USA

⁵Blue Planet Marine, Amberley Business Centre, 1060 Hay St, West Perth, Western Australia 6005, Australia

⁶Opération Cétacés, BP 12827, 98802 Nouméa, New Caledonia

⁷IRD UMR9220 ENTROPIE, Université de Perpignan, 52 avenue Paul Alduy, 66860 Perpignan Cedex, France

⁸Cook Islands Whale Research, PO Box 3069, Avarua, Rarotonga, Cook Islands

⁹British Antarctic Survey, Madingley Road, High Cross, Cambridge, Cambridgeshire CB3 0ET, UK

¹⁰Marine Mammal Research Program, BP 698, Maharepa, Moorea, French Polynesia

¹¹Department of Statistics, University of Auckland, Private Bag 92019, Auckland, New Zealand

ABSTRACT: Capture–recapture studies offer a powerful tool to assess abundance, survival and population rate of change (λ). A previous capture–recapture study, based on DNA profiles, estimated that the IUCN-listed Endangered Oceania population of humpback whales had a super-population size of 4329 whales (95% confidence limits, CL: 3345, 5315) and $\lambda = 1.03$ (95% CL: 0.90–1.18) for the period 1999–2005. This low estimate of λ contrasts with the high estimated λ for the neighbouring east Australia population (1.11; 95% CL: 1.105–1.113). A future assessment of Oceania humpbacks through capture–recapture methodology has been proposed to meet 3 objectives: (1) estimate population size with a coefficient of variation of <20%, and detect if λ is significantly different from (2) 1.00 or (3) λ of east Australia. The proposed survey design involves using DNA profiles to identify whales on principal breeding grounds within Oceania in proportion to the abundance of whales on these grounds over the 10 to 12 wk wintering period, to minimise capture heterogeneity between individuals and to maximise capture probabilities. Simulations of the idealised survey design incorporating data from the previous surveys (1999–2005) with 3 new survey years were conducted under a range of scenarios for the ‘true’ demographic status of the population. Simulations of the entire Oceania region showed that the proposed design will give sufficient power to meet objectives (1) under all scenarios, (2) if the true $\lambda \geq 1.05$ and (3) if the true $\lambda \leq 1.05$. Region-specific simulations suggested there was scope to test for differences in recovery between principal breeding sites within Oceania.

KEY WORDS: Capture–recapture · DNA profile · Heterogeneity · *Megaptera novaeangliae*

INTRODUCTION

Accurate estimates of demographic parameters, such as abundance, population rate of change and survival, are critical for making informed manage-

ment decisions, particularly in the context of endangered or depleted species. Such information is typically based on long-term time series of photo-ID catalogues (Forcada & Aguilar 2000), genetic sampling (Taberlet et al. 1997, Dreher et al. 2007, Wade

*Corresponding author: elc6@st-andrews.ac.uk

et al. 2011), or distance or line-transect surveys (Borchers et al. 1998) of a particular area or population. However, long-term data series may be logistically difficult or expensive to collect, and yet high-quality data are required to make management decisions. For example, the International Union for the Conservation of Nature (IUCN) requires evidence of a recent or projected decline of 50 to 70 % in the past 10 yr, or 3 generations, for a population or species to be considered endangered (IUCN 2012).

Given limited time and resources, it is important to assess whether an ongoing or proposed research programme will meet its goal of providing accurate demographic parameters for management and conservation decisions. Key questions include the length of the time series required and whether existing data can be incorporated into the analysis. Here we assess the design and power of a proposed capture–recapture study of a migratory species for which availability for capture and capture probabilities vary by sex and breeding status: the IUCN-listed, Endangered Oceania population of humpback whales, *Megaptera novaeangliae* (Childerhouse et al. 2008).

The Oceania population of humpback whales congregates seasonally to breed during the austral winter in the South Pacific: from New Caledonia in the west (~160° E) to French Polynesia in the east (~120° W) (Garrigue et al. 2002, Poole 2002). Whales from Oceania then migrate to high-latitude, productive Antarctic feeding grounds in the austral summer (Dawbin 1966). Individuals have been recorded to move between Oceania and feeding grounds including International Whaling Commission (IWC) management areas known as Areas I, V and VI (Southern Ocean waters spanning 130° E to 50° W) based on discovery marks (Dawbin 1966), photo-identification (Robbins et al. 2011), genotype identification (Steel et al. 2008, Constantine et al. 2014) and satellite tag studies (Hauser et al. 2010, Horton et al. 2011).

The contemporary Oceania humpback whale population shows differential patterns of habitat use across the 8 million square kilometres of the South Pacific. The principal known breeding grounds are New Caledonia, Tonga and French Polynesia, to which individual whales can show high levels of site fidelity (Garrigue et al. 2011a). In addition, there are areas that function more as migratory corridors, such as the Cook Islands, where the re-sight rate is much lower (Hauser et al. 2010). There is a significant difference in the frequency of maternally inherited mitochondrial DNA haplotypes among the main breeding sites within Oceania, suggesting that site fidelity may limit female-mediated gene flow, leading

to population sub-structuring (Olavarría et al. 2007). However, there is additional evidence from molecular, photo-identification and song studies suggesting connectivity between these regions (Helweg et al. 1998, Garrigue et al. 2011a, Garland et al. 2013). Furthermore, the Oceania population is considered a distinct management unit, separate from east Australia, by the IWC. This is based on comparisons of the movement of individuals identified using both photo-identification and DNA profiles (Garrigue et al. 2002, 2011b, Anderson et al. 2010) and significant differentiation between east Australia and Oceania breeding grounds based on the analyses of mitochondrial DNA (Olavarría et al. 2006).

Historically, the Oceania population was estimated to number between 10 000 and 20 000 whales (IWC 2015). However, late 19th century and mid-20th century whaling killed an estimated 45 000 humpback whales in the Southern Ocean areas associated with the Oceania, and other, wintering grounds (Areas V and VI) (Clapham et al. 2009, Ivashchenko & Clapham 2014). Illegal Soviet whaling from 1947 to 1973, most notably the killing of 20 000 whales over the summers of 1959–1960 and 1960–1961 in IWC Area V, south of eastern Australia and New Zealand, drove the population into a demographic bottleneck (Jackson et al. 2008, Clapham et al. 2009).

To assess the current status of the Oceania humpback whale population after such intense exploitation, the South Pacific Whale Research Consortium (SPWRC) undertook a large-scale survey of Oceania during the austral winters of 1999 to 2005. Over this 6 yr period, the SPWRC identified individual whales using a combination of photographs of natural markings (photo-ID, $n = 660$) and DNA profiles from skin biopsy samples ($n = 840$). The sighting histories of these individuals were used in a capture–recapture framework to estimate abundance with the POPAN formulation of the Jolly Seber model developed by Schwarz & Arnason (1996). The superpopulation (N_S) estimate for Oceania from 1999 to 2005 was 4329 (95 % confidence limits, CL: 3345, 5315) whales and the estimated annual population growth rate for this period was $\lambda = 1.03$ (95 % CL: 0.90–1.18) based on the DNA profile data (Constantine et al. 2012). This is considerably lower than the estimated rate of increase for east Australia of 10.9 % per annum, corresponding to $\lambda = 1.11$ (95 % CL: 1.105–1.113; Noad et al. 2011), although the wide confidence interval (CI) from Oceania includes the CI from east Australia. Given the apparent low rate of recovery in Oceania, there is a strong need to improve estimates of abundance and trend information for this population.

