

Running fast in the slow lane: rapid population growth of humpback whales after exploitation

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ABSTRACT: Humpback whales were hunted almost to extinction in the 20th century, providing an opportunity to measure their post-exploitation population growth rates. Variation in growth rates may be related to many factors, and little work has been done to understand the differences among populations. First, we provided an estimate of the growth rate for the Brazilian breeding stock of humpback whales using models that consider imperfect detection applied to a long-term and broad-scale dataset collected through systematic aerial surveys. Then, a review of the literature on the population growth rates of this species worldwide and a meta-analysis were conducted to explore the differences in growth rates and their determinants. A finite growth rate of 12% yr⁻¹ (95% CI = 8–16%; CV = 17%) for the population wintering in Brazil was estimated from aerial surveys conducted from 2002 to 2011 and may be regarded as an empirical estimate of its intrinsic growth rate. The meta-analysis shows that there are geographical differences in growth rates, with substantial heterogeneity among studies. Growth rates of populations in the Northern Hemisphere are predicted to be lower than those in the Southern Hemisphere. The geographical differences in population parameters may be explained by spatial variability in productivity and prey availability, human impact and distinct hunting histories. Moreover, the differences in population growth rates are linked to genetic variability, with populations with higher haplotype diversity growing at faster rates. Long-term studies on dynamics of baleen whale populations reduced by whaling are invaluable to investigate the population growth and regulation of these cetaceans.

KEY WORDS: *Megaptera novaeangliae* · Population dynamics · Population growth rate · Exponential growth · Distance sampling · Meta-analysis

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INTRODUCTION

The exponential growth of populations when there are enough resources and the environment remains unchanged is one of the oldest and more pervasive

concepts of ecology (Turchin 2003, Kolasa 2011). Although the instantaneous growth rate parameter (r) has different meanings according to the subdisciplines of ecology (Fagan et al. 2010), it measures the per capita population growth rate during an infini-

tesimally small period of time. The growth rate is a 'unifying variable linking the various facets of population ecology' (Sibly & Hone 2002). Ultimately, the population growth rate is linked to the fate of populations and is vital for a variety of models with different purposes in ecology (e.g. Morris & Doak 2002).

Most populations have a growth rate that fluctuates around a mean of zero (Fryxell et al. 2014). Thus, opportunities for estimating the maximum rate of population growth or the intrinsic growth rate (r_{\max}) in the wild are rare. Such opportunities arise when populations are reduced well below their carrying capacity or when a species is introduced to an environment with abundant resources and no natural enemies, such as islands (Hone et al. 2010). Due to this limitation, a common alternative to obtaining the intrinsic growth rate is to use population models that require other parameters that are easier to obtain, such as body mass and the age of females at first reproduction (Caughley & Krebs 1983, Hone et al. 2010). When applied to cetaceans, such models have shown great variation in life histories (Taylor et al. 2007), which is most likely linked to the great variation in body sizes within the group. At one extreme, many species live in the 'fast lane' (see Read & Hohn 1995), which includes groups such as small porpoises, some delphinids and river dolphins, which mature relatively early and have rapid reproduction. At the other extreme of life history variation within cetaceans are the baleen whales, the largest animals that have ever lived on Earth, with slow reproduction, a longer lifespan and later maturity. Accordingly, the intrinsic rate of population growth tends to decrease with larger body sizes (Caughley & Krebs 1983).

Commercial whaling targeted the largest species, with more than 2 million whales from at least 8 species being severely hunted and many populations being depleted almost to extinction (Clapham & Baker 2009). Whaling in the 20th century was the greatest wildlife exploitation event in human history (Clapham et al. 2008). The decline in the whaling industry and the worldwide embargo issued by the International Whaling Commission (IWC) in 1966 allowed many populations to recover and provided a unique opportunity to measure their post-exploitation population growth rates (Best 1993). Despite its associated controversy, commercial whaling in the first half of the past century may be regarded as a huge ecological uncontrolled 'experiment' (Laws 1977, Witting 2013). Of course, this large-scale human intervention cannot be called an experiment in the strictest statistical sense, but it surely offers the chance to better understand the dynamics of the

Southern Ocean ecosystem. The removal of whales, for example, may have resulted in a surplus of prey and an increase in the abundance of other krill consumers, such as penguins and seals (Laws 1977).

In the present study, we focus on the post-exploitation growth rate of humpback whales *Megaptera novaeangliae*. There is a consensus among researchers that most or all populations of this species of the marine megafauna have been growing worldwide (e.g. Zerbini et al. 2010). Although many studies on the population growth rates of humpback whales exist, with much variability in the growth rates observed among them, the possible causes of such differences have been poorly investigated. First, we used a long-term dataset from this recovery period to study the dynamics of the humpback whale population that winters in Brazil. Our first question was: What is the growth rate for this humpback whale population? The instantaneous rate of population growth was estimated for this population using statistical methods that account for imperfect detection (King 2014). The second question was: How do the growth rates vary among populations and what variables may explain such variation? To answer this, available estimates on the annual growth rate of different populations of this species around the globe were reviewed and explored using a meta-analysis approach (Côté & Jennions 2013).

