

Robust assessment of population trends in marine mammals applied to New Caledonian humpback whales

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ABSTRACT: Estimating population trends for long-lived, migratory animals is challenging but essential for managing populations. Here we propose using a simple but potentially robust method, the direct estimation of population growth rate (PGR) from capture–recapture data. We considered an Endangered population of humpback whales *Megaptera novaeangliae* breeding and calving annually in the southern lagoon of New Caledonia. Studied since 1996, this population is known to exhibit a strong signal of transience, i.e. the presence of individuals that pass through the sampling area once, inducing detection heterogeneity. Another difficulty is that a more recently discovered second breeding and calving habitat (offshore seamounts to the south) has been surveyed with less intensity. Current direct PGR estimation models cannot deal with spatial sampling heterogeneity. In order to assess the reliability of the proposed method—in general and for our population in particular—we evaluated its robustness using simulations: first, when there are transient individuals; then, when the study area is split into 2 unequally sampled parts. We found no bias in PGR in the presence of transients. The bias with 2 unequally sampled parts depends on the amount and direction of exchanges, but appears negligible in our case study. The constant yearly PGR of the New Caledonian humpback whale population at the level of the 2 habitats was estimated at 1.15 (95% CI 1.11–1.20), suggesting outside recruitment. Whenever capture–recapture is feasible, we recommend the Pradel approach to estimate the PGR, validated with appropriate simulations, in order to assess population welfare.

KEY WORDS: *Megaptera novaeangliae* · Capture–recapture · Transients · Multi-site · Population growth rate · Pradel Model · Population trend

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INTRODUCTION

Estimating abundance and demographic parameters of marine mammals is essential for management and conservation decisions. In particular, estimating the population growth rate (PGR) allows us to assess whether a population is declining, thriving, or stable. Capture–recapture (CR), where individually recognizable animals are sampled repeatedly in a population, is a popular and useful method for studying the

population dynamics of several species of birds, reptiles, and mammals (Williams et al. 2002, Amstrup et al. 2006). With regard to cetaceans, the ability to recognize individuals from natural markings makes it possible to apply the CR technique based on photo-identifications (e.g. Hammond et al. 1990). CR is becoming widely used for estimating cetacean abundance (e.g. Cerchio et al. 2009, Carroll et al. 2011, Constantine et al. 2012), but it has seldom been used for estimating PGR.

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Most often, PGR is calculated as the ratio of successive population abundances N_{t+1}/N_t . When estimating population abundance, in order to guard against widespread detection heterogeneity among individuals, use of a robust design protocol is recommended (Pollock 1982), where the main sampling occasions between which the population changes are themselves subdivided into secondary sampling occasions sufficiently close in time to consider that the population does not change. In this way, robust estimators of population abundance for closed populations can be used (e.g. Huggins 1989, Chao et al. 1992). The formula estimating N (White et al. 2001), a derived parameter, is complex, and the derivation of estimates of precision of PGR, their running ratio, with the delta method is possible (e.g. Clark et al. 2010) but difficult. In these circumstances, testing the influence of a covariate on PGR would require a generalized least squares approach and would be even more difficult, as the full variance matrix would be needed. This sets a practical limit to the robust design approach. Another less used approach to estimating PGR from CR data (Pradel 1996) has PGR among its fundamental parameters. This so-called Pradel method is simple to implement, produces direct estimates of PGR with their associated measures of precision, accounts for sampling correlation between successive PGR estimates, and allows testing the influence of covariates in a model selection framework. Additionally, it does not require a robust design protocol but functions on the same encounter histories used to estimate survival with Cormack-Jolly-Seber models. The difference between the Cormack-Jolly-Seber model for survival estimation and the Pradel model for PGR estimation is that the latter analyses the encounter histories simultaneously forward and backward in time (and not just forward) within a single likelihood. In this way, it makes full use of the information available, unlike an analysis that would proceed by steps: estimating first survival and then recruitment with a reverse time analysis (Pradel 1996). Hence, this direct approach presents advantages over the robust design approach in (1) alleviating fieldwork (no need for a robust design protocol) and (2) providing more possibilities for modeling PGR and hence examining factors potentially acting at this level. It is also robust in the face of variable capture probabilities for individuals (Hines & Nichols 2002, Pradel et al. 2010, Marescot et al. 2011), the primary motivation for development of the robust design. However, it makes stronger assumptions, e.g. there is only one site and no transients. There is another approach worth mentioning that is

sometime used to estimate actual PGR, although it is more commonly used for predicting the theoretical PGR under different scenarios, namely, the population matrix approach (Caswell 2001). This approach demands a detailed knowledge of the population dynamics, e.g. first-year survival and immigration and emigration rates. In cases when one parameter is missing or poorly known, the PGR may become unreliable (Courtney et al. 2004). Hence, the matrix population approach should be reserved for well-studied populations.