Here we consider the design of a new set of surveys to assess the recovery of the Oceania population of humpback whales through capture–recapture analysis, and undertake simulations to assess the power of these proposed surveys to meet 3 objectives: (1) determine population size with a coefficient of variation (CV) of <20%, (2) detect whether λ is significantly different from 1.0 (i.e. the population is increasing or decreasing) and (3) detect whether λ for Oceania is significantly different from that of east Australia. We discuss appropriate survey designs to meet these objectives and investigate the power of the proposed surveys under various postulated scenarios for the true demographics of the population, on both a regional and Oceania-wide basis.

RATIONALE AND METHODS

Rationale

We discuss and describe the proposed survey design, including the model to be used and its assumptions. We then discuss the idealised survey design with these assumptions in mind and conduct simulations to test the power of the proposed surveys. In addition, we consider the impact of heterogeneity in capture probability between regions, and between males and females, on the power of the proposed survey design.

Model selection

In order to estimate population growth rate, we will need to use an open capture–recapture model, as these account for population removals (deaths/emigration) and additions (births/immigration). The POPAN model (Schwarz & Arnason 1996, Arnason & Schwartz 1999), a derivative of the Jolly-Seber model (Jolly 1965, Seber 1965), estimates N_S , defined as the total number of individuals that are ever exposed to capture between the first and last survey occasions, comprising individuals that join the population between the first and last surveys in addition to individuals present at the start of the first survey. A proportion of the N_S enters the survey area during each survey occasion and is available for capture: this is estimated by a parameter termed the probability of entry for each survey occasion. The standard POPAN model and an extension of it, termed the λ -POPAN model (Carroll et al. 2013), both provide estimates of N_S , the number of animals in the survey area each

year (N_t) and the annual apparent survival rate (Φ). However, the λ -POPAN model is also able to directly estimate λ , and as λ is a key parameter of interest, we decided to use the λ -POPAN model rather than the standard POPAN model.

Model assumptions and survey design

The primary assumptions of the POPAN model are general to most capture–recapture models and include: (1) the study area is constant, (2) marks are permanent and read correctly, (3) all individuals (within a demographic class) have equal capture probability and (4) all individuals have equal survival probability (Schwarz & Arnason 1996). These assumptions will be dealt with in turn in the following sections.

Assumption 1: constant study area

The basic survey design is boat-based surveys on the principal Oceania humpback population wintering grounds. Previous work suggests that most whales were captured within these core regions, and increasing regional coverage did not lead to a significant increase in estimated abundance (Constantine et al. 2012). Therefore, we suggest that the proposed sampling regime will be concentrated at 3 core sites that are the principal wintering grounds: Tonga, New Caledonia and French Polynesia. To meet Assumption 1, a consistent geographic area at each core site should be surveyed during each survey occasion.

Assumption 2: permanent marks

The surveys will collect photographs of natural markings for photo-identification and skin biopsy samples for identification by DNA profiling, following a previously described methodology that met Assumption 2 (Constantine et al. 2012).

Assumption 3: equal capture probability

Heterogeneity in capture probability is typically thought of as an intrinsic characteristic of an individual that will create a downward bias in abundance estimates if unaccounted for (Seber 1982). Despite some advances (Pledger 1998, 2000), open models

such as λ -POPAN cannot account for heterogeneity in capture probability other than as a function of covariates. Therefore, the heterogeneity between individuals in both timing of migratory arrivals and duration of stay on Oceania wintering grounds may be considered and accounted for by fitting appropriate covariates or appropriate survey design. Here we summarise available information on the sources of heterogeneity in capture probability between individuals and under 'Recommendations for proposed survey design' address these with suggestions on the appropriate survey design.

Humpback whales show heterogeneity between individuals in migratory behaviours, whereby whales of different sex, age, or breeding status (henceforth referred to as demographic classes) leave high-latitude summer feeding areas and arrive at low-latitude winter breeding areas at different times (Chittleborough 1965). This occurs in a generally set sequence: the first whales to leave Antarctica are the lactating females and yearlings, followed approximately 12 d later by immature whales of both sexes, with mature males, non-pregnant females and pregnant females leaving approximately 20, 23 and 31 d later, respectively. In general, the earliest and last whales in each demographic class travel approximately 6 wk before and after the central peak for that category (Dawbin 1966).

Across-season re-sightings suggest that females tend to arrive at and depart from the breeding grounds earlier in years when they do not have a calf than in years when they give birth (Glockner & Venus 1983, Craig et al. 2003, Burns et al. 2014). As humpback whales have a modal reproductive cycle of 2 or 3 yr (although it can vary between 1 and 5 yr), the migratory timing and habitat use patterns of individual females, and therefore availability for capture on wintering grounds, appears to vary across years depending on reproductive status (Baker et al. 1987, Craig et al. 2003). While females are likely to return quickly to the feeding grounds after becoming pregnant, mature males remain on the breeding grounds longer, presumably in an attempt to increase mating opportunities. Therefore, males are likely to have a higher capture probability than females on wintering grounds (Craig et al. 2001, 2003, Clapham 2002, Dulau-Drouot et al. 2012, Burns et al. 2014). This is reflected in the male bias in genetic samples from the Oceania wintering grounds (Constantine et al. 2012), as well as in sighting histories of whales from Hawaii (Herman et al. 2011).

Overall, recent evidence suggests that whales remain on winter breeding areas for 3 to 8 wk (Craig

et al. 2001, Garrigue et al. 2001, Dulau-Drouot et al. 2012, Burns et al. 2014). On the return journey south, newly pregnant or resting females and immature whales leave tropical waters first, followed 10 d later by mature males, and finally mothers with calves leave a further 6 d later (Dawbin 1966, 1997).

Assumption 4: equal survival

Adult humpback whales typically have a high annual apparent survival of ≥ 0.94 (Clapham et al. 2003, Robbins 2007, Zerbini et al. 2010, Orgeret et al. 2014). However, calf survival has been estimated to be lower: 0.82 (95% CI: 0.48–0.98) for the North Pacific (0 to 6 mo; Zerbini et al. 2010) and 0.66 (95% CI: 0.52–0.78) in the Gulf of Maine (6 to 18 mo; Robbins 2007). For this reason, the typical method used to reduce the heterogeneity in survival in baleen whale datasets is to exclude dependent calves from the analyses (Wade et al. 2011, Constantine et al. 2012), and we shall follow this convention.

Recommendations for proposed survey design

We recommend that the 3 principal wintering grounds of Tonga, New Caledonia and French Polynesia should be consistently surveyed to meet Assumption 1. To achieve approximately equal capture probability among sites, we suggest that effort (e.g. number of boats or researchers) is allocated in proportion to the current estimates of the relative abundance of humpback whales at these sites. In theory, this could reduce the number of capture probability parameters that need to be estimated and thereby increase the power of the study design.

The heterogeneity in availability for capture and capture probabilities between individuals is directly linked to the variation in the timing of migratory arrivals and duration of stay between demographic classes, particularly between males and females. Therefore we recommend sampling in a way that allows for the identification of sex, implying a preference for biopsy sampling, which has previously met Assumption 2 of providing permanent marks that are consistently identifiable (Wade et al. 2011, Constantine et al. 2012).

