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▶ **To cite this version:**

HAL Id: hal-03502433
https://hal.science/hal-03502433

Submitted on 25 Dec 2021

Robust assessment of population trends in marine mammals applied to the New Caledonia Humpback Whales

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ABSTRACT: Estimating population trends for long-lived, migratory animals is challenging but essential for managing populations. We propose to use a simple but potentially robust method, the direct estimation of population growth rate (PGR) from capture recapture data. As motivating study, we consider an endangered population of humpback whales *Megaptera novaeangliae* breeding and calving annually in the south 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 second breeding and calving habitat (offshore seamounts to the south) more recently discovered has been surveyed with less intensity. Now, the 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 two unequally sampled parts. We found no bias in PGR in presence of transients. The bias with two 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-Caledonia humpback whale population at the level of the two habitats was estimated at 1.15 [1.11; 1.20], hinting at outside recruitment. Whenever capture-recapture is feasible, we recommend the Pradel approach to estimating the PGR, validated with appropriate simulations, in order to assess population welfare. (250)

KEYS WORDS: *Megaptera novaeangliae*, Capture-Recapture, transients, multi-site, population growth rate, Pradel Model, population trend.

Running title: Assessing marine mammals populations trends

INTRODUCTION

Estimating abundance and demographic parameters of marine mammals is essential for management and conservation decisions. In particular, estimating the population growth rate (PGR) will permit to know 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 little been used for estimating PGR.

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, it is recommended to use a robust design protocol (Pollock 1982), where the main sampling occasions between which population changes, are themselves subdivided into secondary sampling occasions sufficiently close in time to consider that population does not change. In this way, robust estimators of population abundance for closed populations can be used (e.g. Chao 1992, Huggins 1989). The formula estimating N (White et al. 2001), a derived parameter, is however complex and the derivation of estimates of precision of PGR, their running ratio, with the delta method possible (e.g. Clark et al. 2010) but painful. In these circumstances, testing the influence of a covariate on PGR would require a generalized least square approach and would be even more painful 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 capture recapture 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 with the Cormack-Jolly-Seber models for survival estimation is that it 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 of a robust design protocol) and 2) providing more possibilities for modelling 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, immigration and emigration rates. In case 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 (L) of New Caledonia (NC) and for which detailed knowledge of the population dynamics is not available. Although previous studies have detected a long term site specific fidelity to this local wintering grounds (Garrigue et al. 2002, 2011a), population specific analyses suggest a phenomenon of transience (Constantine et al. 2012, Madon et al. 2012), i.e. the presence of individuals that do not remain in the study area and have a zero probability of being recaptured during the remaining of the entire study. Transience is a frequent phenomenon. It has been detected repeatedly in animal populations (e.g.,

95 Rosenberg et al. 1999, Chaloupkas & Limpus 2002, Perret et al. 2003, Cam et al. 2004),
96 including cetaceans (Ramp et al. 2006 and 2010, Silva et al. 2009, Conn et al. 2011, Madon
97 et al. 2012). Its impact on the estimation of PGR using Pradel's method is unknown, which
98 might explain why this method has seldom been used with cetaceans (but see Mizroch et al.
99 2004, Cerchio et al. 2009, Verborgh et al. 2009, Ryan et al. 2011, Constantine et al. 2012).
100 Our first task in this paper will be to examine the influence of transience on the estimation of
101 PGR using the Pradel model.
102   A new breeding and calving habitat for humpback whales has recently been discovered,
103 the offshore seamounts (Garrigue et al. 2010) located some 200 km south of the Southern
104 Lagoon. Madon et al. (2012) suggested that some transients observed in the Southern
105 Lagoon could have originated from the seamounts. If so, examining the humpback whale
106 population at the level of the two habitats may be more appropriate. However, sampling effort
107 has been very unequal between the two sites. As no previous study has examined the
108 impact of unequal sampling effort of different parts of a study area on the estimation of PGR,
109 we will also examine this point. Because the extent of the bias likely depends on the amount
110 of exchanges and on the intensity of transience, we will first estimate these quantities in the
111 NC humpback whale population by means of a two-site capture-recapture analysis (Arnason
112 1973, Schwarz et al. 1993). The detection parameters estimated for each habitat will guide
113 our choice of simulated scenarios while the transience and movement parameters will allow
114 us to situate the real population within the range of simulated scenarios.
115   In the light of the expected biases, we will then estimate and interpret the PGR of our
116 population over a 17-year period.