Our work was motivated by the study of a small and Endangered population of humpback whales (Childerhouse et al. 2008) that congregates to breed and calve during austral winter in the southern lagoon of New Caledonia and for which detailed knowledge of the population dynamics is not available. Although previous studies have detected long-term, site-specific fidelity to this local wintering ground (Garrigue et al. 2002, 2011a), population-specific analyses suggest a phenomenon of transience (Constantine et al. 2012, Madon et al. 2013), i.e. the presence of individuals that do not remain in the study area and have a 0 probability of being recaptured during the remainder of the study. Transience is a frequent phenomenon. It has been detected repeatedly in animal populations (e.g. Rosenberg et al. 1999, Chaloupka & Limpus 2002, Perret et al. 2003, Cam et al. 2004), including cetaceans (Ramp et al. 2006, 2010, Silva et al. 2009, Conn et al. 2011, Madon et al. 2013). Its impact on the estimation of PGR using Pradel's method is unknown, which might explain why this method has seldom been used with cetaceans (but see Mizroch et al. 2004, Cerchio et al. 2009, Verborgh et al. 2009, Ryan et al. 2011, Constantine et al. 2012). Our first task in this study was to examine the influence of transience on the estimation of PGR using the Pradel model.

A new breeding and calving habitat for humpback whales has recently been discovered, viz. offshore seamounts (Garrigue et al. 2010) located some 200 km south of the southern lagoon. Madon et al. (2013) suggested that some transients observed in the southern lagoon could have originated from the seamounts. If so, examining the humpback whale population at the level of the 2 habitats may be more appropriate. However, sampling effort has been very unequal between the 2 sites. As no previous study has examined the impact of unequal sampling effort of different parts of a study area on the estimation of PGR, we also examined this issue. Because the extent of the bias likely depends on the amount of exchanges and on the intensity of transience, we first estimated these quantities in the New Caledonia humpback whale popula-

tion by means of a 2-site CR analysis (Arnason 1973, Schwarz et al. 1993). The detection parameters estimated for each habitat guided our choice of simulated scenarios, while the transience and movement parameters allowed us to situate the real population within the range of simulated scenarios. In light of the expected biases, we then estimated and interpreted the PGR of our population over a 17 yr period.

MATERIALS AND METHODS

Humpback whale study

New Caledonia is located in the southwest Pacific Ocean (22°S, 166°E). The principal survey areas cover approximately 1100 km² for the southern lagoon (22°30'S, 166°55'E) and 185 km² for the seamounts (23°25'S, 168°05'E). CR data were obtained via regular surveys between 1996 and 2012, with the exception of 2008 for the southern lagoon, and between 2008 and 2011 for the seamounts. Data collection occurred during the wintering season on a daily basis between July and September, but sampling effort varied among years, with 37 ± 14 (SD) days on average, August being the only month sampled in all years. When a group of whales was encountered, an attempt was made to photograph the underside of the fluke of each individual for photo-identification (Katona et al. 1979) and to get a skin sample for molecular identification of sex (Olavarria et al. 2007). Photographs were reviewed for quality control to rank their quality following a protocol developed by Calambokidis et al. (2001). In total, 784 whales were photographically identified, of which 658 were sexed (397 males and 261 females). Encounter histories based on photo-identification only were built for each individual on a yearly basis using 0 for the years where the individual was not encountered and 'L' or 'S' when the encounter originated in the southern lagoon or the seamounts, respectively. On 23 occasions, an individual was identified in both sites within the same year. In each case, we retained the location where the highest number of observations was made. When the number of observations was equal in both places (10 occasions), we assigned the location randomly with 50:50 probability. The data structure did not lend itself to the robust design approach because there was no simple way to isolate secondary occasions *a posteriori*, closure being especially problematic even over the short term due to the amount of transience.

The multi-site model and proportion of transients

We used the Arnason-Schwarz multi-site open-population model (Arnason 1972, 1973, Schwarz et al. 1993, Lebreton et al. 2009) to estimate site-specific adult apparent survival (ϕ^L , ϕ^S) and movement probability among sites (ψ^{LY} , ψ^{SL}) (following the notation of Lebreton et al. 1992).

In order to estimate the proportion of transients (Pradel et al. 1997, 2005), we fitted models with 2 age-classes on the survival probability, where age in a CR context is the time elapsed since first capture. More precisely, the transient proportion among the unmarked τ was estimated as:

$$\tau = 1 - \frac{\phi_1}{\phi_2} \quad (1)$$

where ϕ_1 is the apparent survival rate of newly captured individuals and ϕ_2 is the survival rate of residents obtained from the individuals captured more than once (Pradel et al. 1997). The proportion of transients in the entire population T_t was then estimated as:

$$T_t = \frac{E(u_t)}{E(u_t + m_t)} \tau \quad (2)$$

where $E(u_t)$ is the expected number of unmarked individuals captured for the first time at occasion t , and $E(u_t + m_t)$ is the expected number of individuals captured at occasion t (marked m_t + unmarked u_t). The observed u_t and $u_t + m_t$ were used as estimates for $E(u_t)$ and $E(u_t + m_t)$, respectively (Perret et al. 2003). A nonparametric bootstrap procedure was used to obtain the confidence intervals for T_t (Davison & Hinkley 1997). Parameter estimation is detailed in the Supplement at www.int-res.com/articles/suppl/m515p265_supp/.