In addition, we propose that sampling efforts focus on males to (1) increase the capture probability and (2) decrease the potential heterogeneity in capture probability, thereby increasing the power of the model to meet the proposed objectives. There is typ-

ically a male bias (1.6:1, male:female) on the Oceania wintering grounds (Constantine et al. 2010), leading to a higher capture probability for males. Females show greater heterogeneity in capture probability linked to reproductive state, and accurately modelling this requires capture probability covariates (Carroll et al. 2013), multi-state models, or estimating transitions between states (Barlow & Clapham 1997). Focusing on males would reduce the number of model parameters, allowing the model to estimate parameters with greater precision.

We also recommend sampling across the entire 10 to 12 wk wintering period. The primary reason is that the season should be long enough to capture all demographic classes within a season, particularly all male age classes. Surveys should also be consistent between seasons to provide the opportunity for recaptures of the same individuals between seasons.

We recommend that the new surveys aim for a minimum capture probability (p) of 0.10 by targeting sample sizes reflecting 10 to 15% of the estimated regional population sizes. Constantine et al. (2012) estimated that the capture probability varied between 0.02 and 0.10 yr⁻¹ (Constantine et al. 2012), largely due to variation in sampling effort by sites and years. We believe that by increasing the duration of the survey, concentrating on 3 principal sites and maintaining consistent effort, a capture probability of 0.10 yr⁻¹ would be achievable. For estimated samples required per year, see the 'Results' section.

We recognise that the capture–recapture modelling of the Oceania population would ideally be stratified by demographic class, and this should be done if the data permit. However, for the rest of the present study we only consider surveys that are focused on males for the reasons outlined above.

Simulations to assess power of surveys

We undertook simulations to determine how effective this survey design would be at estimating abundance and detecting trends in the Oceania population. These simulations are based on the following assumptions about the survey design and population, as well as the standard assumptions for open capture–recapture models:

(1) Correct capture–recapture identification of male humpback whales (i.e. genotypes) in Oceania.

(2) The proposed surveys have a capture probability of $p = 0.10$ for males. We believe this is achievable given previous estimates of capture probability and proposed sampling intensities.

(3) A constant λ and Φ over sites and survey occasions for all surveys, where Φ denotes annual apparent survival probability.

The simulation process involved 3 steps: (1) fitting the λ -POPAN model to the historical Oceania data to provide realistic parameters for simulation, (2) simulating capture histories using an individual-based model and (3) fitting the λ -POPAN model to the simulated capture histories to assess the power of the proposed survey design. We then used additional individual-based simulations to explore the impact of heterogeneity in capture probability between regions, and between males and females, on the power of the proposed survey design.

To provide realistic suites of parameters for the simulations, we fitted the λ -POPAN model to the historical male genotype capture-history data for New Caledonia (NC; available for 1999–2005), Tonga (TG; 2000–2003 and 2005) and the synoptic Oceania region (1999–2005) from Constantine et al. (2012). In cases where not all model parameters were estimable, or estimates at boundary values were returned, some parameters were constrained during this initial model fitting process. This included: (1) apparent survival was fixed at 0.95 (Constantine et al. 2012) and/or (2) years in which similar sample sizes were collected (taken as a proxy for survey effort) were constrained to have the same capture probability. We then used the best-fitting λ -POPAN model(s) as an individual-based model to simulate future scenarios assuming 3 new surveys will take place, in either an annual (2014, 2015, 2016) or biennial (2014, 2016, 2018) configuration.

To determine the appropriate N_S for the simulated periods 1999–2016 or 1999–2018, we note that the true N_S depends upon the true values of λ and Φ , as well as the time period examined. For this reason we selected a baseline absolute abundance for 1999 to be common to all simulation scenarios for each region. The estimated number of males in the population in 1999 was derived from the demographic parameters in the best-fitting model from the 1999–2005 data. This common N_{1999} value was used to produce scenario-specific N_S values for the time period 1999–2016 or 1999–2018, for $\lambda = 0.98, 1.03, \text{ or } 1.05$, and for Φ fixed at 0.95.

To generate simulated capture histories for each scenario, we simulated 1000 replicate populations of males from 1999–2016 or 1999–2018 using the chosen value of N_S , λ and Φ . These simulations were run employing the capture probabilities from the best-fitting 1999–2005 model for simulating captures in the corresponding years and capture probabilities of

$p = 0.10$ for simulating captures from 2014 onwards. For each simulated population of N_S males, we simulated capture histories of individuals for each survey from 1999–2005 and 2014 onwards. Our individual-based λ -POPAN simulation model is described in the Appendix and implemented in program R.

We then fitted the simulated capture histories with λ -POPAN to estimate N_S , λ , Φ and p , to enable us to investigate the power to detect population trends under the proposed survey design. For each set of simulated data, we fitted 11 parameters: N_S , λ , Φ , 7 capture probabilities for the 7 yr from 1999 to 2005 and 1 capture probability for the 3 new surveys from 2014 onwards. We used only 1 capture probability for the 3 new surveys, in order to test the proposed survey design. For all other parameters, the 11-parameter model reflects the maximum complexity for a λ -POPAN model, to ensure a stringent test of power. The only variation concerned the Tongan regional analysis where only 5 surveys occurred from 1999 to 2005, so only 9 parameters were fitted in total.

To investigate the power under each scenario to estimate abundance, we calculated the mean estimate of N_S and the mean estimated CV of N_S from the 1000 simulations. The biological relevance of N_S is limited in itself, but the trio N_S , λ and Φ encode the values of all $EN_{1999}, \dots, EN_{2018}$, where EN_t is the expected number alive in Year t (Appendix). We illustrate the estimation of EN_t using EN_{2014} as an example. The expected numbers alive do not incorporate demographic stochasticity (randomness in births and deaths). Therefore, rather than quoting a CV for EN_{2014} , we estimated the CV of N_{2014} itself for each scenario by simulating an instance of N_{2014} from each of the 1000 fitted models and using the sample CV of the 1000 instances. The resulting CV of N_{2014} incorporates demographic stochasticity as well as uncertainty in model fitting.

To estimate the power under each scenario to determine if λ was significantly different from 1.0, we calculated the percentage of simulations where the 95% CIs of λ were entirely <1.0 and >1.0 , for simulations where $\lambda = 0.98$ and 1.03 or 1.05, respectively. We also investigated the power of each scenario to detect whether λ was significantly different from the east Australian growth rate of $\lambda = 1.10$ (95% CL: 1.105–1.113).

Analyses: Oceania-wide and region-specific

We simulated the power of the proposed surveys on the overall Oceania population. This combines the

data from New Caledonia, Tonga and French Polynesia. In addition, we simulated the power of the proposed surveys on 2 regions: New Caledonia (NC: Stock E2) and Tonga (TG: Stock E3). French Polynesia (Stock F) was explored, but the low recapture rate in the previously collected data prohibited a region-specific power analysis.

Effect of capture heterogeneity and covariate model

We conducted further simulations to investigate the impact of heterogeneity in capture probability on the precision of λ estimates and power to detect trends. We divided N_S into 2 equally sized groups, one of which was designated to have higher capture probabilities than the other. All individuals were allotted the same values of λ and Φ . We simulated data in the same individual-based model (Appendix) using these disparate capture probabilities, but ignored the disparity when fitting the model to the simulated data, such that all individuals were fitted with the same set of capture probabilities. Doing this enables us to investigate robustness to unmodelled heterogeneity when estimating λ .