MATERIAL AND METHODS

The humpback whale study

121   New Caledonia is located in the south west Pacific Ocean (22°S-166°E). The principal
122 survey areas cover approximately 1100 km² for the southern lagoon (22°30'S, 166°55'E) and
123 185 km² for the seamounts (23°25'S, 168°05'E). CR data were obtained via regular surveys
124 between 1996 and 2012, with the exception of 2008 for the southern lagoon and between
125 2008 and 2011 for the seamounts. Data collection occurred during the wintering season on a
126 daily basis between July and September but sampling effort varied among years with 37+/-14
127 days on average, August being the only month sampled in all years. When a group of whales
128 was encountered, an attempt was made to photograph the underside of the fluke of each
129 individual for photo-identification (Katona et al. 1979) and to get a skin sample for molecular
130 identification of sex (Olavarria et al. 2007). Photographs were reviewed for quality control
131 (QC) to rank their quality following a protocol developed by Calambokidis et al. (2001). A
132 total of 784 whales were photographically identified among which 658 were sexed (397
133 males and 261 females). Encounter histories based on photo-identification only were built for
134 each individual on a yearly basis using 0 for the years where the individual was not
135 encountered and "L" or "S" when the encounter originated in the southern lagoon or the
136 seamounts respectively. On 23 occasions, an individual was identified in both places in the
137 same year. In each case, we retained the location where the highest number of observations
138 was made. When the number of observations was equal in both places (10 occasions), we
139 assigned the location randomly with 50:50 probability. The data structure did not lend itself to
140 the robust design approach because there was no simple way to isolate secondary
141 occasions a posteriori, closure being really problematic even on the short term due to the
142 amount of transience.

The Multisite model & Transience proportion

145

146   We used the Arnason-Schwarz multi-site (MS) open-population model (Arnason 1972,
147   1973, Schwarz *et al.* 1993, Lebreton et al. 2009) to estimate site-specific adult apparent
148   survival (ϕ^L, ϕ^S) and movement probability among sites (ψ^{LS}, ψ^{SL}) (following Lebreton et al.
149   1992 notation).
150   In order to estimate the proportion of transients (Pradel et al. 1997, Pradel et al. 2005), we
151   fitted models with two age-classes on the survival probability, where age in a CR context is
152   the time elapsed since first capture. More precisely, the transient proportion among the
153   unmarked τ was estimated as:

$$\tau = 1 - \frac{\Phi_1}{\Phi_2}$$

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

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

157   where $E(u_t)$ is the expected number of unmarked individuals captured for the first time at
158   occasion t and $E(u_t + m_t)$ is the expected number of individuals captured at occasion t
159   (marked m_t + unmarked u_t). The observed u_t and $u_t + m_t$ were used as estimates for $E(u_t)$ and
160    $E(u_t + m_t)$, respectively (Perret et al 2003). A nonparametric bootstrap procedure was used to
161   obtain the confidence intervals for T_t (Davison & Hinkley, 1997). Parameter estimation is
162   detailed in the supplementary material.

163

164

The Pradel model

166

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

174   ρ=ϕ/γ

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

186   The Pradel model being a variant of the Jolly-Seber model (Jolly 1965, Seber 1965), the
187   fit of its time-dependent version can be assessed with the tests developed by Burnham et al.
188   (1987) and Pradel et al. (2005); those include tests of trap dependence and transience. In
189   case of lack-of-fit, an overdispersion factor can be calculated and used in any analysis of
190   capture-recapture data. Models are then compared based on the QAICc instead of the AICc
191   (Burnham & Anderson 2002).
192
193
194   **Study of bias by simulations**
195
196   Two different simulation studies were conducted. First, in order to test robustness of the
197   Pradel model to transiency, data sets including transients were simulated. Then the
198   robustness of the model to unequal sampling intensity of different parts of the study area was
199   tested by simulating data sets with different detection probabilities in two subsites. PGRs
200   were estimated for each simulated data set using the Pradel model. We evaluated the bias of
201   the ρ estimator, $\hat{\rho}$, by subtracting the true value of the PGR used in the simulations from the
202   mean $\hat{\rho}$. If the difference comes near to 0, then $\hat{\rho}$ is an unbiased estimator of the PGR.
203

