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Reproductive capacity of an endangered and recovering population of humpback whales in the Southern Hemisphere

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ABSTRACT: Estimating demographic parameters is essential to assessing the recovery potential of severely depleted populations of marine mammal species such as the baleen whales, which were decimated by commercial whaling of the past century. The Oceania humpback whale *Megaptera novaeangliae* population is classified as endangered by the IUCN because of low numbers and a slow recovery rate. Nevertheless, an anomalously strong increase has recently been detected in the New Caledonia breeding population. To determine the drivers of population growth, reproductive parameters were estimated for the first time for a humpback whale population of Oceania. Based on an extensive monitoring program (1995–2018), recapture histories were reconstructed for 607 females and incorporated in multi-event capture–recapture models. As the females' ages were generally unknown (87%), 2 models with contrasting age scenarios were investigated. For females of unknown age, the mature scenario assumed maturity at the first encounter, while the immature scenario assumed immaturity within 7 yr after the first encounter, unless the female was encountered breeding. These models respectively resulted in a calving interval of 1.49 yr (95% CI: 1.21–2.08) or 2.83 yr (95% CI: 2.28–3.56) and a calving rate of 0.67 or 0.35. The relatively high calving rate modelled by the mature model is consistent with high pregnancy rates recently observed in the migratory corridors of the Kermadec Islands and on the feeding grounds of the Antarctic Peninsula. Therefore, our results suggest that the recovery of the New Caledonia humpback whale population from past exploitation may be partially driven by an increased reproductive capacity.

KEY WORDS: Calving interval · Calving rate · Humpback whales · New Caledonia · Pacific population · Recovery · Sexual maturity

1. INTRODUCTION

In the context of biodiversity loss and decrease in natural populations (Barnosky et al. 2011, Pimm et al. 2014), understanding the recovery of a population following intense exploitation is an important issue in conservation. Baleen whale populations were heavily impacted by commercial whaling over the last century, with an estimated 2 million whales hunted (Clapham & Baker 2002). When commercial exploitation was officially brought to an end, humpback whale *Megaptera novaeangliae* populations were near extinction (Tønnessen & Johnsen 1982, Jackson et al. 2015), leading the IUCN to classify them as an endangered species worldwide in 1986. Since then, most of the populations have increased, and in 2008 the species' status was changed from Vulnerable to Least Concern, with the exception of the Arabic and Oceania populations that were changed to Endangered (Childerhouse et al. 2008, Minton et al. 2008).

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Long-lived mammal species, such as humpback whales, are characterized by low temporal fluctuation in survival rate (canalization theory, Gaillard & Yoccoz 2003), thus slowing down the resilience of populations following intense exploitation (Gaillard & Yoccoz 2003, Gamelon et al. 2014). Moreover, because of their large size, they theoretically invest more energy in survival than reproduction, leading to a low potential growth rate and a slow population recovery (Lebreton 2006). The average intrinsic growth rate of humpback whale populations has been estimated at between 7.3 and 8.6% yr^{-1}, with a maximum plausible rate of 11.8% yr^{-1} (Zerbini et al. 2010). This maximum growth rate was estimated primarily using reproductive parameters obtained for Northern Hemisphere populations (Clapham & Mayo 1987, Barlow & Clapham 1997). More recently, Wedekin et al. (2017) conducted a meta-analysis to explore the differences in worldwide growth rate and predicted a higher growth rate for Southern Hemisphere populations (12.2%) than for Northern Hemisphere ones (7.7%). The authors suggest that Southern Hemisphere humpback whales may display shorter inter-birth intervals and higher survival rates and possibly breed at a younger age when conditions are favourable. However, parameters such as calving rates have rarely been calculated for Southern Hemisphere populations (Rankin et al. 2014).