If the source of heterogeneity in capture probability is observable, for example, due to sex or sampling region, we can create a covariate model in which the heterogeneity is accommodated by assigning different capture probabilities to different groups. In addition to fitting each simulated dataset as a single group to investigate the robustness of λ , we also fitted the covariate model to assess the power to detect $\lambda > 1$ when the correct 2-group model is fitted. We conducted these simulations for varying levels of heterogeneity, from none to extreme. These simulations were based on values of N_S , λ and Φ derived from Scenario O5 (see 'Results').

Incorporating females

Our previous simulations have focused on males in order to test our survey design in a worst-case scenario in which the pattern of female availability and capture is too complex to incorporate into estimating λ and abundance. We conducted a final set of simulations in the same individual-based model under the assumption that female capture probabilities are a simple multiple of male capture probabilities. Explicitly, if the male capture probability for year t is p_t , then the female capture probability is αp_t , where α is a single constant parameter to be estimated. Assum-

ing that male and female superpopulation sizes are equal, we investigate the impact on power and precision of incorporating females by fitting the single extra parameter α , compared with using the data on males only. These simulations were based on values of N_S , λ and Φ derived from Scenario O5 (see 'Results').

RESULTS

Power analysis: Oceania-wide results

The best-fitting model for the male genotype dataset for Oceania was $\lambda(\cdot)p(t)\Phi(0.95)$ (Table S1 in the Supplement at www.int-res.com/articles/suppl/n028p147_supp.pdf). This model gave the following capture probabilities: $p_{1999} = 0.02$, $p_{2000} = 0.07$, $p_{2001} = 0.12$, $p_{2002} = 0.08$, $p_{2003} = 0.03$, $p_{2004} = 0.04$ and $p_{2005} = 0.09$. The simulations were run using these capture probabilities and $N_{1999} = 1019$, and annual (2014:2016) and biennial (2014, 2016, 2018) surveys with a constant $p = 0.10$ for the new, proposed surveys.

The results of simulations for the Oceania region are given in Table 1: Scenarios O1 to O3 simulated

annual surveys from 2014 to 2016, while Scenarios O4 to O6 simulated 3 biennial surveys from 2014. Objective 1 was met, as both N_S and N_{2014} were estimated with a CV < 20% in all simulated scenarios. There was high (>95%) power to meet Objectives 2 and 3 ($\lambda > 1.00$ and $\lambda < 1.10$, respectively) when the true $\lambda = 1.05$, under both annual and biennial survey designs. There was moderate power to meet Objective 2 under annual and biennial surveys (65 and 77% power, respectively) when $\lambda = 1.03$, but strong power (100%) to meet Objective 3. Under both survey configurations (annual and biennial surveys), when $\lambda = 0.98$, simulations have a low power ($\leq 30\%$) to meet Objective 2 but a high power to meet Objective 3. Typically, power is increased 5 to 10% when the new surveys are biennial rather than annual.

Power analysis: region-specific results

New Caledonia

There were 3 models that fit the NC data within ΔAIC (Akaike's information criterion) of 3 (see Table S2 in the Supplement at www.int-res.com/articles/

Table 1. Parameters used to simulate a capture–recapture study of the Oceania humpback whale *Megaptera novaeangliae* wintering ground, and the results from 1000 simulations of each scenario. The parameters used for each simulated scenario (O1–O6) are listed: superpopulation size (N_S), population growth rate (λ) and apparent survival (Φ). The capture probabilities for each survey year are as follows: $p_{1999} = 0.02$, $p_{2000} = 0.07$, $p_{2001} = 0.12$, $p_{2002} = 0.08$, $p_{2003} = 0.03$, $p_{2004} = 0.04$, $p_{2005} = 0.09$ and $p = 0.10$ for all new surveys. Survey years indicate whether the proposed new set of surveys is annual (2014:2016) or biennial (2014, 2016, 2018), and, under the simulated scenario, the unique male sample size required for each new survey year is shown. Statistics from simulation results show the mean estimate and mean coefficient of variation (CV) for N_S and N_{2014} from the 1000 simulations. λ :power also shows the proportion of simulations with 95% CIs that were entirely <1 or >1, depending on the scenario. The λ :overall power data show the percentage of simulated scenarios with CIs that are greater or less than the given λ value (1, 1.05, 1.1). For example, 98% of simulations of Scenario O1 had CIs below or above 1.05

	O1	O2	O3	O4	O5	O6
Survey years	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014, 2016, 2018	1999:2005 2014, 2016, 2018	1999:2005 2014, 2016, 2018
N_S	1436	2793	3652	1506	3066	4130
λ	0.98	1.03	1.05	0.98	1.03	1.05
Φ	0.95	0.95	0.95	0.95	0.95	0.95
Year: sample size (unique males)	2014: 75 2015: 74 2016: 72	2014: 159 2015: 164 2016: 168	2014: 212 2015: 222 2016: 236	2014: 75 2016: 72 2018: 69	2014: 159 2016: 169 2018: 179	2014: 212 2016: 236 2018: 258
Summary statistics from simulations						
Mean N_S	1438	2806	3669	1515	3082	4155
N_S CV	0.08	0.07	0.07	0.08	0.07	0.07
Mean N_{2014}	779	1697	2277	795	1707	2289
N_{2014} CV	0.18	0.12	0.11	0.18	0.13	0.11
λ :power	<1:26%	>1:65%	>1:99%	<1:30%	>1:77%	>1:100%
λ:overall power						
1	26	65	99	30	77	100
1.05	98	39	4	99	41	5
1.1	100	100	99	100	100	100

Table 2. Parameters used to simulate a capture–recapture study of the New Caledonian humpback whale *Megaptera novaeangliae* wintering ground, and the results from 1000 simulations of each scenario. The parameters used for each simulated scenario (N1–N12) are listed: superpopulation size (N_S), population growth rate (λ) and apparent survival (Φ). Scenarios N1–N6 (conservative case) had a baseline of 210 whales in 1999, whereas Scenarios N7–N12 (high case) had a baseline of 326 whales in 1999. The capture probabilities for each survey year are as follows: $p_{1999} = 0.05$, $p_{2000} = 0.09$, $p_{2001} = 0.13$, $p_{2002} = 0.05$, $p_{2003} = 0.13$, $p_{2004} = 0.05$, $p_{2005} = 0.13$ and $p = 0.1$ for all new surveys. Survey years indicate whether the proposed new set of surveys is annual (2014:2016) or biennial (2014, 2016, 2018), and, under the simulated scenario, the unique male sample size required for each new survey year is shown. Statistics from simulation results show the mean estimate and mean coefficient of variation (CV) for N_S and N₂₀₁₄ from 1000 simulations. λ: power also shows the proportion of simulations that were <1 or >1, depending on the scenario. The λ: overall power data show the percentage of simulated scenarios with CIs that are greater or less than the given λ value (1, 1.05, 1.1). For example, 95% of simulations of Scenario N1 had CIs < 1.10