$$Bias(\hat{\rho}) = E(\hat{\rho}) - PGR \qquad Eq. 1$$

204
205   Data were simulated with parameter values of survival and capture probabilities similar to
206   those of the New-Caledonian humpback whale population, derived from the two-site capture-
207   recapture analysis mentioned above (see supplementary material for details). Each
208   simulation ran over 10 sampling periods and started with 500 individuals at the first occasion,
209   sex was not considered as parameter estimates were similar for males and females. In these
210   simulations, we were interested only in a positive PGR. At each subsequent occasion, new
211   individuals were added to replace those expected to die plus a supplementary number to
212   ensure the target growth rate according to the formula $N_{t-1}(1-\phi)+(\rho-1)N_{t-1}$ (Hines & Nichols,
213   2002). These new recruits survived and were detected with the same probabilities as the
214   others.
215   When studying the effect of transience, only one site was considered. The proportion of
216   transients was kept constant over time in each simulation but varied from 0.1 to 0.6 among
217   simulations in order to cover a large range of situations. To study the effect of unequal
218   sampling between two areas of the study site, fixed detection probabilities, chosen to reflect
219   the conditions found in the New-Caledonian humpback whale study, were simulated on each
220   site. Movement probabilities Ψ_1 (site1 toward site2) and Ψ_2 (site2 toward site1) were varied
221   independently from 0.1 to 0.9 again to cover a wide range of situations. A total of 250
222   datasets were simulated for each scenario, i.e. for each transient proportion (study of the
223   effect of transience) or for each one of the 81 combinations of movement probabilities (study
224   of the effect of unequal sampling), and the Pradel model with constant parameters was fitted
225   to estimate PGR each time. The mean $\hat{\rho}$ over the 250 datasets with the same simulation
226   parameters was used to assess the bias in the corresponding scenario according to Eq. 1.
227   Simulations were done with R 2.14.1 (2011, R Foundation for Statistical Computing) and the
228   package RMark (Laake, 2013) which calls MARK from R. The R code is made available in
229   the supplementary material.
230
231

RESULTS

The analysis of the data set with two-site Arnason-Schwarz capture-recapture 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 supporting information for details). Similar values of the estimates were found for females and males. The annual survival was estimated around 94%. The annual shifts from the southern lagoon to the seamounts around 28% and 45% in the reverse direction respectively, which means that individuals move more often in direction of the southern lagoon. The detection probability was estimated at 28% in the southern lagoon and at 15% in the seamounts respectively. We found that around 40% of the individuals newly captured each year at the level of the two habitats (South lagoon plus seamounts) were transients (see supporting information for details). These values are in good agreement with previous studies (Madon 2010, Garrigue et al. 2011a, Madon et al. 2012, Constantine et al. 2012).

### Effect of transience on the estimation of population growth rate

Data were simulated with survival ϕ=0.90, detection probability p=0.3 and PGR ρ=1.10 (increasing population). These values were chosen in the light of the two-site analysis and of previous studies of the same population. They are probably realistic for several cetacean studies (for example, Ramp et al 2010, Silva et al 2009, Verborgh et al 2009, 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 (Table S4).
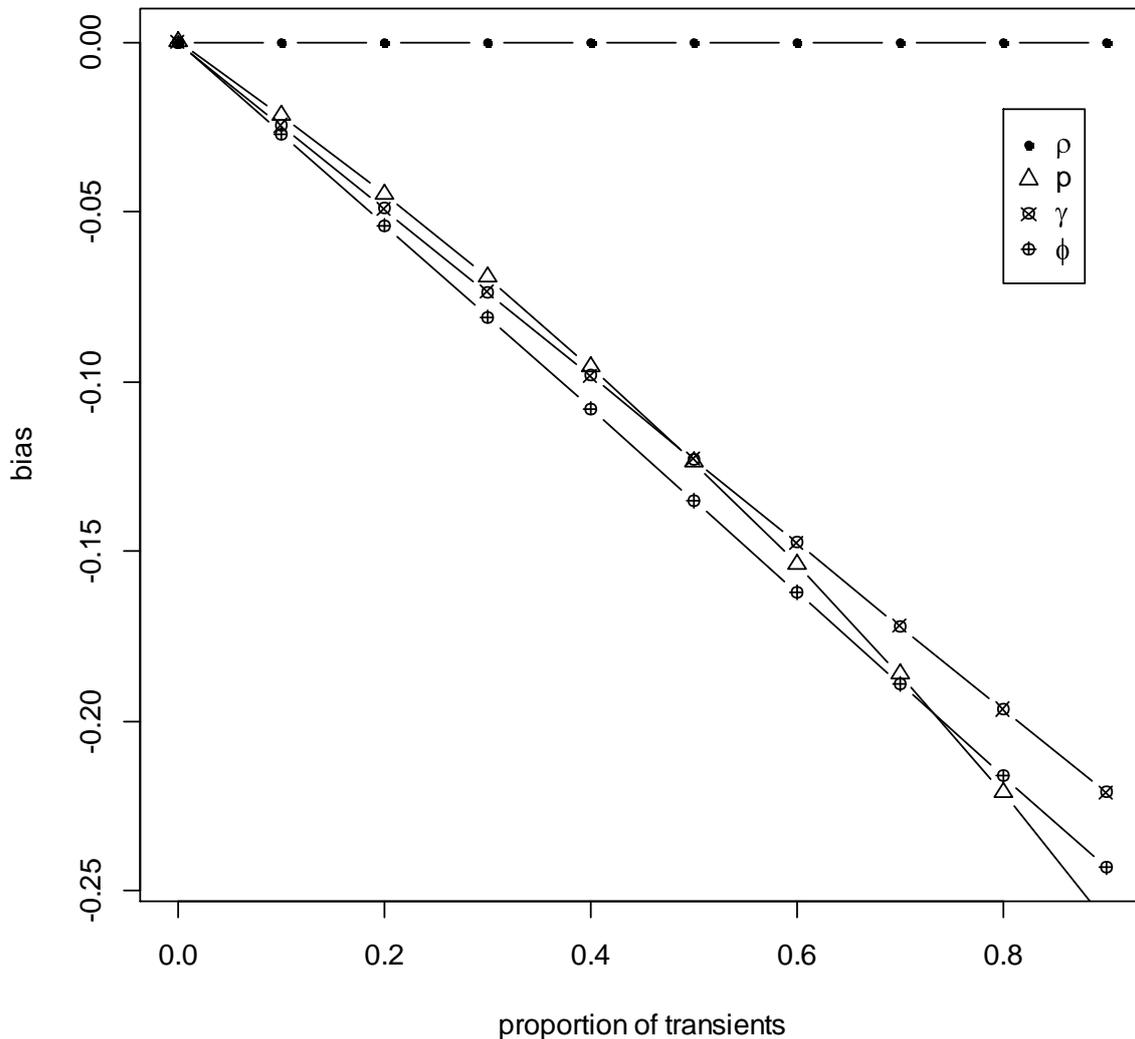
Fig. 1. *Absolute bias in population growth rate compared to that in other parameters using Pradel model (Y-axis) as a function of an increasing proportion of transients (X-axis)*