The potential recovery of an endangered population in the Southern Hemisphere — the humpback whale population of Oceania (including humpback whales wintering in the South Pacific islands from New Caledonia to French Polynesia; Childerhouse et al. 2008) — has recently been investigated through population dynamics analysis. Jackson et al. (2015) estimated a population growth rate of 8.2% yr^{-1} between 2010 and 2015 and suggested that the population size was at 47% of pre-exploitation levels in 2015. The humpback whale breeding sub-stock E2 (IWC 2005), which migrates annually from feeding areas in the Southern Ocean to breeding grounds in New Caledonia, belongs to this population (Constantine et al. 2012). Sub-stock E2 has recently been characterized by an anomalous increase in abundance and a high realized growth rate of 15% (Garrigue et al. 2012, Orgeret et al. 2014), well above the maximum plausible rate of 11.8% calculated by Zerbini et al. (2010). Although previous work has put forward immigration as a possible cause of the high growth rate (Orgeret et al. 2014), we suggest breeding capacity as an alternative hypothesis. Based on an extensive monitoring program conducted for more than 2 decades in New Caledonia, we provide the first estimation of reproductive parameters for a humpback whale population in Oceania.

2. MATERIALS AND METHODS

2.1. Data collection

Humpback whale surveys were conducted in the austral winter (July–September) between 1995 and 2018 in the breeding ground of New Caledonia, South Pacific (Garrigue et al. 2001). The survey effort was determined to maximize the chances of a whale encounter while accounting for common cetacean survey limitations: weather conditions, harbour proximity and vessel capacity (Derville et al. 2018). The search effort primarily focused on the coastal waters of the South Lagoon aboard a 6 m rigid-hulled inflatable boat. Surveys did not follow a systematic or explicitly randomized sampling technique but rather a haphazard sampling regime to maximize encounters with whales (Derville et al. 2019). Surveys were conducted in closing mode, as cetaceans were approached upon detection, and a focal follow was conducted at each group encounter. The presence or absence of a calf was recorded. Humpback whales were approached to photograph the underside of their fluke and to collect a skin sample (biopsy, Lambertsen 1987). Humpback whales were then individually identified by photo-identification (Katona & Whitehead 1981) and/or genotyping on 16 previously published micro-satellite loci (Garrigue et al. 2004, Olavarría et al. 2007, Baker et al. 2013). To identify the sex of each individual sampled, molecular sexing was performed by amplification of a male-specific SRY marker with a positive control ZFX/ZFY (Aasen & Medrano 1990, Gilson et al. 1998) as described in Garrigue et al. (2004).

Capture–recapture histories were then constructed for females that had been genetically identified at least once in their life. During each encounter, females' identity was validated via genotyping, photo-identification or a combination of the 2 methods. Based on the recapture histories, 2 breeding statuses were defined: a female observed with a calf was considered as a breeding female (B), and a female without a calf was considered a non-breeding female (NB). In addition, females were not necessarily genetically identified and genetically sexed upon their first encounter (in the case when females were only identified via photo-identification at the time). Including these encounters prior to the year of the first genotyping may bias survival estimates, but is useful to estimate breeding parameters. Hence, to estimate survival only after genotyping occurred, the first year of genotyping was also recorded in the capture–recapture history (see GI in Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m643p219_supp1.xlsx). To estimate survival only after genotyping occurred, female status at each encounter was assigned a code whether the female had been genotyped upon its first encounter (GI) or not (NG). Genetic identification is usually performed several times throughout a female's history of capture, but only the first one is referenced for the purpose of this study. In summary, for each breeding season included in this study, females could either be not encountered, encountered non-breeding and genetically identified (NB-GI), encountered breeding and genetically identified (B-GI), encountered non-breeding and not genetically identified (NB-NG) or encountered breeding and not genetically identified (B-NG, Table S1).

2.2. Multi-event model description

As a preliminary approach to understanding the data structure, we ran goodness of fit (GOF) tests designed for the conditional Arnason-Schwarz model (CAS, Pradel et al. 2003), where survival, breeding and detection probabilities are time specific, using the R2ucare package (Gimenez et al. 2018). The only detected departure from the assumptions of the CAS model is a high frequency of individuals observed only once (Test 3.GR, $p = 0.001$, see Pradel et al. 2005 for details of the test). This is usually interpreted as the presence of transient individuals in the sample, but may also result from the inadequacy of the CAS model to account for other differences among individuals (Genovart & Pradel 2019).