MATERIALS AND METHODS

Humpback whale populations

Humpback whales typically migrate between summer feeding grounds at high latitudes, and winter breeding and calving sites in the tropical seas of both hemispheres (Kellogg 1929). Fidelity to distinct breeding and feeding grounds promotes the worldwide population structure, and the subpopulations are considered to be independent demographic units (Baker et al. 1993). There is limited genetic exchange between ocean basins, leading to the definition of 3 populations or subspecies (Baker et al. 1993, Jackson et al. 2014): North Atlantic, North Pacific and Southern Hemisphere. Furthermore, 7 breeding stocks are recognized in the Southern Hemisphere (IWC 2011); whales from these stocks are known to be genetically differentiated (Olavarria et al. 2007, Rosenbaum et al. 2009). Additionally, a non-migratory population is found in the Arabian Sea (Mikhalev 1997). Whales wintering off Brazil congregate in shallow and warm habitats on the continental shelf (Andriolo et al. 2010) and correspond to breeding stock A (IWC 2011).

Aerial surveys

Aerial surveys covered the main area of concentration of humpback whales on the Brazilian coast (from 12° 10' to 20° 42' S) during 7 breeding seasons, from 2001 to 2005 and 2008 and 2011 (for more details see Andriolo et al. 2006, 2010). The sampling was stratified into 5 geographical regions that had differences in whale density, including waters from the coastline to the 500 m isobath (Supplement 1 in the supplementary material at www.int-res.com/articles/suppl/m575p195_supp.pdf). The surveys were conducted during the peak of the breeding season, from mid-August to mid-September. The study area was flown systematically from north to south.

The first aerial survey of our time series (2001) was excluded from the estimation of the population growth rate to minimize a possible bias in terms of the increased efficiency of the observers over time, which could have caused an overestimation of the growth rate. The aerial surveys employed a 2-engine high-wing aircraft ('Aerocommander') equipped with bubble windows. The survey altitude was 152.4 m, except in 2008, when the survey altitude was 304.8 m. Whenever a group of whales was detected, the declination angle was measured with a hand-held clinometer to estimate the perpendicular distance. Observers recorded groups of whales at unlimited distance from the transect lines.

Distance sampling analyses

Density and abundance were estimated using multiple covariate distance sampling (Marques & Buckland 2003, 2004). A key feature of this method is fitting a detection function to the data, which describes how different covariates affect the rate at which the probability of detecting a group decreases with distance. Hazard-rate and half-normal parametric functions were considered as detection functions because of their desirable properties and shapes (Buckland et al. 2001). Additional adjustment terms (cosine, simple polynomial or Hermite polynomial) were also considered to improve model fitting when necessary. The covariates were included in the detection function through a scale term (Marques & Buckland 2003).

For the estimation of density and abundance, year-specific detection functions were fitted to the data (Supplement 2). The year-specific detection functions were estimated to account for interannual differences in survey altitudes, teams of observers and environmental conditions. The following covariates

were considered each year: individual observer, sun glare (%), cloud cover (%), sea state on the Beaufort scale (as a factor or numerical), sighting conditions (poor, regular, good or excellent), cluster size, sighting cue (body, aerial behavior or blow) and geographical region.

The stepwise approach was used to build detection probability models for the distance data considering different covariates (Marques & Buckland 2003; see details in our Supplement 3). Model selection considered Akaike's information criterion differences (ΔAIC), which represents the difference between the AIC of the best model ($\Delta AIC = 0$) and the AIC of the model being considered (Burnham & Anderson 2002). Models with $\Delta AIC < 2$ have a substantial level of empirical support and were considered for inference (Burnham & Anderson 2002).

Global density estimates were calculated as the mean density of each stratum weighted by the stratum area. A global detection function (as opposed to a region-specific one) was fitted to the data for each year, and maximum likelihood estimates (MLE) were obtained using the software Distance, version 6.2 (Thomas et al. 2010). Abundance was calculated through a Horvitz-Thompson-like estimator (Borchers & Burnham 2004, Marques & Buckland 2004). Whales were detected in clusters, and total abundance was estimated as number of groups multiplied by mean cluster size within the program Distance.