	Conservative case						High case					
	N1	N2	N3	N4	N5	N6	N7	N8	N9	N10	N11	N12
Survey years	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014, 2016, 2018	1999:2005 2014, 2016, 2018	1999:2005 2014, 2016, 2018	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014, 2016, 2018	1999:2005 2014, 2016, 2018	1999:2005 2014, 2016, 2018
N _S	302	576	752	310	632	851	468	894	1168	482	981	1322
λ	0.98	1.03	1.05	0.98	1.03	1.05	0.98	1.03	1.05	0.98	1.03	1.05
Φ	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95
Year:	2014 to 2016:	2014: 33 2015: 34 2016: 35	2014: 44 2015: 46 2016: 48	2014: 16 2016: 15 2018: 14	2014: 33 2016: 35 2018: 37	2014: 44 2015: 46 2018: 53	2014: 24 2015: 24 2016: 23	2014: 51 2015: 52 2016: 54	2014: 68 2015: 71 2016: 75	2014: 24 2016: 23 2018: 22	2014: 51 2016: 54 2018: 57	2014: 68 2016: 75 2018: 82
Summary statistics from simulations												
Mean N _S	309	594	772	317	651	879	471	911	1186	487	1000	1352
N _S CV	0.16	0.15	0.14	0.17	0.18	0.17	0.12	0.12	0.11	0.12	0.13	0.13
Mean N ₂₀₁₄	166	355	481	165	357	482	256	555	744	256	556	748
N ₂₀₁₄ CV	0.31	0.24	0.22	0.31	0.25	0.22	0.26	0.20	0.18	0.27	0.21	0.18
λ: power	<1:10%	>1:17%	>1:62%	<1:13%	>1:21%	>1:73%	<1:15%	>1:31%	>1:80%	<1:19%	>1:37%	>1:89%
λ: overall power												
1.00	10	17	62	13	21	73	15	31	80	19	37	89
1.05	62	17	4	67	18	4	81	19	4	82	22	4
1.10	95	82	62	96	85	67	99	94	77	100	94	82

suppl/n028p147_supp.pdf). Therefore we used 2 N₁₉₉₉ values: a high case of 326 whales and a conservative case of 210 whales. We used the capture probabilities from the model that produced a value of λ (1.03, 95% CL: 0.96, 1.11) and Φ (fixed at 0.95) most similar to the overall findings for Oceania in Constantine et al. (2012). This model had the following capture probabilities: $p_{1999} = 0.05$, $p_{2000} = 0.09$, $p_{2001} = 0.13$, $p_{2002} = 0.05$, $p_{2003} = 0.13$, $p_{2004} = 0.05$ and $p_{2005} = 0.13$. The conservative case (N1–N6) and high case (N7–N12) scenarios were both simulated for annual (2014:2016) and biennial (2014, 2016, 2018) surveys with a constant $p = 0.10$.

The simulation results are given in Table 2. Under all simulated scenarios, Objective 1 is met and N_S, although not N₂₀₁₄, is estimated with a CV < 20%. There is moderate (62–73%) and high power (80–89%) to meet Objective 2, under the conservative and high case, respectively, when the true λ = 1.05. There is 62 and 77% power to meet Objective 3, under the annual survey design under conservative and high cases, respectively, when the true λ = 1.05. This power is increased 5 to 10% when the new surveys are biennial rather than annual. There is little power (<50%) to meet Objective 2 under any scenario when the true λ ≤ 1.03. However, there is high power to meet Objective 3 under all scenarios when λ = 0.98 and under the high case when λ = 1.03; this decreases to moderate power (82 to 85%) under the conservative case when λ = 1.03.

Therefore, at lower rates of growth, the proposed survey design is sufficient to detect that the population growth rate in New Caledonia is different from that in East Australia. When the true λ = 1.05, the power to meet Objectives 2 and 3 is enhanced by conducting biennial surveys from 2014.

Tonga

The historical data used for Tonga were limited to 2000–2003 and 2005. There were no data for Tonga from 2004, and the sample size for Tonga for 1999 was <10; therefore, these years were omitted. There were 3 models that fit the Tongan data within a Δ AIC of 3 (see Table S3 in the Supplement at www.int-res.com/articles/suppl/n028p147_supp.pdf). Therefore, we used 2 N_{1999} values: a high case of 1397 whales and a conservative case of 639 whales. We note that the high case is larger than the estimate used for Oceania. This high variability in N_S is due to the large impact that small variations in very low capture probabilities have on the overall estimate of population size. Again, the sparseness and short time frame of the data meant that we used model constraints in some cases. We used the capture probabilities from the best-fitting model: $p_{2000} = 0.02$, $p_{2001} = 0.04$, $p_{2002} = 0.04$, $p_{2003} = 0.04$ and $p_{2005} = 0.02$. The conservative case (T1–T6) and high case (T7–T12) scenarios were both simulated for proposed annual (2014: 2016) and biennial surveys (2014, 2016, 2018) with constant $p = 0.10$.

The simulation results are given in Table 3. Under almost all simulated scenarios, Objective 1 is met and N_S and N_{2014} are estimated with a CV < 20%. However, a CV > 20% for N_S and N_{2014} was obtained when $\lambda = 0.98$ for the conservative case (both annual and biennial surveys).

There was strong power (>90%) to meet Objective 2 only under the high case with biennial surveys, when $\lambda = 1.05$. There was moderate power (>65%) to meet Objective 2 when $\lambda = 1.05$, under the high case with annual surveys and the conservative case with biennial surveys. There was high power (>89%) to meet Objective 3 when the true $\lambda \leq 1.03$, except when annual surveys were conducted under the conservative

Table 3. Parameters used to simulate a capture–recapture study of the Tongan humpback whale *Megaptera novaeangliae* wintering ground, and the results from 1000 simulations of each scenario. The parameters used for each simulated scenario (T1–T12) are listed: superpopulation size (NS), population growth rate (λ) and apparent survival (Φ). Scenarios T1–T6 (conservative case) had a baseline of 639 whales in 1999, whereas Scenarios T7–T12 (high case) had a baseline of 1397 whales in 1999. The capture probabilities for each survey year are as follows: $p_{2000} = 0.02$, $p_{2001} = 0.04$, $p_{2002} = 0.04$, $p_{2003} = 0.04$, $p_{2005} = 0.02$ and $p = 0.1$ for all new surveys. Survey years indicate whether the proposed new set of surveys is annual (2014:2016) or biennial (2014, 2016, 2018), and, under the simulated scenario, the unique male sample size required for each new survey year is shown. Statistics from simulation results show the mean estimate and mean coefficient of variation (CV) for N_S and N_{2014} from 1000 simulations. λ : power also shows the proportion of simulations that were <1 or >1, depending on the scenario. The λ :overall power data show the percentage of simulated scenarios with CIs which are greater or less than the given λ value (1, 1.05, 1.1). For example, 95% of simulations of Scenario T1 had CIs <1.10