Effect of unequal sampling of the study area on the estimation of population growth rate

The simulated study area consisted of two unequally sampled zones. The detection probability was 30% and 10% for sites 1 and 2 respectively mimicking the situation of the study population; survival was set at 90%. Bias on $\hat{p}$ varied with the movement rates (Fig. 2) but remained always low (<0.02). The strongest biases were obtained for asymmetric exchanges, especially when movements were mainly directed towards the site with low detection.
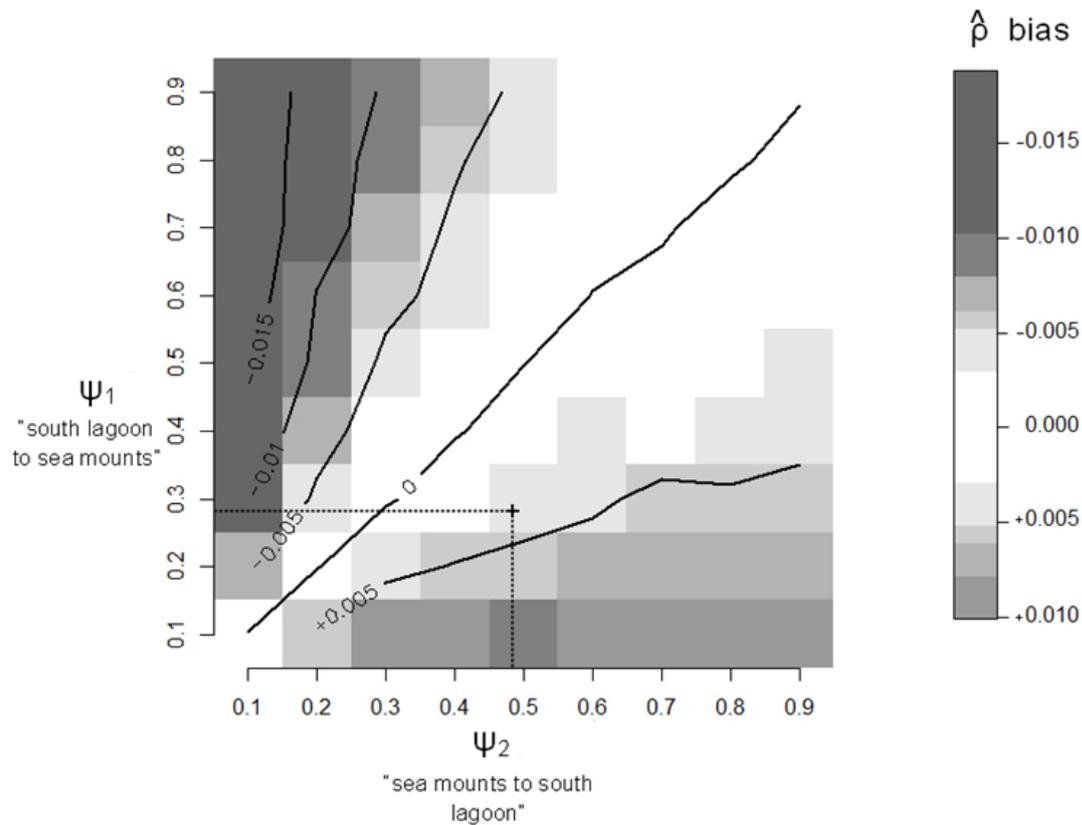
271
272   Fig. 2. *Absolute bias in growth rate estimation using the constant-parameter Pradel model*
273   *as a function of movement probabilities (ψ1 and ψ2) between the two sites (site1 and site 2*
274   *according have detection probability of 0.3 and 0.1 respectively). The darker the color, the*
275   *stronger the bias. The "white zone" illustrates a combination of values of ψ1 and ψ2 for which*
276   *the estimation of lambda is unbiased. The dot line and the cross indicate the New-*
277   *Caledonian humpback whale population case.*