The annual finite population growth rate (λ) and the instantaneous growth rate (r) were derived from a continuous exponential growth model fitted to the abundance estimates. The instantaneous growth rate (r) corresponds to the slope (β_1) of a linear regression model with the abundance estimates transformed by the natural logarithm: $\ln(\hat{N}) = \beta_0 + \beta_1 \times (\text{year})$, where \hat{N} is the abundance estimate and β_0 is the intercept of the model. This log-linear model is equivalent to the density-independent exponential population dynamics model ($N_t = N_0 e^{rt}$, where N_t is the abundance in time t , N_0 is the abundance in time zero or initial abundance, r is the intrinsic population growth rate and e is the Euler's number, the base of the natural logarithm) and is therefore adequate to estimate the instantaneous population growth rate. Weighted linear regression was used to account for the variable precision through the coefficient of variation (CV) of the abundance estimates (weight = $1 / CV(N_t)^2$). The relationship between the finite growth rate and the instantaneous growth rate was given by $\lambda = e^r$. We will refer to λ simply as the 'population growth rate' throughout the article. The growth rate may also be referred to as 'rate of increase' in the literature.

Meta-analysis

Peer-reviewed articles and unpublished technical documents reporting the growth rates of humpback whales were scanned from the literature (see Supplement 5). We chose an arbitrary cutoff precision level for the parameter estimates and eliminated growth rates with CVs that were higher than 30% from the analysis. Studies that did not include any information on the precision of estimates were also excluded from the analysis (see Supplement 5 for details).

The standard error (SE) was used as a measure of precision for the studies considered here. Because many of these studies only reported the CIs of the parameter estimates as error measures, we calculated an approximate normal standard error estimate using the 95% CIs with the following equation: $SE = (\text{upper CI} - \text{lower CI}) / 3.92$. The validity of this approach was confirmed by comparing the SE computed from the 95% CIs with the estimated SE from studies for which both SE and 95% CIs were available.

A meta-regression was then used to investigate the causes of variation in the estimates of the annual population growth rates reported in the literature (Chen & Peace 2013) using the R package 'metafor' (Viechtbauer 2010). Meta-regression is similar to a multiple regression approach, where it is possible to assess whether one or more explanatory variables have an influence on the size of the effect of different studies. Using random effects models, it was possible to consider the variation within and between studies (heterogeneity) and the contribution of the covariates in explaining the heterogeneity found in the dataset. The SEs were used as weights in the meta-regression model.

The following covariates were considered separately in the model selection procedure (for more details and rationale see Supplement 6): (1) length of the study in years; (2) study method (capture–recapture, naïve count-based or count-based with distance sampling); (3) study platform (airplane, vessel or shore-based); (4) hemisphere; (5) ocean; (6) breeding stock; (7) time lag from the year when 90% of the whales were captured; (8) time length in years that the population was hunted; (9) total whales captured by whaling activities; (10) haplotype diversity.

A set of models was considered as plausible hypotheses explain-

ing the variability found in the dataset, and model selection was carried out using AIC. The total amount of heterogeneity accounted for by the explanatory variables (heterogeneity explained) included in each model was also calculated as a rough measure of the explanatory power of the model. The heterogeneity explained (pseudo- R^2 statistic) by each model was calculated from the τ^2 index (=the variance of the true effect sizes as seen in the random-effects model) (Raudenbush 2009), which may be regarded as a measure of among-study variance (Chen & Peace 2013).

RESULTS

Trends in abundance from aerial surveys

In total, 1638 groups of humpback whales over a distance of more than 21 000 km were observed during the aerial surveys conducted from 2002 to 2011 (Table 1). While the mean group size varied slightly among years, the sighting rates increased steadily over the years.

The half-normal function with no adjustment terms was selected by AIC for all of the years as the most supported detection probability model and generally had fewer problems with convergence than the hazard-rate function. The covariates that influenced the shape of the detection function varied among years. Cue was the most common covariate affecting the detection probability, with aerial behaviors and blows being detected at greater distances than the bodies of whales either near the surface or submerged. In some years, the different observers also had an effect on the detection function. Finally, sea conditions (as measured by the Beaufort scale) had an influence on detection in 2004.

Table 1. Effort and sightings of humpback whales during aerial surveys from 2002 to 2011

Year	Line transects	Effort (km)	Groups detected	Mean group size	Group size (% CV)	Sighting rate (groups km ⁻¹)	Sighting rate (% CV)
2002	76	3730.9	178	1.53	3.45	0.015	68.68
2003	76	3928.4	207	1.79	3.79	0.053	10.65
2004	77	4011.2	267	1.57	3.00	0.067	9.09
2005	77	4004.1	304	1.61	3.22	0.076	8.23
2008	42	2373.7	268	1.58	3.59	0.113	12.19
2011	54	3122.4	414	1.54	2.50	0.246	9.16
TOTAL	402	21170.7	1638	–	–	–	–