	Conservative case						High case					
	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12
Survey years	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014:2016	1999:2005 2014:2016
N_S	905	1669	2151	931	1836	2437	1976	3650	4702	2036	4014	5327
λ	0.98	1.03	1.05	0.98	1.03	1.05	0.98	1.03	1.05	0.98	1.03	1.05
Φ	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95
Year:	2014: 48	2014: 97	2014: 127	2014: 48	2014: 97	2014: 127	2014: 105	2014: 211	2014: 277	2014: 105	2014: 211	2014: 277
sample size	2015: 47	2015: 100	2015: 133	2016: 46	2016: 103	2016: 140	2015: 103	2015: 218	2015: 290	2016: 101	2016: 224	2016: 305
(unique males)	2016: 46	2016: 103	2016: 140	2018: 44	2018: 109	2018: 154	2016: 101	2016: 225	2016: 305	2018: 97	2018: 238	2018: 336
Summary statistics from simulations												
Mean N_S	922	1738	2208	955	1883	2475	2002	3730	4745	2039	4046	5329
N_S CV	0.22	0.18	0.15	0.21	0.15	0.13	0.14	0.11	0.09	0.13	0.10	0.08
Mean N_{2014}	492	1027	1358	484	1028	1359	1060	2249	2949	1053	2232	2938
N_{2014} CV	0.23	0.18	0.16	0.25	0.19	0.17	0.17	0.13	0.11	0.18	0.14	0.12
λ :power	<1:4%	>1:18%	>1:40%	<1:7%	>1:29%	>1:65%	<1:7%	>1:30%	>1:70%	<1:16%	>1:51%	>1:94%
λ:overall power												
1.00	4	18	39	7	30	65	7	30	70	16	51	94
1.05	45	6	4	72	13	2	89	15	5	98	26	4
1.10	95	71	41	99	89	70	100	97	74	100	100	98

case (power decreases to 71%). There was also high power to meet Objective 3 when $\lambda = 1.05$ under the biennial survey design in the high case, and moderate power when $\lambda = 1.05$ under the annual survey design in the high case (74%) and biennial survey design in the conservative case (71%).

Biennial surveys will increase the power to meet Objectives 2 and 3 by up to 30% if the true $\lambda = 1.05$. Due to the low recapture rate and high variance in the models fitted to the Tongan dataset, the simulated scenario may not be an accurate representation of the population.

Effect of capture heterogeneity and covariate model

We used Scenario O5 with $\lambda = 1.03$ as the basis for simulations to investigate the impact of heterogeneity in capture probability, because it represents the better biennial design, and displays only moderate power to detect $\lambda > 1$ (Table 1). This leaves scope for discerning either an upward or a downward trend in power under the influence of heterogeneity.

We divided the estimated superpopulation of $N_S = 3066$ males from Scenario O5 into 2 groups of 1533 each. For 1999–2005, we set the baseline capture probability at 0.065, corresponding to the average in the real-data Oceania analysis for 1999–2005. For 2014, 2016 and 2018, we set the baseline capture probability at 0.1 in accordance with our survey design. These baseline capture probabilities represent the average across the 2 groups under the simulated scenarios.

We introduced heterogeneity by adding or subtracting quantity ϵ from the baseline probabilities. Group 1 individuals were each given capture probabilities $0.065 - \epsilon$ and $0.1 - \epsilon$ for the 1999–2005 and 2014–2018 sessions, respectively. Group 2 individuals were each given capture probabilities $0.065 + \epsilon$ and $0.1 + \epsilon$. We tested values of ϵ ranging from 0 to 0.05. The value $\epsilon = 0$ corresponds to no disparity between groups, with capture probabilities of 0.065 and 0.1 for all individuals. The value $\epsilon = 0.05$ generates extreme disparity with Group 1 probabilities of 0.015 and 0.05 and Group 2 probabilities of 0.115 and 0.15.

When testing the robustness of λ to this heterogeneity, we treated all simulated individuals as a single group. We fitted 2 models to each simulated dataset, to mimic the real-life situation of model-selection uncertainty. The first model fitted just 1 p -parameter throughout 1999–2018, and the second

allowed 2 p -parameters, one for 1999–2005 and the other for 2014–2018; the best model according to AIC was picked to go forward for each simulation.

The resulting estimates of λ and EN_{2014} are shown in Fig. 1A,B, based on 500 simulations for each value of ϵ . The boxplots show that estimates of λ and EN_{2014}

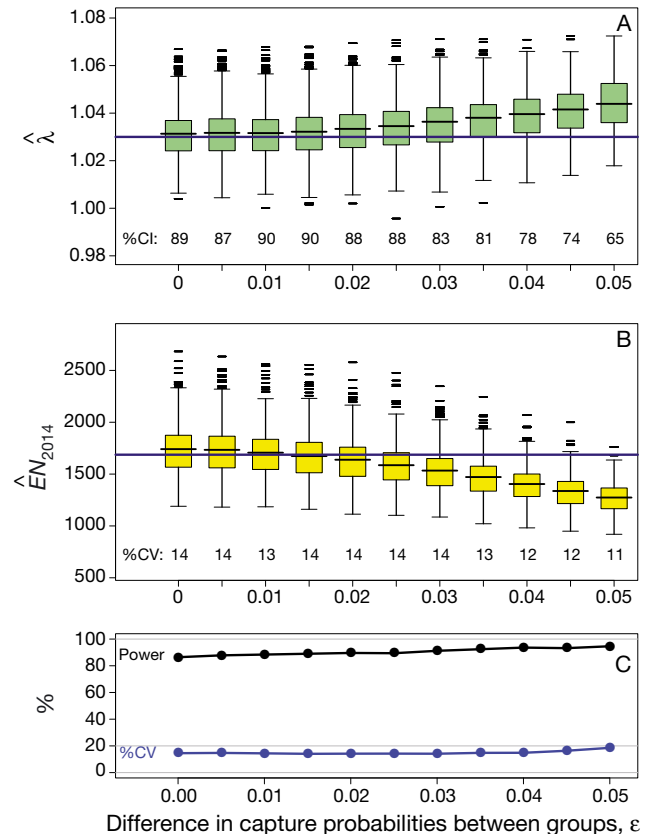


Fig. 1. Impact of heterogeneity in capture probability on estimates of population growth rate (λ) and the expected number alive in 2014 (EN_{2014}). Boxplots show (A) point estimates of λ and (B) point estimates of EN_{2014} when group heterogeneity is ignored and all animals are fitted with the same capture probabilities. The boxplots show the results of 500 simulations for each value of the disparity-parameter ϵ ranging from $\epsilon = 0$ (no disparity between groups) to $\epsilon = 0.05$ (extreme disparity between groups). The true values $\lambda = 1.03$ and EN_{2014} are marked by bold horizontal lines across the plots, and the mean estimate for each value of ϵ is shown by the horizontal line across each box. Boxes are drawn between the upper and lower quartiles of the point estimates; whiskers extend to the last observation within 1.5 times the interquartile range from the quartiles; outliers are marked by short horizontal lines beyond the whiskers. %CI: percentage confidence interval coverage for nominal 95% confidence intervals. %CV: percentage coefficient of variation gained from the standard deviation of the 500 estimates divided by their mean. Panel (C) shows trends in the percentage power to detect $\lambda > 1$ and the percentage CV of EN_{2014} when heterogeneity is correctly modelled by allotting different capture probabilities to the 2 groups

remain fairly robust until heterogeneity reaches $\varepsilon = 0.025$. This represents marked heterogeneity, with capture probabilities for Group 1 being 0.04 and 0.075 and those for Group 2 being nearly double at 0.09 and 0.125, for the 1999–2005 and 2014–2018 survey periods, respectively. The confidence interval coverage for λ is lower than the nominal 95%, even when there is no heterogeneity when $\varepsilon = 0$. This unexpected result was found to be due to model-selection uncertainty: when $\varepsilon = 0$, all of the iterations in which the incorrect single- p model was selected resulted in a confidence interval that did not enclose the true value of λ . When only the results from the correct, 2- p model were examined, confidence interval coverage was a little conservative at 97.5%.