Reproductive parameters were calculated using E-SURGE software (Choquet et al. 2009) based on multi-event models (Pradel 2005). Two separate multi-event models were implemented to account for age to sexual maturity. Zerbini et al. (2010) and Rankin et al. (2014) reported humpback whale sexual maturity at 5.9 to 11 and 4.23 to 13.50 yr, respectively. Furthermore, in our dataset, females of known age (first encountered as calves, 13% of individuals) were at least 8 yr old when they were encountered with a breeding status ($n = 2$ females). Hence, all females of known age were considered mature 8 yr after their first encounter as calves. For other females, the true age was unknown, and sexual maturity was therefore introduced through 2 different scenarios which were analysed independently: one where females were considered as mature at the first encounter (SMa), and another where females were considered immature at the first encounter unless encountered breeding (SIm). In the latter scenario, maturity was acquired either 7 yr after their first encounter or at the first breeding event encountered within 7 yr after their first encounter.

A first initial state matrix was set up to define whether individuals were genetically identified and sexed or not at first encounter (C currently and L latter status in state matrix π, given in Supplement 2, www.int-res.com/articles/suppl/m643p219_supp2.pdf). A second matrix defined the known or presumed age of the individual at first encounter, depending on the scenario (SIm or SMa). The model included the proportion of breeders among the mature individuals observed for the first time (SMa scenario only), the survival probabilities (ϕ), the probabilities of transition between breeding statuses (ψ) and the detection probabilities (p), each described by a separate matrix (Supplement 2). Survival was estimated as constant over time, and related to 2 age classes: survival over the first year (calf survival), and survival over the rest of the whales' lives (juvenile and adult survival). Transition probabilities were also considered constant within each breeding status, to obtain a mean reproductive capacity in the population. Detection probability and initial state were tested as either constant or fluctuating over time, the former additionally depending on breeding status. Finally, we also considered the possibility that there were transient females, by estimating a separate survival probability for newly encountered individuals (effect [c] on survival). We tested several model parameterizations and selected the most parsimonious combination using Akaike's information criterion (Burnham & Anderson 2002).

2.3. Reproductive parameters

Multi-event models allowed the estimation of distinct breeding probabilities p following a breeding episode:

$$\mathrm{p}(\mathrm{breeding}_t|\mathrm{breeding}_{t-1}) = \mathrm{p}(B|B) \quad (1)$$

and not following a breeding episode:

$$\mathrm{p}(\mathrm{breeding}_t|\mathrm{not\ breeding}_{t-1}) = \mathrm{p}(B|NB) \quad (2)$$

These 2 conditional probabilities allowed the calculation of the probability γ_t, that 2 calving events were separated by a time interval t:

$$\gamma_1 = \mathrm{p}(B|B) \quad (3)$$

$$\gamma_2 = \mathrm{p}(B|B) \times \mathrm{p}(B|NB) \quad (4)$$

$$\gamma_3 = \mathrm{p}(NB|B) \times \mathrm{p}(NB|NB) \times \mathrm{p}(B|NB) \quad (5)$$

The maximum interval considered was 10 yr, as it was the longest calving interval observed in the

Table 1. Summary relating the number of parameters and evaluation metrics for the 4 best multi-event models under 2 different scenarios applied to 607 female humpback whales encountered in New Caledonia between 1995 and 2018. The 2 **bold** models are the ones selected. Multi-event models were based on an initial matrix π, survival parameters ϕ, transition probabilities ψ and detection probabilities p. Parameters could be constant (.), fluctuate in time (t), vary by breeding status only (b), be related to age (a) and be the first genetic identification (g). The initial matrix could account for sexual maturity following the 2 extreme scenarios, SMa and SIm. With the exception of individuals of known age, the immature scenario (SIm) considered all females as immature within 7 yr after their first encounter (the model was also tested with a maturity of 5 yr) unless encountered breeding before then, and the second scenario (SMa) considered all females as mature at the first encounter. These models tested the impact of considering age at maturity and model structure. Akaike's information criterion (AIC), the difference of AIC across models (ΔAIC), AIC weight and deviance are reported