278

279   **Estimation of the population growth rate of the New-Caledonia humpback whale**
280   **population**

281

282   As there are many exchanges of individuals between the two sites, it may be considered
283   that this is a single population. Therefore, the data used in the two-site analysis was modified
284   by recoding "L" and "S" as a single site. Also, females and males were not distinguished as
285   preliminary analyses did not find marked differences between them in any parameter. With
286   the recoded data set, an over-dispersion factor of 1.89 was estimated with program U-CARE
287   (Choquet et al. 2009) and was used to account for lack-of-fit. A series of Pradel models were
288   then fitted using program MARK and sorted by increasing QAICc (Table 1). Models varied on
289   whether the three types of parameters (survival, population growth rate, and detection
290   probability) were constant or time-dependent with all 8 possible combinations being
291   investigated.
292   The first model, with constant survival and PGR but variable detection probabilities over
293   the years was much better than any other (QAICc weight of 1). The estimated population
294   growth is 1.15 [1.11; 1.20] which corresponds to an increase of 15% per year. Given the
295   insensitivity of this estimator to the presence of transients, bias might only come from the
296   exchanges of individuals between the two zones that constitute the sampling area. Given the

detection probabilities estimated in the two-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), 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. A constant increase for this population > 10% seems thus ascertained.

Table 1. *Model selection results for Pradel's analysis of the population growth rate. Models are ordered according to the quasi Akaike Information Criterion (QAICc) value. ϕ indicates survival, p detection and ρ the PGR. The dot and t indicate constant and time effects respectively*

No	Model	QAICc	ΔQAICc	No par	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

DISCUSSION

Given the high amount of exchanges between the two habitats in the New-Caledonian humpback whale case study, we may reasonably consider that they belong to a unique population. At the two-habitat level, the identified violations of assumptions of the Pradel model for the estimation of the population growth rate have been found to have negligible impact in terms of bias. There might be other undetected violations of assumptions though. 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 have protected ourselves against undetected departures from assumptions. It can also be noted that 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) have detected a spurious trend over years and Pradel et al. (2010) have 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 rates

estimates are biased (see Fig.1). We have currently 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 of supplements).

Regarding movement between two 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 is close to a situation where the population concentrates in one site with poor monitoring: overall population size may not be changing, but its concentration in the "poor" zone makes it appears 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 appears to be thriving. When movements are symmetric, no bias is expected as all the individuals have on average an equal chance of being on 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 yet been fully treated recently (Pradel et al. 2010) and little bias seems to ensue anyway (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 population growth rate 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 parameters from life-history 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. 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 NC 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 had 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 population growth rate 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 to a stable population 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 (Garrigue et al. 2011b, Jackson et al. 2012, Olavarria et al. 2007). However, a certain degree of interconnectivity has been demonstrated with the cultural transmission of the song from the 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 farther grounds, which may correspond to the detected transients in recent and the present studies.

<div align="center">

<u>Conclusion</u>

</div>

This 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 little and sometimes not at all sensitive to frequent phenomenons 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.

<div align="center">

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