Pradel model

The Pradel model analyzes encounter histories with forward time modeling, which yields the estimates of apparent survival (ϕ), and also simultaneously with reverse time modeling from the last captures backwards yielding a seniority probability (γ) defined as the probability that an individual did not enter the population between the previous and current occasions. This approach relies on a relationship that states that the ratio of successive population sizes—hence the PGR—is under certain assumptions equal to the ratio of the 2 above quantities (Pradel 1996):

$$\rho = \phi/\gamma \quad (3)$$

This relationship is embedded in a likelihood function, rendering direct modeling of the realized PGR ρ possible. From a practical point of view, Pradel models are available in the free popular software MARK (White & Burnham 1999) under 3 alternative parameterizations (note that MARK, rather than the original notation ρ , uses λ , which is confusing as this is the usual notation of the projected PGR in Leslie matrix scenarios). Although the method was established under strong assumptions (same survival and catchability for all individuals on each occasion, and a single study area), it has been found to be remarkably robust to a number of departures (Hines & Nichols 2002, Williams et al. 2002, Pradel et al. 2010, Marecot et al. 2011), but its robustness to the presence of transients or to unequal sampling intensity of different parts of the study area has not been demonstrated yet.

Given that the Pradel model is a variant of the Jolly-Seber model (Jolly 1965, Seber 1965), the fit of its time-dependent version can be assessed with the tests developed by Burnham et al. (1987) and Pradel et al. (2005); those include tests of trap dependence and transience. In case of lack-of-fit, an overdispersion factor can be calculated and used in any analysis of CR data. Models are then compared based on the quasi Akaike's information criterion (QAICc) instead of the AICc (Burnham & Anderson 2002).

Study of bias by simulations

Two different simulation studies were conducted. First, in order to test robustness of the Pradel model to transiency, data sets including transients were simulated. The robustness of the model to unequal sampling intensity of different parts of the study area was then tested by simulating data sets with different detection probabilities in 2 subsites. PGRs were estimated for each simulated data set using the Pradel model. We evaluated the bias of the ρ estimator $\hat{\rho}$ by subtracting the true value of the PGR used in the simulations from the mean $\hat{\rho}$. If the difference is near 0, then $\hat{\rho}$ is an unbiased estimator of the PGR.

$$\text{Bias}(\hat{\rho}) = E(\hat{\rho}) - \text{PGR} \quad (4)$$

Data were simulated with parameter values of survival and capture probabilities similar to those of the New Caledonian humpback whale population, derived from the 2-site CR analysis mentioned above (see Supplement). Each simulation ran over 10 sampling periods and started with 500 individuals on the

first occasion; sex was not considered, as parameter estimates were similar for males and females. In these simulations, we were interested only in a positive PGR. On each subsequent occasion, new individuals were added to replace those expected to die plus a supplementary number to ensure the target growth rate according to the formula $N_{t-1}(1 - \phi) + (\rho - 1)N_{t-1}$ (Hines & Nichols 2002). These new recruits survived and were detected with the same probabilities as the others.

When studying the effect of transience, only one site was considered. The proportion of transients was kept constant over time in each simulation but varied from 0.1 to 0.6 among simulations in order to cover a large range of situations. To study the effect of unequal sampling between 2 areas of the study site, fixed detection probabilities, chosen to reflect the conditions found in the New Caledonian humpback whale study, were simulated for each site. Movement probabilities Ψ_1 (Site 1 toward Site 2) and Ψ_2 (Site 2 toward Site 1) were varied independently from 0.1 to 0.9 again to cover a wide range of situations. In total, 250 datasets were simulated for each scenario, i.e. for each transient proportion (study of the effect of transience) or for each of the 81 combinations of movement probabilities (study of the effect of unequal sampling), and the Pradel model with constant parameters was fitted to estimate PGR each time. The mean $\hat{\rho}$ over the 250 datasets with the same simulation parameters was used to assess the bias in the corresponding scenario according to Eq. (4). Simulations were done with R 2.14.1 (R Foundation for Statistical Computing) and the package RMark (Laake 2013) which calls MARK from R. The R code is provided in Supplement 2.

RESULTS

The analysis of the data set with 2-site Arnason-Schwarz CR models was first conducted in order to estimate average survival, movement, and detection parameters in the New Caledonian population and to guide our simulation studies (see the Supplement for details). Similar values of the estimates were found for females and males. Annual survival was estimated around 94%. The annual shifts from the southern lagoon to the seamounts were around 28%, vs. 45% in the reverse direction, which means that individuals move more often in the direction of the southern lagoon. The detection probability was estimated at 28% in the southern lagoon and at 15% in the seamounts. We found that around 40% of the

individuals newly captured each year at the level of the 2 habitats (southern lagoon plus seamounts) were transients (see Supplement 1 for details). These values are in good agreement with previous studies (Madon 2010, Garrigue et al. 2011a, Constantine et al. 2012, Madon et al. 2013).