Model	Age class	Age at maturity	Parameters (n)	Deviance	AIC	ΔAIC	AIC weight
SIm model							
$\boldsymbol{\pi(\mathrm{SIm}.g).\phi(.).\psi(a.b).p(b)}$	2	7	8	2051.7	2065.77	0	$9.7e^{-1}$
$\pi(\mathrm{SIm}.g.t).\phi(.).\psi(a.b).p(b)$	2	7	31	2011.41	2073.41	7.7	$2.0e^{-2}$
$\pi(\mathrm{SIm}.g.t).\phi(.).\psi(a.b).p(b)$	2	5	31	2316.3	2352.1	286	$6.3e^{-63}$
$\pi(\mathrm{SIm}.g).\phi(.).\psi(a.b).p(b)$	2	5	8	2344.6	2362.6	296.9	$3.3e^{-65}$
SMa model							
$\boldsymbol{\pi(\mathrm{SMa}.g).\phi(.).\psi(a.b).p(b)}$	2	7	8	2776.64	2792.6	0	$8.5e^{-1}$
$\pi(\mathrm{SMa}.g).\phi(.).\psi(a.b).p(b)$	2	5	8	2780.1	2796.1	3.5	$1.4e^{-1}$
$\pi(\mathrm{SMa}.g.t).\phi(.).\psi(a.b).p(b)$	2	7	31	2746.21	2808.2	15.6	$3.4e^{-4}$
$\pi(\mathrm{SMa}.g.t).\phi(.).\psi(a.b).p(b)$	2	5	31	2749.6	2811.6	19.0	$6.3e^{-5}$

Table 2. Values (±SE) of the reproductive and population parameters estimated for 2 scenarios in a multi-event model calculated on 607 female humpback whales encountered in New Caledonia between 1995 and 2018. With the exception of individuals of known age, the immature scenario (SIm) considers all females as immature within 7 yr after their first encounter unless encountered breeding before then, and the second scenario (SMa) considers all females as mature at the first encounter. Four different parameters are reported for each class: probability of breeding during 2 consecutive years p(B|B), probability of breeding the first year and not breeding the second year p(B|NB), the calving interval (yr) estimated from the best multi-event model and the calving rate (inverse value of the calving interval)

Parameter	Immature scenario (SIm)	Mature scenario (SMa)
Survival 1 yr	0.50 ± 0.14	0.33 ± 0.10
Survival >1 yr	0.87 ± 0.01	0.90 ± 0.01
Detection NB	0.06 ± 0.01	0.11 ± 0.02
Detection B	0.28 ± 0.04	0.06 ± 0.01
p(B|B)	0.01 ± 0.01	0.82 ± 0.04
p(B|NB)	0.54 ± 0.07	0.36 ± 0.07
Calving interval (yr)	2.83 (95% CI: 2.28–3.56)	1.49 (95% CI: 1.21–2.08)
Calving rate	0.35	0.67

dataset. The mean calving interval was then calculated based on the different probabilities as:

$$\sum_{t=1}^{10} t\gamma_t \qquad (6)$$

The calving rate was calculated as the inverse of the calving interval, to represent the annual proportion of females that breed (Civil et al. 2017).

3. RESULTS

A total of 607 females were individually genotyped, representing 39% of the total number of humpback whales genetically identified in New Caledonia (sex ratio: 1.5:1 [M:F]). Among these females, 26% (n = 156) were observed at least once with a breeding status, and 13% (n = 78) were first observed as calves. A total of 859 encounters were made, including 221 encounters where a calf accompanied a female. Breeding in consecutive years was observed in only 1 case.

Only the 4 best models are presented for each scenario (Table 1). Although the GOF test had detected a signal of transience, the best-supported multi-event model did not retain transience (in bold in Table 1). It included constant survival on 2 different age classes. It also included detection and transition probabilities depending on the breeding status (breeder or non-breeder) and age at maturity (see Supplement 2). The SIm model had a lower deviance than the SMa model (2051.7 and 2776.64, respectively, Table 1).

In both the SIm and the SMa models, survival was considerably lower for the first year as a calf (respectively 0.50 ± 0.14 and 0.33 ± 0.10, Table 2), compared to subsequent years (0.87 ± 0.01 and 0.90 ± 0.01). The probability of detection differed between the 2 breeding statuses in the SIm model (NB detection 0.06 ± 0.01 vs. B detection 0.28 ± 0.04) but not as much in the SMa model (NB detection 0.11 ± 0.02 vs. B detection 0.06 ± 0.01).