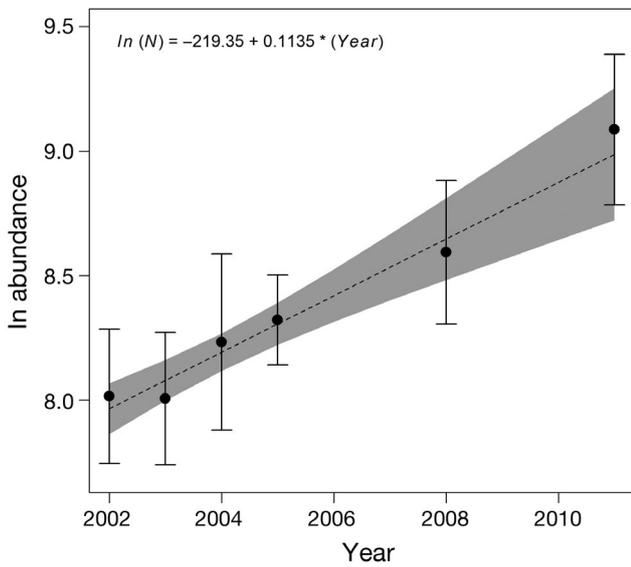


Fig. 1. Abundance estimates (natural log scale) from aerial surveys for humpback whales on the Brazilian coast from 2002 to 2011. The log-linear regression fit to the data is indicated by the black dashed line (gray area corresponds to the 95% confidence bands). Error bars are SE

Except for the first 2 years (2002 and 2003), which had similar abundance estimates, the uncorrected abundance estimates for the humpback whales on the Brazilian coast increased monotonically from 2003 to 2011. The precision of the uncorrected estimates was reasonably high, with the CV ranging from 9 to 18% (Table 2). The linear regression model with the log-transformed abundance estimates from 2002 to 2011 yielded an instantaneous growth rate (r)

Table 2. Uncorrected abundance estimates for the humpback whale population from 2002 to 2011, and covariates included in the best model of detection. Truncation refers to elimination of data on shortest or longest distances from the transect line to improve fit. N = uncorrected abundance estimate; p = probability of group detection

Year	Covariates	Truncation (m)	N	N (% CV)	p	p (% CV)
2002	Observer (obs)	>2500	3026	13.2	0.44	7.0
2003	Cue	>2500	2999	13.1	0.52	5.0
2004	Beaufort (factor)	>2500	3763	17.9	0.52	14.0
2005	Cue	>2500	4113	9.0	0.55	5.0
2008	Cue + obs	>4000	5399	13.6	0.40	6.0
2011	Cue + obs	>2500	8832	14.1	0.43	4.0

of 0.1135 (SE = 0.0130) (Fig. 1). The trend was significantly different from zero ($F = 76.59$; $df = 1, 4$; $p < 0.001$), and the model fit the data well (adjusted $R^2 = 0.938$). A finite growth rate of $12.02\% \text{ yr}^{-1}$ (95% CI = 8.06–16.13%; CV = 17%) was derived from the instantaneous growth rate. A linear model of population growth also fit our data well (adjusted $R^2 = 0.8821$).

Meta-analysis

The bibliographic review resulted in 28 documents reporting growth rates of humpback whale populations worldwide (Supplement 5). A total of 14 docu-

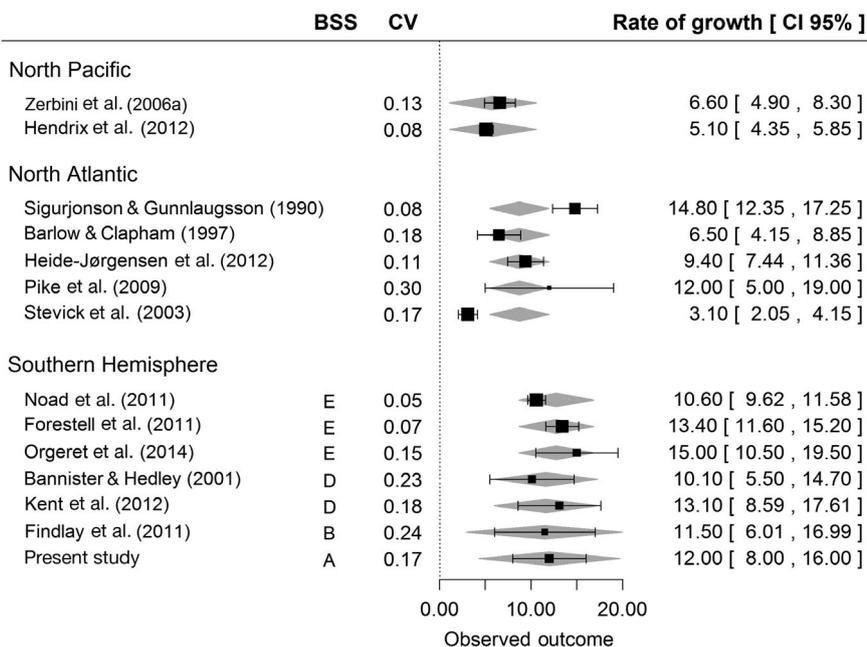


Fig. 2. Annual growth rates of the global humpback whale populations reported by the studies included in the meta-analysis ($n = 14$). Black boxes correspond to growth rate estimates, and their sizes are proportional to the weights (precision) considered in the meta-regression model. Gray diamonds indicate the predicted growth rates from a meta-regression model with breeding stock as an explanatory variable. BSS = Southern Hemisphere breeding stock. Error bars are SE