Effect of transients on the PGR estimation

Data were simulated with survival $\phi = 0.90$, detection probability $p = 0.3$, and PGR $\rho = 1.10$ (increasing population). These values were chosen in the light of the 2-site analysis and of previous studies of the same population. They are probably realistic for several cetacean studies (for example, Silva et al. 2009, Verborgh et al. 2009, Ramp et al. 2010, Zerbini et al. 2010), although the PGR may be unusually high. A higher survival value of 0.975 was also tried and gave essentially the same results (not shown). Independently of the proportion of transients introduced, bias in the PGR estimator ($\hat{\rho}$) was always close to 0 (Fig. 1, see Table S4 in Supplement 1).

Effect of unequal sampling of the study area on the PGR estimation

The simulated study area consisted of 2 unequally sampled zones. The detection probability was 30 and 10% for Sites 1 and 2, respectively, mimicking the situation of our study population; survival was set at 90%. Bias on $\hat{\rho}$ varied with the movement rates (Fig. 2) but always remained low (<0.02). The strongest biases were obtained for asymmetrical exchanges, especially when movements were mainly directed towards the site with low detection.

Estimation of the PGR of the New Caledonian humpback whale population

As there are many exchanges of individuals between the 2 sites, it may be considered that this is a single population. Therefore, the data used in the 2-site analysis were modified by recoding 'L' and 'S' as a single site. Also, females and males were not distinguished, as preliminary analyses did not find marked differences between them in any parameter. With the recoded data set, an over-dispersion

factor of 1.89 was estimated with the program U-CARE (Choquet et al. 2009) and was used to account for lack of fit. A series of Pradel models were then fitted using MARK and sorted by increasing QAICc

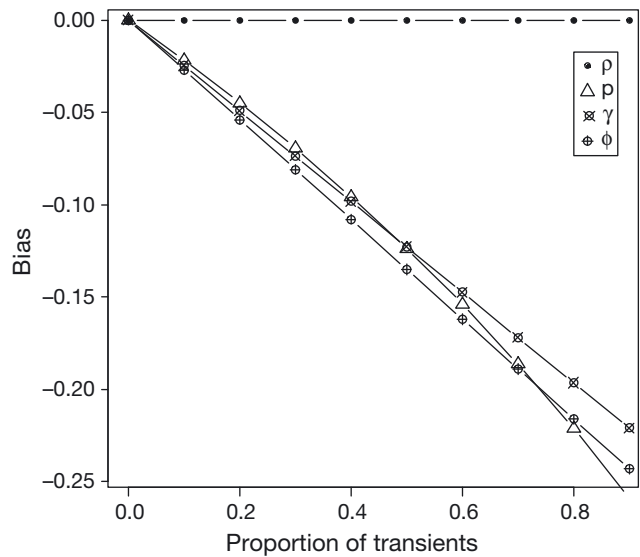


Fig. 1. Absolute bias in population growth rate compared to that in other parameters using the Pradel model (y-axis) as a function of an increasing proportion of transients (x-axis)

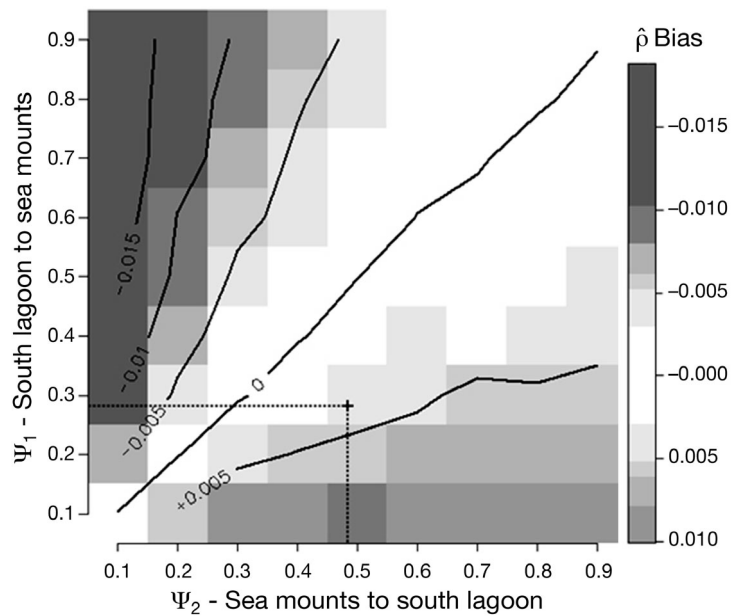


Fig. 2. Absolute bias in growth rate estimation using the constant-parameter Pradel model as a function of movement probabilities (Ψ_1 and Ψ_2) between 2 sites (Site 1 and Site 2 have a detection probability of 0.3 and 0.1, respectively). Darker colors indicate stronger bias. The 'white zone' illustrates a combination of values of Ψ_1 and Ψ_2 for which the estimation of lambda is unbiased. The dotted line and the cross indicate the case of the New Caledonian humpback whale *Megaptera novaeangliae* population