Finally, the SMa model showed a probability to breed in consecutive years of 0.82 and a probability to breed the second year if non-breeding the first year of 0.36. As a result, the calving interval in this mature scenario averaged 1.49 yr (95% CI: 1.21–2.08), and the calving rate was estimated at 0.67 (Table 2). On the other hand, the SIm model showed a probability to breed in consecutive years of 0.01 and a probability to breed the second year if non-breeding the first year of 0.54. Hence, the calving interval in this immature scenario averaged 2.83 yr (95% CI: 2.28–3.56), and the calving rate was estimated at 0.35 (Table 2).

4. DISCUSSION

In this study, we used a 24 yr recapture dataset where age was unknown to estimate female reproductive parameters and survival for the endangered humpback whale population of New Caledonia, while accounting for the impact of age at sexual maturity. This study provides the first estimates of calving rates for a humpback whale population breeding in Oceania.

4.1. Detection of females on breeding grounds

Although the GOF test detected a signal, which could be due to transience, transience was not retained in the final multi-event model. The transience signal detected by the GOF test reflects a lower probability of reencountering newly captured females. Here, such signal is likely to be due to age (Genovart & Pradel 2019). Indeed, younger females have lower survival (Table 2) and may therefore die before being recaptured. True transience (i.e. individuals transiting through but not belonging to the study population, Genovart & Pradel 2019) may not occur in New Caledonia. Indeed, interchange levels across neighbouring populations and breeding grounds of the South Pacific are marginal in comparison to breeding site fidelity (Garrigue et al. 2002, 2011, Olavarría et al. 2007). Although recent genetic analyses have highlighted potential exchanges between New Caledonia and the east Australian migratory corridor (Valsecchi et al. 2010, Steel et al. 2018), the genetic differentiation of females of both subpopulations is significant (Bonneville et al. 2017). The probability for a female of the New Caledonian subpopulation to occasionally give birth outside these waters is therefore expected to be low.

The transience effect detected by the GOF could also result from a lack of detection of whales otherwise present in the New Caledonian study region, which covers multiple breeding aggregations, some of them recently discovered. Given the heterogeneous levels of survey effort across years and especially across breeding aggregations (Derville et al. 2018), it is possible that some individuals favouring certain breeding aggregations over others (Garrigue et al. 2017) may have different detectability.

Alternatively, it is possible that newly captured females are not reencountered in New Caledonia, because they did not migrate and overwintered in their feeding grounds in some years. Indeed, based on the sex ratio measured over the east Australian migratory corridor (2.4:1 [M:F]) and in whaling catches, Brown et al. (1995) suggested that about half of the females in Antarctic area V did not migrate each year. Nevertheless, the sex ratio measured in New Caledonia over our study period (1.5:1 [M:F]) suggests a lower sex bias, indicating a potentially smaller proportion of non-migrant females.

Finally, in the SIm model, breeding females had a higher detection probability (0.28 ± 0.04) than non-breeding females (0.06 ± 0.01). This is easily explained, as breeding females tend to stay longer in breeding grounds (Chittleborough 1965, Dawbin 1966), hence increasing their probability to be observed within a given season.

4.2. Survival of females

The survival of females >1 yr old between 0.87 and 0.90 estimated by our models is slightly lower than the survival of the entire population, estimated at 0.94 (Orgeret et al. 2014). It is also lower than the survival estimated for females from various populations of the Northern and Southern hemispheres (Table 3, Barlow & Clapham 1997, Rosenbaum et al. 2002, Ramp et al. 2010, Rankin et al. 2014), even if some annual survivals as low as 0.566 (CI: 0.418–0.733) have been measured in the Gulf of Maine, North Atlantic (Rosenbaum et al. 2002). These low survival values could be explained in part by the presence of juveniles in our dataset, whose survival is expected to be lower than that of mature individuals (Caughley 1966). Moreover, survival is likely to increase progressively after sexual maturity, as older females might be able to withstand higher energetic expenses for calving, nursing and lactation because of their larger size (Robbins 2007). Finally, early breeding in a female's life may affect its survival, as energy is allocated to reproduction rather than growth.