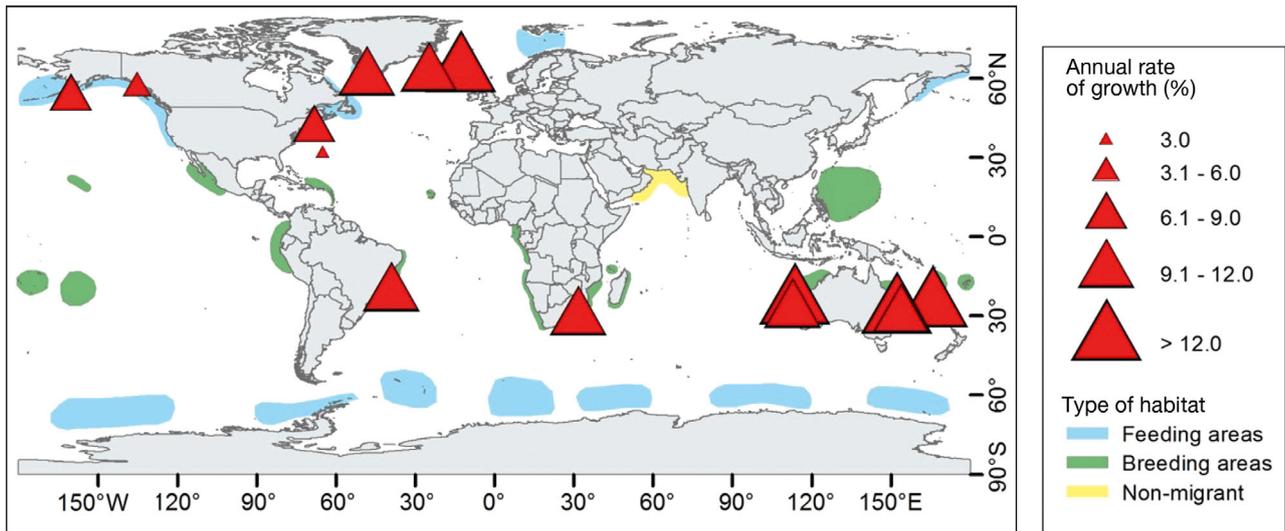


Fig. 3. Locations of the studies reporting annual growth rates of humpback whale populations that were included in the meta-analysis ($n = 14$). Size of the red triangles is proportional to the growth rate reported by each study. Polygons showing different types of habitats are approximations of the true distributions

ments that satisfied our criteria for inclusion in the meta-analysis, including that of precision, were considered (Figs. 2 & 3). If we consider a meta-regression with random effects and no moderator, the typical annual growth rate for the humpback whales would be 10.46% (95% CI = 8.55–12.37%). The heterogeneity was high among studies, with an estimated $I^2 = 90.9\%$ (see Higgins et al. 2003). I^2 refers to the index of heterogeneity and represents the ratio of excess dispersion to total dispersion

Table 3. Meta-regression models of the growth rates of the global humpback whale populations as functions of different explanatory variables. % Het = percentage of among-study heterogeneity explained; AIC = Akaike's information criterion; Δ AIC = AIC difference between the model and the best model (lowest AIC value). Akaike weight measures the weight of evidence in favor of the model and may be interpreted as the model probability

Model description	% Het	AIC	Δ AIC	Akaike weight
Breeding stock	12.3	57.4	0	0.782
Ocean	20.1	60.1	2.7	0.203
Haplotype diversity	38.8	67.4	10.0	0.005
Hemisphere	34.2	68.4	11.0	0.003
Research method	5.7	68.6	11.2	0.003
Research platform	0.0	69.6	12.2	0.002
Total whales hunted	14.5	70.9	13.5	0.001
Period whaling	0.0	73.0	15.6	0
Years research	0.0	73.0	15.6	0
Lag years of 90% captures	0.0	73.3	15.9	0
Null random effects	–	75.9	18.5	
Null fixed effects	–	286.5	229.1	

The meta-regression models were constructed considering 10 explanatory variables (Table 3). The most parsimonious meta-regression model according to AIC included the breeding stock as an explanatory variable but accounted for only 12.3% of the among-study heterogeneity. The second-most parsimonious model included ocean as an explanatory variable, predicting the lowest growth rates in the North Pacific and North Atlantic oceans, respectively (Fig. 4). The model that included the haplotype diver-