Table 1. Model selection results for Pradel's analysis of the population growth rate (PGR). Models are ordered according to the quasi Akaike's information criterion (QAICc) value. ϕ indicates survival, p is detection probability, and ρ is the PGR. NP is the number of identifiable parameters in the model. The dot (.) and t indicate constant and time effects, respectively

No.	Model	QAICc	Δ QAICc	NP	Deviance
1	$\phi(.) p(t) \rho(.)$	3104.31	0.00	18	299.73
2	$\phi(.) p(t) \rho(t)$	3126.08	21.77	33	289.91
3	$\phi(.) p(.) \rho(t)$	3126.11	21.80	18	321.53
4	$\phi(t) p(t) \rho(.)$	3130.40	26.08	33	294.22
5	$\phi(t) p(.) \rho(t)$	3145.34	41.03	33	309.18
6	$\phi(t) p(t) \rho(t)$	3152.59	48.28	47	286.07
7	$\phi(.) p(.) \rho(.)$	3188.45	84.14	3	414.52
8	$\phi(t) p(.) \rho(.)$	3213.85	109.54	18	409.27

(Table 1). Models varied based on whether the 3 types of parameters (survival, PGR, and detection probability) were constant or time dependent, with all 8 possible combinations being investigated.

The first model, with constant survival and PGR but variable detection probabilities over the years, was much better than any other (QAICc weight of 1). The estimated population growth was 1.15 (95% CI 1.11–1.20), which corresponds to an increase of 15% yr⁻¹. Given the insensitivity of this estimator to the presence of transients, bias might only come from the exchanges of individuals between the 2 zones that constitute the sampling area. Given the detection probabilities estimated in the 2-site analysis, the probability of shifting from the southern lagoon to the seamounts is equivalent to Ψ_1 in the simulations, and the probability of the reverse movement is equivalent to Ψ_2 . Therefore the expected bias is approximately 0.003 (Fig. 2) and thus negligible in regard to the precision of the estimator. The extra precaution of using a variance inflation factor guarantees that the confidence interval has been correctly inflated to account for lack of fit of the model considered. We therefore estimated a constant increase for this population of >10%.

DISCUSSION

Given the large amount of exchanges between the 2 habitats in the New Caledonian humpback whale case study, we may reasonably consider that they belong to a unique population. At the 2-habitat level, the identified violations of the Pradel model assumptions for the estimation of the PGR had a negligible impact in terms of bias. However, there may be other

undetected violations of assumptions. For instance, some studies have reported capture heterogeneity between sexes for humpbacks on breeding grounds. Although we did not detect such heterogeneity in our study, we cannot rule it out entirely; also, there might be among-individual capture heterogeneity unrelated to sex. However, previous studies have found that the estimate of PGR is robust to capture heterogeneity (Hines & Nichols 2002, Pradel et al. 2010, Marescot et al. 2011). Additionally, by correcting for lack of fit with the introduction of a variance inflation factor in the models and using the QAICc for selection, we protected against undetected departures from assumptions. The ρ estimator has up to now proved extremely robust to many kinds of departures from assumptions (Hines & Nichols 2002, Williams et al. 2002, Franklin et al. 2004, Pradel et al. 2010, Marescot et al. 2011). The magnitude of the ρ estimate thus appears reliable. More caution is needed yet when studying time patterns. For instance, in a simulation study of capture heterogeneity, Hines & Nichols (2002) detected a spurious trend over years and Pradel et al. (2010) observed a delayed timing in the detection of the yearly peak of abundance of a small mammal in a seasonal study.

The results of our study are particularly remarkable regarding the transients. There appears to be no bias at all in the PGR estimate, while the survival and seniority rate estimates are biased (see Fig. 1). We currently have no explanation why biases in survival and seniority compensate each other in producing the estimate of PGR, but preliminary results indicate that this might no longer be true if the transience rate varies over time (Table S4 in Supplement 1).

Regarding movement between 2 unequally sampled zones, we note that the worst bias is registered when individuals depart from the intensively monitored area to join the poorly monitored one with no return movements. This is understandable, as this approximates a situation where the population concentrates at one site with poor monitoring: overall population size may not be changing, but its concentration in the 'poor' zone makes it appear to be declining. The opposite happens when individuals move from the poorly monitored zone into the intensively monitored one: their concentration in the 'good' zone makes the population appear to be thriving. When movements are symmetric, no bias is expected, as all individuals have on average an equal chance of being at each site in the long run and thus share the same average detection probability. The opposite happens if individuals move so little that they are virtually segregated into individuals with a

high and a low detection probability (depending on where they are stationed). The case of individual heterogeneity of detection has recently been explicitly modelled (Pradel et al. 2010) and appears to cause little bias (Hines & Nichols 2002, Pradel et al. 2010, Marescot et al. 2011).