The survival of calves estimated by the SIm and SMa models was also lower than the estimates made in other populations of humpback whales around the

Table 3. Humpback whale reference values of survival rates estimated across the globe

Age	Hemisphere	Region	Survival rate	Reference
<1 yr	Northern	Gulf of Maine, USA	0.875 (SE: 0.047)	Barlow & Clapham (1997)
		Gulf of Maine, USA	0.664 (CI: 0.517–0.784)	Robbins (2007)
		Gulf of Maine, USA	0.702	Rosenbaum et al. (2002)
		Hawaii and Alaska, USA	0.482–0.759	Gabriele et al. (2001)
>1 yr (females only)	Northern	St Lawrence, Canada	0.992 (CI: 0.985–0.999)	Ramp et al. (2010)
		Gulf of Maine, USA	0.96 (SE: 0.008)	Barlow & Clapham (1997)
		Gulf of Maine, USA	0.964 (CI: 0.946–0.976)	Rosenbaum et al. (2002)
	Southern	Hervey Bay, Australia	0.98 (CI: 0.96–0.99)	Rankin et al. (2014)

world (Baker et al. 1987, Clapham & Mayo 1987, Barlow & Clapham 1997, Craig & Herman 2000). However, it must be noted that our values are not directly comparable to those available in the literature, as they were estimated (1) in a breeding area and (2) for female calves only. Hence, the differences observed could be caused by higher mortality of female calves compared to males or by higher mortality over the first calf's migration from breeding to feeding grounds. Moreover, survival of calves has been shown to vary greatly from one year to another (Rosenbaum et al. 2002), with exceptionally low survival estimated in some years (e.g. 0.142 [CI: 0.022–0.550] in 1994–1995 in the Gulf of Maine, Rosenbaum et al. 2002).

4.3. Calving interval

In the absence of information on the exact age of females, we estimated the mean calving interval for 2 different sexual maturity scenarios, which we analysed separately. In essence, neither of these 2 sexual maturity scenarios is an exact reflection of the reality, as the real proportion of immature females in the population remains unknown. The reality lies in-between the 2 scenarios, as do the resulting estimates of the females' reproductive parameters.

While they were applied to the same recapture dataset, the SIm model had a lower deviance than the SMa, hence indicating a better fit. In addition, the SIm model may be considered more conservative, as it estimated reproductive parameters using only the parts of recapture histories during which females were mature without doubt. The values issued from SIm (calving interval at 2.83 yr [95% CI: 2.28–3.56] and calving rate at 0.36) are in agreement with the estimates from the Northern Hemisphere (2.38 yr in the Gulf of Maine, Barlow & Clapham 1997) and the Southern Hemisphere (2.78 yr in Australia, Rankin et al. 2014). The resulting calving rate estimated in southeastern Alaska (0.37, Baker et al. 1987) is also consistent with the SIm model's output. However, the comparison between populations originating from the 2 hemispheres must be considered with caution, as Wedekin et al. (2017) showed significant geographic differences in growth rate, especially between the Southern (12.21%) and Northern (7.74%) hemisphere populations. These differences were attributed to spatial variability in productivity and prey availability (Brodie 1975, Murphy et al. 2007). The only other Southern Hemisphere study currently comparable to our results was conducted on the east coast of Australia using a multi-event model and yielded a calving interval of 2.78 yr (95% CI: 2.23–3.68, Rankin et al. 2014).