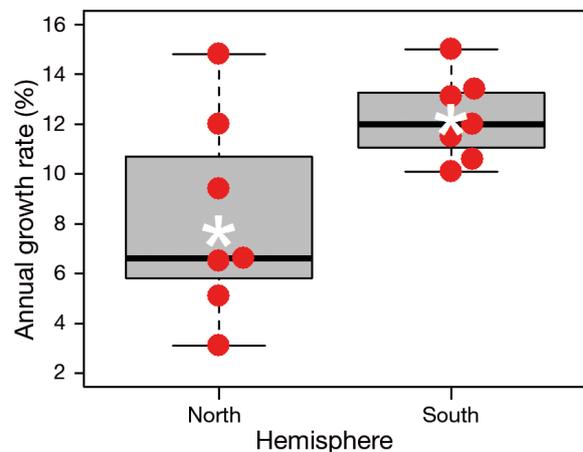


Fig. 4. Annual population growth rates of humpback whales according to hemisphere as reported by studies included in the meta-analysis ($n = 14$). The black line within the box indicates the median, box indicates the 1st and 3rd quartiles, and the whiskers indicate range of values. White asterisks indicate the predicted population growth rates for both hemispheres based on the meta-regression model with hemisphere as an explanatory variable

sity as an explanatory variable was the model that accounted for the most among-study heterogeneity (~39%). This model predicts higher rates of growth with increasing genetic diversity. The model that included hemisphere as a moderator also accounted for substantial heterogeneity (~34%), predicting higher growth rates in the Southern Hemisphere (12.21% yr⁻¹) and lower rates in the Northern Hemisphere (7.74% yr⁻¹) (Fig. 4). Other models that included variables related to methodology or the history of hunting did not fit the data well and did not explain much of the among-study heterogeneity.

DISCUSSION

Potential biases in the growth rates

Two types of errors resulting from animals being missed by observers may affect distance sampling methods (Marsh & Sinclair 1989): availability bias, which is caused by animals that are not available to be detected, and perception bias, which is caused by the ability of an observer to detect the animals. If the parameter of interest was the absolute abundance of the population, a correction factor to account for availability bias caused by animals that were underwater when the airplane passed should be applied (Barlow et al. 1988). It is reasonable to assume that the availability bias for humpback whales did not vary among years, and thus the uncorrected estimates of abundance were used as proxies for the total population size to obtain the growth rates. However, our assumption of constant perception bias among years remains to be tested. An important improvement for future aerial surveys is to include a double observer platform (Borchers et al. 1998) to test whether perception bias plays an important role in the estimates of abundance and growth rates, and whether it varies among years. Any change in the survey method, however, needs to be done in a manner that still allows comparisons over the long term.

Distance sampling estimates of growth rate may also be affected by temporary or permanent migration. It has been hypothesized that the high growth rates of some populations of humpback whales may be the result of a combination of true growth and temporary immigration, driven by a tendency to aggregate for mating (Clapham & Zerbini 2015). In essence, whales would abandon former breeding grounds in favor of other sites with higher densities. Such unidirectional movements could bias growth rate estimates from both mark-recapture and distance sampling methods.

Movements between breeding grounds were detected in the Southern Hemisphere, including a whale that was sighted in Madagascar and Brazil (Stevick et al. 2011) and another whale sighted in Ecuador and Brazil (Stevick et al. 2013). Connections between the stocks of Africa and Brazil have been suggested by song behavior and genetics (Darling & Sousa-Lima 2005, Rosenbaum et al. 2009), despite the fact that the majority of whales from Brazil retain their fidelity to this breeding ground (Rosenbaum et al. 2009). These authors estimated an immigration rate from stock B (West Africa) to stock A (Brazil) of approximately one individual per year (or 29 per generation). Such few migrants per generation may allow some genetic exchange among breeding stocks but would not be enough to significantly affect their population structure (Rosenbaum et al. 2009). Thus, the contribution of migration to the population growth rate for Brazilian humpback whales is assumed to be small or negligible.

Growth rate of the stock of Brazilian humpback whales

Humpback whales from Brazil were intensively hunted both in their feeding and breeding grounds, with figures in the order of tens of thousands of whales caught (Williamson 1975, Findlay 2001, de Moraes et al. 2017). It has been estimated that this population reached a depletion level of 1 to 13% and remained low for 4 decades (Zerbini et al. 2011). Almost 10 years after the commercial whaling moratorium issued by the IWC in 1966, the occurrence of this species in the whaling grounds of the northeastern coast of Brazil was considered rare (Williamson 1975).

In recent decades, multiple lines of evidence have indicated that the Brazilian stock of humpback whales is growing. Previous studies reporting the growth rates of these whales, however, have shown contrasting growth rates (Freitas et al. 2004, Ward et al. 2011). The first study considered a mark-recapture dataset collected from the Abrolhos Bank, estimating an annual growth rate of 31% from 1996 to 2000 (CV = 48%; Freitas et al. 2004). Such a high growth rate may be overestimated by the use of a population model with 100% survival or by the failure to control for differences in effort in terms of space or time among years. The mark-recapture estimates for this period are apparently overestimated when compared with the growth rates obtained through count methods.