Given the previous considerations, it is unlikely that the high value of 15% estimated for the realized yearly humpback whale PGR over the study period is an artifact of the method. It is much higher than the maximum rate of increase for humpback whale populations (11.8%) calculated by Zerbini et al. (2010) using life history parameters obtained in different studies: a review of life history parameters was done and growth rate was computed to obtain plausible growth rate for humpback whale as a species. However, the contradiction is only apparent because the estimate of Zerbini et al. (2010) represents the demographic potential of the species, while the actual growth rate is under the influence of migration in addition to that of demography. It is thus highly likely that the migration balance is positive and contributes significantly to the change in the New Caledonian population size. It is more difficult to conclude whether the increase is due to a regular migration flow or to a main pulse. While the best model found by selection in the present study indicates a constant rate of increase, a recent abundance study of the southern lagoon found an anomalous increase between 2008 and 2011 (Garrigue et al. 2011b). However, both methods have their weaknesses: as indicated above, the estimate of the realized PGR may fail to correctly detect the timing of changes over time, and the estimate of abundance is very sensitive to the presence of transients.

In the context of Oceania, our findings complement the results of Constantine et al. (2012). Using the Pradel model, these authors found a rate of increase not statistically different from 1 for Oceania and concluded that the population was stable between 1999 and 2004. The longer length of our study may have permitted the detection of a previously non-significant increase, but it may also be that the population is indeed relatively stable at the level of Oceania and that the local increase in New Caledonia is mainly due to the redistribution of individuals within the region. Unfortunately, few data are available on humpback whales around New Caledonia prior to whaling, and none provide information on past abundance or behavior (du Pasquier 1990). We can only advance hypotheses about the possible origin of immigrants in New Caledonia. Considering that immigrants from a depleted population drawn into

another breeding ground could inflate the apparent rate of increase (social aggregation hypothesis, Clapham & Zerbini 2006), the Fijian breeding populations could be responsible for part of the immigration, as this historically healthy population does not show any sign of recovery yet (Gibbs et al. 2004). On the other side, the eastern Australian population has shown a strong rate of increase (10.9%) for several years (Noad et al. 2011) and could also act as a source of immigrants for the New Caledonian population. To date, limited exchanges between the east Australian population and the rest of Oceania have been documented using photo and genotypic identifications (Olavarria et al. 2007, Garrigue et al. 2011b, Jackson et al. 2012). However, a certain degree of interconnectivity has been demonstrated with the cultural transmission of the song from east Australia eastwards through Oceania (Garland et al. 2011). New Caledonia being the closest island to Australia, it is most likely to receive immigrants and individuals en route to more distant grounds, which may correspond to the transients detected in recent studies as well as in this one.

CONCLUSION

Our and previous studies have focused on the main effects that general departures from assumptions of the Pradel models have on the estimation of PGR with CR data. It appears that these models are very robust, being minimally (and sometimes not at all) sensitive to frequent phenomena that badly affect survival and/or abundance estimates. They can thus be considered as very reliable tools for assessing the general welfare of a population. However, it is not clear whether they can be used to detect subtle effects. For instance, in their present form, they seem unable to detect the precise timing of changes in abundance. Also, more complex scenarios than the ones we have examined might be worth studying because they are likely to occur. For instance, transience in a real population may vary randomly over years or even present a temporal trend as suspected in the east Australian humpback whale population (Clapham & Zerbini 2006) and departures of different natures can compound to create a bias in the PGR estimator. Thus, we recommend the use of simulations to assess the effects of the particular conditions of each study as well as the extra precaution of introducing a variance inflation factor and the use of the QAICc for model selection. In conclusion, we recommend the estimation of PGR to assess the status of a

population when individual longitudinal monitoring is possible such as is often the case for marine mammals but also for other marine species like shellfish. Although this parameter cannot make the distinction between immigration and biological recruitment, it appears to be able to provide an accurate estimate of the trend of a population under various circumstances.