Fig. 1C shows the impact of fitting the correctly specified covariate model to each simulated dataset. Interestingly, the power to detect $\lambda > 1$ improves as the disparity between groups worsens. This is probably due to the extreme disparities producing high capture probabilities for Group 2 individuals, improving the overall precision of λ . The percentage CV of EN_{2014} , gained from the standard deviation of the 500 estimates divided by their mean, worsens a little only at the most extreme values of ε , and remains below the benchmark value of 20% for all settings.

Incorporating females

As above, we used Scenario O5 to test the impact of incorporating females. We simulated a superpopulation of 3066 males and 3066 females. Male capture probabilities for 1999–2005 were those given in the legend to Table 1, and those for 2014–2018 were 0.1. Female capture probabilities were given by male probabilities multiplied by α , for various values of α from 0.5 to 1. This α -model was fitted to all simulated datasets, with the parameter α being estimated along with the other demographic and capture parameters. We conducted model selection for each simulated dataset by fitting models with variously 1 p -parameter or 3 p -parameters for 2014–2018, and selecting the better model by AIC. All models fitted 7 separate p -parameters for the 1999–2005 surveys.

Fig. 2 shows that reasonable improvements can be gained by incorporating females into the analysis, if female capture probabilities can be modelled by this simple pattern. For this scenario with true value $\lambda = 1.03$, power to detect $\lambda > 1$ rises from 76% for the male-only analysis to 86% in the worst-case scenario where females are incorporated with $\alpha = 0.5$, and to

97% in the best-case scenario at $\alpha = 1$ where females are incorporated with capture probabilities equal to those of males. The percentage CV of EN_{2014} shows more modest improvement, from 13.6% for the male-only analysis, falling only to 13.0% when $\alpha = 0.5$, but then decreasing substantially to 8.8% when $\alpha = 1$. These results show that the male-only analyses presented in the rest of the paper are reasonably indicative of what is likely to be achieved, even if it is possible to create a simple covariate structure to incorporate females into the analysis.

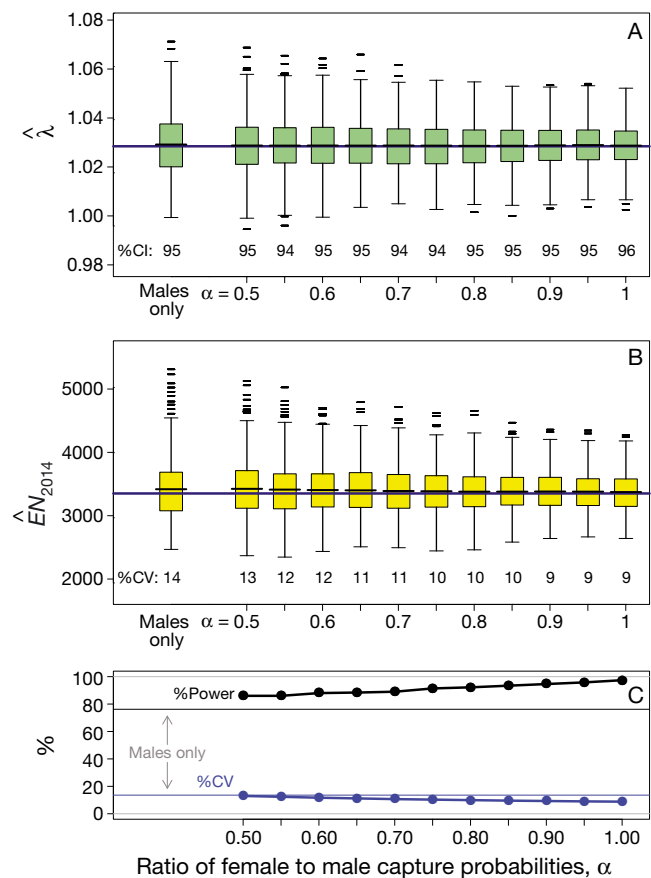


Fig. 2. Impact of including females in population size estimation when female capture probabilities are given by male probabilities multiplied by α . Boxplots show (A) point estimates of λ and (B) point estimates of EN_{2014} as α ranges from $\alpha = 0.5$ (female captures severely downweighted) to $\alpha = 1$ (female captures equal to male capture). Results from male-only models are shown in the boxplots on the left. Male-only results for EN_{2014} are doubled to gain an estimate of the overall population size. The true values $\lambda = 1.03$ and EN_{2014} are marked by bold horizontal lines across the plots. (C) shows trends in percentage power (%Power) to detect $\lambda > 1$ and the percentage of CV of EN_{2014} (%CV) as α ranges from 0.5 to 1. The thin lines across (C) show the corresponding results from the male-only analysis that yielded 76% power to detect $\lambda > 1$ and 13.6% CV for EN_{2014} .

DISCUSSION

Here we assess the power of a proposed set of surveys of the endangered Oceania humpback whale population to provide estimates of abundance and annual population growth for management purposes. Under all scenarios investigated for Oceania, the desired precision on both N_S and N_{2014} was obtained (Objective 1). In addition, under the simulated scenarios for Oceania, incorporating data from the previous genotype surveys from 1999 to 2005 with 3 new survey years will give sufficient power to detect if the growth rate is significantly >1 (Objective 2) if the true $\lambda = 1.05$. Objective 3, the ability to detect if the growth rate is significantly lower than that of east Australia, was met if the true $\lambda \leq 1.05$. Restricting analyses to only the proposed 3 new annual or biennial surveys, it was found that the precision around λ was very poor (results not shown). Inclusion of the full time series is therefore necessary to obtain the required precision around λ . Typically, a modest (5 to 10%) increase in power to detect whether the true λ is different from 1.0 was found when the proposed surveys were biennial rather than annual in Oceania.

The Oceania population of humpback whales is, in many ways, a unique population that requires careful consideration when it comes to designing surveys. The difficulties in surveying such a large geographic area over a long migratory period, in addition to logistical and financial considerations constraining the survey design to fewer sampling occasions, are more pronounced than, for example, studying an easily accessible terrestrial mammal. However, other problems encountered when monitoring the Oceania population are common to many other species, including accounting for heterogeneity between individuals. In this case, we focused on designing the survey to minimise the heterogeneity between demographic classes by surveying over the entire 10 to 12 wk wintering period. We also chose to focus on males to: (1) increase the capture probability due to the male bias on wintering grounds and (2) increase the precision of estimates of N_S and λ by avoiding parameter-intensive modelling of heterogeneity in females due to the reproductive cycle. Despite this intentional focus on males, data will likely be collected from all whales encountered, as it is difficult to distinguish sex in the field due to a lack of sexual dimorphism. Once DNA profiles have been constructed and sex identified, it could be possible to model female-specific or combined male and female demographic parameters if sufficient data are col-

lected. For example, models that account for the reproductive state through modification of capture probabilities could be used in an open population framework (Carroll et al. 2013). Our simulation exercise indicated that if female capture probabilities can be modelled as a simple multiple of male capture probabilities, there is a modest power gain.