Counts of whales from boat surveys around the National Marine Park of Abrolhos (same core sampling area and period of the mark–recapture effort) yielded a growth rate of $7.4\% \text{ yr}^{-1}$ from 1995 to 1998 ($CV = 48\%$; Ward et al. 2011). The limited area covered by the boat surveys used to count whales, however, could result in a negative bias in the growth rate determined in this study because only core habitats were surveyed, and these areas may become saturated first relative to more marginal habitats (Ward et al. 2011).

The aerial surveys covered a wider study area and show that the growth rate may vary among regions (see Supplement 4). The highest density area observed in this study in the central region of the Abrolhos Bank roughly matches the area covered by the boat counts and indeed has lower growth rates than adjacent regions. This provides further evidence for the hypothesis that the growth rate presented by Ward et al. (2011) was an underestimate, as their study did not sample the entire habitat of this population. Some regions within the Brazilian breeding ground presented growth rates too high to be caused only by births (see Supplement 4). The spatial organization resulting from movements of whales may bias growth rate estimates because whales born in a high density region of the breeding ground may occupy adjacent regions in following seasons. Moreover, potential biases of the studies reviewed by us in the meta-analysis, including growth rates too high to be biologically plausible, may be due to sampling a particular region within the breeding ground.

The dataset presented here, which was collected during a later time period than those discussed above, yielded relatively high estimates of annual growth for this population. As judged by its good precision, a more rigorous sampling procedure and broader spatial coverage of the breeding area, we consider that aerial surveys provided a robust empirical estimate of the instantaneous growth rate (r) for this population. The estimate of an increase of $12\% \text{ yr}^{-1}$ is very close to what was proposed as the biologically plausible limit using a theoretical population model (Zerbini et al. 2010) and thus is most likely close to the intrinsic growth rate for this species. Moreover, the confidence interval of the growth rate presented here covers the theoretical maximum proposed for the species, suggesting that they are not significantly different.

Whaling activities did not last long enough to hamper the genetic diversity of the Brazilian stock, which is one among the highest of the humpback whale populations of the Southern Hemisphere (Engel et al.

2008). Recent abundance estimates for this stock suggest that the population is nearly half of its pre-exploitation abundance of 24 558 whales (Zerbini et al. 2011). According to the logistic model and other models of population growth with density dependence, this population is growing at its maximum rate. Furthermore, with the depletion of most populations of other baleen whales in the Southern Hemisphere, millions of tons of krill were available for other whales and consumers in the Southern Ocean (Laws 1977). This 'krill surplus' may have favored consumers in the Southern Ocean, creating the necessary conditions for the observed growth of this population (but see Balance et al. 2006 for a more complex picture).

The recovery of humpback whale populations worldwide through the moratorium of commercial whaling may be regarded as an emblematic example of conservation success. Recently, the International Union for Conservation of Nature has revised the Red List status of humpback whales worldwide to Least Concern (IUCN 2016) and the Brazilian Ministry of the Environment reclassified the species in national waters to Near Threatened (ICMBio 2014). Unfortunately, commercial whaling had many negative consequences, some of which were irreversible. Humpback whales were once abundant around South Georgia in the Southern Ocean and now are recorded at low numbers, despite the presence of krill in the region (Moore et al. 1999). Furthermore, the moratorium occurred too late to preclude the local extinction of some species (e.g. gray whale in the North Atlantic, blue whale at South Georgia and off Japan), and other species have not yet achieved full recovery (e.g. North Atlantic right whale, humpback whales at South Georgia and New Zealand) (Clapham et al. 2008, Clapham 2016).

Among-population differences in growth rate

The meta-analysis suggests that a substantial amount of the heterogeneity among studies in the growth rates of humpback whales is attributable to geographical differences. The predicted growth rate of humpback whales in the Northern Hemisphere was lower than that in the Southern Hemisphere. A remarkable difference between the polar ecosystems of the south and the north is the absence of geographical barriers in the Southern Hemisphere. The Antarctic Circumpolar Current runs eastward around the Antarctic continent, creating gyres and upwellings, and therefore enhancing the mixing and

productivity of the Southern Ocean ecosystem (see Murphy et al. 2007). The absence of geographical barriers in the Southern Hemisphere may also affect the population dynamics and structure of baleen whales. Migration of whales between different stocks may decrease the risk of extinction through a 'rescue effect' (Hanski 1999).