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LITERATURE CITED

- Amstrup S, MacDonald L, Manly B (2006) Handbook of capture-recapture analysis. Princeton University Press, Princeton, NJ
- Arnason AN (1972) Parameter estimates from mark-recapture experiments on two populations subject to migration and death. *Res Popul Ecol (Kyoto)* 13:97–113
- Arnason AN (1973) The estimation of population size, migration rates and survival in a stratified population. *Res Popul Ecol (Kyoto)* 15:1–8
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, NY
- Burnham KP, Anderson DR, White GC, Brownie C, Pollock KH (1987) Design and analysis methods for fish survival experiments based on release-recapture, Vol 5. American Fisheries Society, Bethesda, MD
- Calambokidis J, Steiger GH, Straley JM, Herman LM and others (2001) Movements and population structure of humpback whales in the North Pacific. *Mar Mamm Sci* 17:769–794
- Cam E, Oro D, Pradel R, Jimenez J (2004) Assessment of hypotheses about dispersal in a long-lived seabird using multi-state capture-recapture models. *J Anim Ecol* 73: 723–736
- Carroll EL, Patenaude NJ, Childerhouse SJ, Kraus SD, Fewster RM, Baker CS (2011) Abundance of the New Zealand subantarctic southern right whale population estimated from photo-identification and genotype mark-recapture. *Mar Biol* 158:2565–2575
- Caswell H (2001) Matrix population models, 2nd edn. Sinauer, Sunderland, MA
- Cerchio S, Ersts P, Pomilla C, Loo J and others (2009) Updated estimates of abundance for humpback whale breeding stock C3 off Madagascar, 2000–2006. International Whaling Commission, Cambridge
- Chaloupka MY, Limpus CJ (2002) Survival probability estimates for the endangered loggerhead sea turtle resident in southern Great Barrier Reef waters. *Mar Biol* 140: 267–277
- Chao A, Lee SM, Jeng SL (1992) Estimating population size for capture-recapture data when capture probabilities vary by time and individual animal. *Biometrics* 48: 201–216
- Childerhouse S, Jackson JA, Baker CS, Gales N, Clapham PJ, Brownell RL Jr (2008) *Megaptera novaeangliae* Oceania subpopulation. IUCN Red List of Threatened Species, Gland. Available at www.iucnredlist.org
- Choquet R, Lebreton JD, Gimenez O, Reboulet AM, Pradel R (2009) U-CARE: Utilities for performing goodness of fit tests and manipulating CAPTURE-RECAPTURE data. *Ecography* 32:1071–1074
- Clapham PJ, Zerbini A (2006) Is social aggregation driving high rates of increase in some Southern Hemisphere humpback whale populations? Paper IWC/58/SH3. International Whaling Commission, Cambridge
- Clark JD, Eastridge R, Hooker MJ (2010) Effects of exploitation on black bear populations at White River National Wildlife Refuge. *J Wildl Manag* 74:1448–1456
- Conn PB, Gorgone AM, Jugovich AR, Byrd BL, Hansen J (2011) Accounting for transients when estimating abundance of bottlenose dolphins in Choctawhatchee Bay, Florida. *J Wildl Manag* 75:569–579
- Constantine R, Jackson JA, Steel D, Baker CS and others (2012) Abundance of humpback whales in Oceania using photo-identification and microsatellite genotyping. *Mar Ecol Prog Ser* 453:249–261
- Courtney SP, Blakesley JA, Bigley RE, Cody ML and others (2004) Scientific evaluation of the status of the Northern Spotted Owl. Sustainable Ecosystems Institute, Portland, OR
- Davison AC, Hinkley DV, Worton BJ (1992) Bootstrap likelihoods. *Biometrika* 1:113–130
- Du Pasquier T (1990) Les baleiniers français de Louis XVI à Napoléon. Kronos, Henri Veyrier, Paris
- Franklin AB, Gutierrez RJ, Nichols JD, Seamans ME and others (2004) Population dynamics of the California spotted owl (*Strix occidentalis occidentalis*): a meta-analysis. *Ornithol Monogr* 54:1–54
- Garland EC, Goldizen AW, Rekdahl ML, Constantine R and others (2011) Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Curr Biol* 21:687–691
- Garrigue C, Aguayo AL, Amanthe-Helweg VLU, Baker CS, Cabellero S (2002) Movements of humpback whales in Oceania, South Pacific. *J Cetacean Res Manag* 4: 255–260
- Garrigue C, Zerbini AN, Geyer Y, Heide-Jørgensen MP, Hanaoka W, Clapham P (2010) Movements of satellite-monitored humpback whales from New Caledonia. *J Mammal* 91:109–115
- Garrigue C, Constantine R, Poole MM, Hauser N and others (2011a) Movement of individual humpback whales between wintering grounds of Oceania (South Pacific), 1999 to 2004. *J Cetacean Res Manag (Spec Issue)* 3: 275–281
- Garrigue C, Albertson R, Jackson JA (2011b) An anomalous increase in the New Caledonian humpback whales breeding sub-stock E2. International Whaling Commission, Cambridge
- Gibbs N, Paton D, Childerhouse S, McConnell H, Oosterman A (2004) A survey of whales and dolphins in the Lomaiviti Island group, Fiji 2003. Department of Environment and Heritage, Canberra
- Hammond PS, Mizroch SA, Donovan GP (eds) (1990) Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. *Rep Int Whal Com Spec Issue* 12:1–440
- Hines JE, Nichols JD (2002) Investigations of potential bias in the estimation of lambda using Pradel's (1996) model for capture-recapture data. *J Appl Stat* 29:573–587
- Huggins RM (1989) On the statistical analysis of capture-