In addition to estimating the precision of the proposed survey design, we also estimated the sample sizes for each of the simulated scenarios (Tables 1 to 3). These numbers represent unique males identified in each year, and need to be adjusted for females (up to 50%) and within-year recaptures (typically 10 to 20%). Even with such adjustments, these sample sizes are reasonable given that the proposed survey design includes 10 to 12 wk concurrent surveys in New Caledonia, Tonga and French Polynesia and the number of samples successfully collected in previous surveys. If the New Caledonia population is growing at a rate comparable with that in east Australia (10% per annum) as suggested by 1 of the 3 best-fitting models (Table S2 and Orgeret et al. 2014), then the required sample sizes would increase from 14–53 to 80–130 unique males per year under the conservative case and from 22–82 to 130–200 unique males per year under the high case.

The simulations also indicated that the proposed survey design is relatively robust to variations in capture probability between regions. There was nearly a 2-fold difference between the capture probability of 2 groups, proxies for regions, before estimates of λ and EN_{2014} became substantially biased. In practice, any new survey data will be closely scrutinised for violations of the assumptions of the proposed survey design, including assessing the fit of models with region-specific capture probabilities. Interestingly, we found that the impact of model selection was not straightforward and likely needs to be investigated on a case-by-case basis.

The primary aim was to assess the power of the proposed surveys on an Oceania-wide level. Despite this, it seems there is reasonable precision in estimates of abundance and λ on a regional level, for New Caledonia and Tonga. Although we were unable to utilise earlier data collected from French Polynesia due to small sample sizes, the proposed Oceania-wide work will provide a useful baseline for measuring trends in this principal breeding ground in the future. With an exclusive economic zone of >4.5 million square kilometres, this is a key area for humpback whales wintering in eastern Oceania and therefore an important locality for future surveys of humpback abundance and recovery.

Limitations and biases

The simulations undertaken in this study are based on the standard assumptions of capture–recapture models and the assumptions set out in the ‘Rationale and methods’ section. Furthermore, the Oceania-level simulations did not attempt to model the process as a multi-site capture–recapture study; rather, the proportional distribution of survey effort aims to account for differences between sites.

There are several further unaccounted for factors that could bias our simulation results, such as heterogeneity in capture probability between age classes of males, movement between breeding grounds and differential rates of population growth and survival rates between breeding grounds across Oceania.

We recommended that the survey period encompasses the 10 to 12 wk wintering period to ensure the availability for capture of all male age classes. However, there may be an association between male maturity and the timing of migratory arrival and duration of stay on the wintering grounds that will introduce heterogeneity in capture probability between male age classes (Dawbin 1966, 1997). If this is detected and there are sufficient data, it could be accounted for in several ways. For example, by stratifying the data by age class identified using videogrammetry (Spitz et al. 2000) or using an epigenetic approach (Polanowski et al. 2014). The use of covariates is another option; for example, one linked to the date of capture could be used to account for immature whales arriving earlier and staying for a shorter time period compared with larger, more mature males. It is also worth noting, while estimates of N_S from λ -POPAN are sensitive to heterogeneity in capture probability between individuals, estimates of λ appear more robust, based on the simulation results by Carroll et al. (2013).

Movements between individual breeding grounds (including east Australia) are very rare compared with recaptures within individual breeding grounds, based on the movement of individuals and small but significant differentiation of mitochondrial haplotype frequencies between breeding grounds (Olavarría et al. 2007, Garrigue et al. 2011a,b). We therefore did not attempt to account for movements between breeding grounds in these simulations, as they are not likely to be influential on estimated trends.

We also assumed constant Φ and λ for the simulations. A recent study estimated the annual population growth rate of New Caledonia to be 1.15 (95% CI: 1.11–1.20), using a Pradel model based on the capture–recapture of whales photo-identified be-

tween 1996 and 2012 (Orgeret et al. 2014). As this value of annual growth rate is above that believed biologically plausible for the species (Zerbini et al. 2010), it is indicative of immigration into the New Caledonian wintering ground (Orgeret et al. 2014). While, as noted above, recaptures within breeding grounds are far more common than recaptures between breeding grounds, humpback whales have been hypothesised to show dynamic social behaviour, termed the social aggregation hypothesis (Clapham & Zerbini 2015). This posits that during the recovery of humpback whales from whaling, new breeding aggregations formed that drew in whales that formerly bred in other areas. This could potentially lead to observed differences in recovery rates between the aggregations that are drawing in individuals and those from which they are being drawn. While we did not explicitly account for this, the power simulations indicated that the proposed survey designs will produce separate estimates of λ for New Caledonia and Tonga for comparison with each other and with the overall value for Oceania. Furthermore, the λ -POPAN model does allow λ to vary across time. For example, 2 values of λ could be estimated for New Caledonia: 1 value before and 1 value after the recent rapid increase in abundance. Using the λ -POPAN model in this way, or multi-strata models, could permit the investigation of regional-specific trends in abundance and λ across Oceania using data collected during the proposed surveys.

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Appendix. Individual-based simulation model

The superpopulation size, N_S , is the total number of males ever exposed to capture during the surveys from 1999 to 2016 or 2018. Animals that are born and die in the survey gap from 2006 to 2013 are not included in the superpopulation. The classical POPAN parameter $p_{\text{ent}(t)}$ is the probability that each of the N_S animals first enters the population at time t , either because time t is the first survey, or because it is the first survey after the animal's birth. Given a value for N_S , we simulate the presence-history of all N_S animals by using a multinomial distribution to allot them to their surveys of first appearance, where the multinomial index is N_S and the probability is $p_{\text{ent}(t)}$ that an animal's first appearance is at time t . We then simulate individual annual survival using parameter Φ , and individual capture outcomes for animals still alive in year t via the capture probabilities p_t .

To derive the probabilities $p_{\text{ent}(t)}$ in terms of λ and Φ , we used the following calculation (Carroll et al. 2013). Let N_t be the number of animals alive in the population at time t , including new entrants at time t and survivors from previous years. The expected numbers under the model, EN_t , satisfy:

$$\frac{EN_{t+1}}{EN_t} = \lambda.$$

Animals in the population at time t are those surviving from time $t-1$, plus new entrants at time t . Thus:

$$EN_t = \Phi EN_{t-1} + p_{\text{ent}(t)} N_S. \quad (\text{A1})$$

Dividing Eq. (A1) by $EN_1 = p_{\text{ent}(1)} N_S$, and noting that $\frac{EN_t}{EN_1} = \lambda^{t-1}$ and $\frac{EN_{t-1}}{EN_1} = \lambda^{t-2}$, we gain:

$$\frac{EN_t}{EN_1} = \lambda^{t-1} = \Phi \lambda^{t-2} + \frac{p_{\text{ent}(t)}}{p_{\text{ent}(1)}},$$

which rearranges to show that the p_{ent} parameters follow the equation:

$$p_{\text{ent}(t)} = p_{\text{ent}(1)} (\lambda - \Phi) \lambda^{t-2} \quad (\text{A2})$$

for $t = 2, 3, \dots, t_{\text{max}}$. The value of $p_{\text{ent}(1)}$ can then be found such that the p_{ent} parameters sum to 1. If there are missing years (for example, from 2006 to 2013), the p_{ent} calculation is adjusted, such that the $p_{\text{ent}(t)}$ value for the next survey t (e.g. the 2014 survey) accommodates the survival and recruitment of the missing intervening years.