The extension of sea ice in the Arctic is smaller than that in the Antarctic, and has decreased in recent decades, while it has increased in the Antarctic (NOAA/NSIDC 2014). Sea-ice habitats are known to favor the recruitment of krill (Atkinson et al. 2004). Additionally, the primary productivity of the North Pacific Ocean has decreased over recent decades (Schell 2000). Most rorqual whales in the Southern Hemisphere are larger in size than in the north, which may be related to higher primary productivity in the south or may be a product of selection for energetics (Brodie 1975). Furthermore, humpback whales in the Northern Hemisphere feed on a larger variety of prey and have a longer feeding season than their counterparts in the south (Brodie 1975). In contrast, prey of humpback whales in the Southern Hemisphere largely consists of dense swarms of krill, which may extend over 10s of kilometers (Nicol 2006). Nevertheless, the distribution and abundance of krill around the Antarctic continent is not uniform and the Scotia Sea is the region that has the highest abundance of krill (Atkinson et al. 2004) and is where the Brazilian humpback whales feed (Stevick et al. 2006, Zerbini et al. 2006b, Engel & Martin 2009). Thus, there are likely differences in the marine biological productivity and availability of prey across distinct feeding grounds of the humpback whale.

Human impact in the Northern Hemisphere is higher and can act with biological processes to create the hypothesized differences in the growth rates of whales between the hemispheres. Shipping lanes and traffic that may threaten some baleen whales are much more widespread and intense in the Northern Hemisphere (Halpern et al. 2008). For example, the North Atlantic right whale *Eubalaena glacialis* is struggling to recover from whaling (Caswell et al. 1999) due to high shipping traffic and collisions (Conn & Silber 2013), among other factors. In contrast, most southern right whale populations are recovering from whaling, with high growth rates reported in recent decades (e.g. Best et al. 2001, Cooke et al. 2001). Shipping strikes may not be an issue for Northern Hemisphere populations of humpback whales but may act synergistically with other human impacts and decrease the overall habitat quality for this species.

Patterns of exploitation by whalers also varied geographically and may account for the hemispheric and longitudinal differences in the population growth rates of this species. In the Southern Hemisphere, the past total catches in the Atlantic and Indian oceans were much larger than in the Pacific Ocean (Mori & Butterworth 2006). Moreover, the breeding stocks of the North Pacific, Brazil and eastern Australia were those that experienced the largest catches (see Supplement 6). The peak period of catches also differed among the populations and, together with the total catches, may determine how far each population is from reaching the carrying capacity and, consequently, its growth rate. However, the explanatory variables related to hunting patterns did not explain the heterogeneity in the growth rates among the populations.

Haplotype diversity explained the largest amount of heterogeneity among the studies. Higher genetic diversity was observed for populations in the Southern Hemisphere; the lowest genetic diversity was observed for the population in the North Pacific (Jackson et al. 2014). Populations that may have passed through a population bottleneck due to commercial whaling and loss of genetic diversity, as in the North Pacific and North Atlantic populations, have the lowest genetic diversity and rates of growth. Loss of genetic diversity may impact populations over the long term by adversely affecting the ability to cope with environmental change (Frankham 2005).

Concluding remarks

The growth rate estimated for the Brazilian breeding population of humpback whales in recent decades ($r = 0.114$) is near the maximum possible growth rate for the species. Allometric models predict lower intrinsic growth rates for this species, with r_{\max} ranging from 0.037 (based on the model by Caughley & Krebs 1983) to 0.058 (based on Schmitz & Lavigne 1984). Thus, its large size could place the humpback whale on the slow extreme of the range of life histories within cetaceans. Moreover, using known demographic parameters, such as the age of first reproduction, inter-birth interval and survival, the instantaneous population growth rate for the humpback whale was estimated to be 0.05 (Taylor et al. 2007). Contrary to most theoretical expectations, at least temporarily, humpback whales show high population growth rates typical of fast living and/or smaller-sized cetaceans. One exception is the prediction based on the relationship between r_{\max} and age

at first reproduction (Hone et al. 2010), which yields an estimate of $r_{\max} = 0.118$ for the humpback whale, considering that first reproduction of this species occurs at 6 yr of age (Clapham 1992). It is reasonable to state that humpback whales may decrease inter-birth interval, increase survival and possibly breed at a younger age when conditions are favorable.

The cessation of commercial whaling, the high genetic diversity of humpback whales and the high abundance of krill were likely the conditions that allowed such a remarkable population growth rate for some stocks. Commercial whaling set the stage for the study of population growth and ecosystem shifts at a global scale. Here, an empirical estimate of the instantaneous growth rate (r) for the humpback whale breeding stock of Brazil is provided. This estimate is close to the intrinsic growth rate of the species (r_{\max}), which is rare to observe for wild animal populations. Our study also highlights the importance of long-term studies in population ecology and conservation biology (Caughley 1977, Gaillard et al. 1998). These studies are invaluable for our understanding of how the Southern Ocean will change with the recovery of large whales, including competitive interactions among krill consumers. Another interesting project would be to study the demographic transition of large whales from high population growth to an equilibrium state and determine how density-dependent processes will act on the population dynamics of this species.

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