- recapture experiments. *Biometrika* 76:133–140
- Jackson JA, Anderson M, Steel DS, Brooks L and others (2012) Multistate measurements of genotype interchange between East Australia and Oceania (IWC breeding sub-stocks E1, E2, E3 and F2) between 1999 and 2004. SC/64/SH22. International Whaling Commission, Cambridge
- Jolly GM (1965) Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225–247
- Katona S, Baxter B, Brazier O, Kraus S, Perkins J, Whitehead H (1979) Identification of humpback whales by fluke photographs. In: Winn HE, Olla BL (eds) Behavior of marine animals, Vol 3. Plenum Press, New York, NY, p 33–44
- Laake JL (2013) RMark: an R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep 2013-01. NOAA, NMFS, Alaska Fisheries Science Center, Seattle, WA
- Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67–118
- Lebreton JD, Nichols JD, Barker R, Pradel R, Spendelov JA (2009) Modeling individual histories with multistate capture-recapture models. *Adv Ecol Res* 41:87–173
- Madon B (2010) An extension of the Jolly-Seber model combining two sources of mark recapture data. PhD dissertation, University of Auckland
- Madon B, Garrigue C, Pradel R, Gimenez O (2013) Transience in the humpback whale population of New Caledonia and implications for abundance estimation. *Mar Mamm Sci* 29:669–678
- Marescot L, Pradel R, Duchamp C, Cubaynes S and others (2011) Capture-recapture population growth rate as a robust tool against detection heterogeneity for population management. *Ecol Appl* 21:2898–2907
- Mizroch SA, Herman LM, Straley JM, Glockner-Ferrari DA and others (2004) Estimating the adult survival rate of central North Pacific humpback whales (*Megaptera novaeangliae*). *J Mammal* 85:963–972
- Noad MJ, Dunlop RA, Paton D, Kniest HE (2011) Abundance estimates of the east Australian humpback whale population: 2010 survey and update. Paper SC/63/SH22. International Whaling Commission, Cambridge
- Olavarria C, Baker CS, Garrigue C, Poole M and others (2007) Population structure of South Pacific humpback whales and the origin of the eastern Polynesian breeding grounds. *Mar Ecol Prog Ser* 330:257–268
- Perret N, Pradel R, Miaud C, Grolet O, Joly P (2003) Transience, dispersal and survival rates in newt patchy populations. *J Anim Ecol* 72:567–575
- Pollock KH (1982) A capture-recapture design robust to unequal probability of capture. *J Wildl Manag* 46:752–757
- Pradel R (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703–709
- Pradel R, Hines JE, Lebreton JD, Nichols JD (1997) Capture-recapture survival models taking account of transients. *Biometrics* 53:60–72
- Pradel R, Gimenez O, Lebreton JD (2005) Principles and interest of GOF tests for multistate capture-recapture models. *Anim Biodivers Conserv* 28.2:189–204
- Pradel R, Choquet R, Lima MA, Merritt JF, Crespin L (2010) Estimating population growth rate from capture-recapture data in presence of capture heterogeneity. *J Agric Biol Environ Stat* 15:248–258
- Ramp C, Bérubé M, Hagen W, Sears R (2006) Survival of adult blue whales *Balaenoptera musculus* in the Gulf of St. Lawrence, Canada. *Mar Ecol Prog Ser* 319:287–295
- Ramp C, Bérubé M, Palsbøll P, Hagen W, Sears R (2010) Sex-specific survival in the humpback whale *Megaptera novaeangliae* in the Gulf of St. Lawrence, Canada. *Mar Ecol Prog Ser* 400:267–276
- Rosenberg DK, DeSante DF, McKelvey KS, Hines JE (1999) Monitoring survival rates of Swainson's thrush *Catharus ustulatus* at multiple scales. *Bird Study* 46(Suppl):S198–S208
- Ryan GE, Dove V, Trujillo F, Doherty PF Jr (2011) Irrawaddy dolphin demography in the Mekong River: an application of mark-resight models. *Ecosphere* 2:art58
- Schwarz CJ, Schweigert JF, Arnason AN (1993) Estimating migration rates using tag-recovery data. *Biometrics* 49:177–193
- Seber GAF (1965) A note on the multiple-recapture census. *Biometrika* 52:249–259
- Silva MA, Magalhães S, Prieto R, Serrão Santos R, Hammond PS (2009) Estimating survival and abundance in a bottlenose dolphin population taking into account transience and temporary emigration. *Mar Ecol Prog Ser* 392:263–276
- Verborgh P, De Stephanis R, Pérez S, Jaget Y, Barbraud C, Guinet C (2009) Survival rate, abundance, and residency of long-finned pilot whales in the Strait of Gibraltar. *Mar Mamm Sci* 25:523–536
- White GC, Burnham KP (1999) Program MARK: survival rate estimation from both live and dead encounters. *Bird Study* 46(Suppl 001):S120–S139
- White GC, Burnham KP, Anderson DR (2001) Advanced features of program MARK. In: Fields R (ed) Integrating people and wildlife for a sustainable future: Proceedings of the Second International Wildlife Management Congress, Gödöllő, Hungary. The Wildlife Society, Bethesda, MD, p 368–376
- Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, CA
- Zerbini AN, Clapham PJ, Wade PR (2010) Assessing plausible rates of population growth in humpback whales from life-history data. *Mar Biol* 157:1225–1236