Alternatively, the SMa model showed an unusually small calving interval of 1.49 yr (95% CI: 1.21–2.08), and the calving rate was estimated at 0.67. This high reproductive capacity suggests a relatively high probability for females to breed in consecutive years. Post-partum ovulation and calving in consecutive years is thought to be rare (Chittleborough 1965), and it was observed only once in our recapture dataset. Nevertheless, a high calving rate in New Caledonia would be in accordance with several recent studies investigating pregnancy rates based on progesterone concentrations in the South Pacific and Southern Ocean (Pallin et al. 2018, Riekkola et al. 2018). Riekkola et al. (2018) estimated that 56.7% of females were pregnant at Raoul Island (Kermadec, New Zealand), an island considered to be part of the southward migratory corridor of the New Caledonian humpback whale population (Garrigue et al. 2016, Riekkola et al. 2018). This value is close to our estimated calving rate of 67%. Pallin et al. (2018) found a pregnancy rate of up to 86% in the Antarctic peninsula, a feeding ground known for its proximity to the

Bellinghausen Sea, where humpback whales of Oceania have been followed with satellite tracking (Garrigue et al. 2018, Riekkola et al. 2018). These results converge towards the hypothesis that the South Pacific populations of humpback whales may be characterized by a high reproductive capacity, which could explain the higher growth rates observed in the Southern Hemisphere.

4.4. High reproductive capacity in the South Pacific

Several hypotheses can be brought forward to explain why humpback whales of the Southern Hemisphere may presently have higher reproductive capacities. First, calving rates may be related to the age structure of a population, as the reproductive capacity of mammals is known to often be related to the age of individuals (Clutton-Brock 1984). Riekkola et al. (2018) investigated the age structure of the humpback whales sampled in Raoul Island, revealing the rarity of individuals more than 30 yr old and an average age of 13.8 yr. Females from this age class sampled in 2015 in Raoul Island would have been born around 2001. Therefore, they would have reached sexual maturity about 8 yr later, around 2009, and could have contributed to the increase in abundance recently measured in New Caledonia (Garrigue et al. 2012). We can hypothesize that younger and more fertile females are more abundant today in the humpback whale populations of Oceania. On average, these young females would therefore have more calves than the older generations that have survived the industrial whaling era. Epigenetic aging of humpback whales (Polanowski et al. 2014) would be of great interest to relate age and reproductive capacity at individual and population levels.

Second, a high reproductive capacity could also be caused by an evolution of the reproductive parameters at the individual level (Conover et al. 2009). The anthropogenic pressure caused by commercial whaling may have led to a modification of breeding parameters in large whales (i.e. age at maturity or birth interval). For instance, Kato (1995) highlighted an increase in the reproductive capacity of Antarctic minke whales *Balaenoptera bonaerensis* following commercial whaling and suggested that this phenomenon was linked to reduced competition with other baleen whales for food resources. As a second hypothesis, the birth interval observed in New Caledonia could therefore be a sign of phenotypic plasticity or early evolution of reproductive capacity (Kato 1995). This hypothesis may only be addressed through long-term individual monitoring of females with calves using genetic and photographic capture–recapture.

Finally, a high reproductive capacity in Oceania could be due to food availability in the Southern Ocean. Indeed, in capital breeding populations (which accumulate resources before producing offspring at a later time, Sainmont et al. 2014), the quantity of food accumulated during the feeding season influences the breeding capacity during the next breeding season (e.g. Southern right whale *Eubalaena australis*, Leaper et al. 2006). Studies have highlighted that female humpback whales that have access to food in larger quantities and of better quality were more likely to produce healthy calves (Robbins 2007) and to have more post-partum ovulations (Chittleborough 1958, Dolphin 1985). As a third hypothesis, higher reproductive capacities in the Southern Hemisphere, and particularly in Oceania, could be supported by enhanced food resources compared to those of the Northern Hemisphere feeding grounds (Pallin et al. 2018). Studying historical and contemporaneous prey availability in Southern and Northern hemisphere feeding grounds would contribute to answering this question.

5. CONCLUSIONS

This study provides the first estimate of reproductive parameters for the New Caledonian part of the Endangered Oceania population of humpback whales and revealed calving intervals between 2.83 and 1.49 yr. These potentially short calving intervals corroborate differences highlighted by Wedekin et al. (2017) between the Northern and Southern hemisphere humpback whales, and could have contributed to the growth rate observed in New Caledonia following the ban on commercial whaling. Three non-exclusive hypotheses are proposed to explain potentially high reproductive capacities in Oceania humpback whales: age structure, phenotypic plasticity and prey availability. This study contributes to a global understanding of the dynamics of recovery for a cosmopolitan species following intense exploitation.

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LITERATURE CITED

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