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Southern Hemisphere Humpback Whale Comprehensive Assessment A synthesis and summary: 2005-2015

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ABSTRACT

The Southern Hemisphere humpback whale Comprehensive Assessment was conducted over 15 years at the International Whaling Commission Scientific Committee. Here we present the results of these assessments, commenting on the significant methodological developments that have occurred over the assessment period and the unresolved questions still to address for future assessments of Southern Hemisphere humpback whales. Assessments suggest around 140,000 humpback whales were present in the Southern Hemisphere prior to modern whaling, and reveal contrasting patterns of population recovery across the Southern Hemisphere oceans today.

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We dedicate this document to the memory of our friend and colleague Professor Peter Best, a world leading whale biologist who has published biological studies on South African humpback whales since the 1960s. Peter was a core member of this assessment team since its inception, chairing the first meeting at which the assessment commenced and providing invaluable inputs and commentary throughout.

INTRODUCTION

Southern Hemisphere humpbacks seasonally migrate long distances between low winter latitude breeding and calving grounds and summer Southern Ocean feeding grounds. At least seven distinct breeding grounds have been identified across the Southern Hemisphere (labeled “Breeding Stocks” [BS] A-G by IWC (1998), Figure 1). At least three of those Breeding Stocks (in the South Pacific, eastern South Atlantic and western Indian Ocean) include multiple sub-stocks[1] based on genetic and

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[1] Stock definitions (i) Stock:- *all the individuals in an area that are part of the same reproductive process, forming a self-contained unit, with emigration/ immigration rates far lower than the intrinsic rate of population growth.*(ii) Sub-stock:- *a consistently identifiable subunit of a stock, distinguished on ecological, behavioural or genetic (e.g., mitochondrial DNA)*

geographical evidence (Olavarría *et al.,* 2007; Rosenbaum *et al.,* In review; Rosenbaum *et al.,* 2009) and sub-stock designations have been applied in such cases (for example BSC is subdivided into BSC1, BSC2 and BSC3).

Over 220,000 humpback whales were killed across the Southern Hemisphere during the modern whaling era between 1904 and 1973, with catches particularly concentrated in the Southern Ocean. Since that time, monitoring of these recovering populations in their breeding habitats has been patchy. Coastal surveys off east and west Australia since the 1970s have provided long-term abundance trends for these populations (Bannister 1991, 1994; Bannister *et al.,* 2001; Bannister *et al.,* 1991; Paterson *et al.,* 1989; Paterson *et al.,* 1994, 2004), whilst more limited surveys were conducted off the east coast of South Africa and Mozambique (Findlay et al., 1994; Findlay and Best, 1996). However surveys on most breeding grounds and migratory routes were limited until the International Whaling Commission 'Comprehensive Assessment' of the Southern Hemisphere humpback whale was initiated in the late 1990s (IWC 1998). The key aims of this assessment have been to

(i) identify breeding populations and sub-populations,

(ii) identify migratory linkages between breeding and feeding grounds,

(iii) measure abundance

(iv) measure trends on breeding and feeding grounds,

(v) compile a comprehensive catch record for the Southern Hemisphere,

(vi) conduct assessments to measure the level of recovery of each breeding population relative to pre-exploitation levels (IWC 2007, 2010a, 2012c, In press).

The assessment took over ten years to complete, as there was significant variation in the quality of data available among breeding grounds, and some regions had complex population structuring that was not well characterized. A significant amount of new information was collected from the various Southern Hemisphere breeding grounds for measuring population structure, abundance and trends. In addition a number of improvements were made to the assessment models in order to accommodate the unique characteristics of the available datasets from each breeding population / set of sub-populations, and the challenges of allocating high latitude catches to low latitude stocks.

Here we provide a synthesis of the results of this effort, focussing on both the key scientific challenges of assessing the Southern Hemisphere humpback whale populations, and the methodological approaches developed in response to these challenges. We also consider some potential directions for re-assessment of these populations in the future. This document is laid out into three main sections: (1) the key components of the assessments; (2) assessment results, and (3) unresolved questions and next steps.

ASSESSMENT COMPONENTS

Southern Hemisphere Breeding Stock structure

Southern Hemisphere humpback whale populations are characteristically high in

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grounds. See p287, IWC IWC (2014b) Annex I: Report of the Working Group on Stock Definition. *J. Cetcean Res. (Supp.)* **15**, 271-288.. In this document, 'stock' and 'population' are considered equivalent, as are 'sub-stock' and 'sub-population'.

genetic diversity and exhibit mitochondrial (mtDNA) genetic differentiation between nearly all geographically distinct breeding grounds (Olavarría *et al.,* 2007; Rosenbaum *et al.,* 2009). Such high genetic diversity is thought to be maintained by substantial reproductive sub-structuring across breeding and feeding populations, since humpback whales sharing the same breeding ground can have migratory fidelity to different high latitude feeding grounds. Breeding grounds appear to be defined by relatively fixed environmental factors such as water depth and a specific temperature range (Rasmussen *et al.,* 2007). Feeding hotspots are likely to be associated with oceanographic fronts and features (Friedlaender *et al.,* 2006), some of which are stable through time and others which may vary with factors such as climate oscillations. Migratory destinations are hereditary, passed down through maternal lines via the experience of the calf during the first year of life (Baker *et al.,* 1990). There can also be more subtle genetic differentiation among individuals within breeding grounds over the long-term, since breeding grounds can be composed of multiple 'demes'[2] of whales with different rates of within-deme reproduction (e.g. Baker *et al.,* 2013). This can be occur due to long-term fidelity to a local area within the breeding ground, or long-term association with other whales on a common migratory route from high latitude feeding grounds. Hence on any breeding ground, humpback population structuring can be determined by both breeding and feeding ground fidelities and sometimes also spatial structuring, or genetic 'isolation by distance' across the breeding ground (driven by long-term fidelity of individuals to a specific breeding site within a large geographically continuous breeding ground).

This diversity and complex sub-structuring also has an additional consequence, in terms of measured genetic differentiation between populations. Significant genetic differentiation has been reported between all breeding grounds using distance based measures such as F_{ST} (e.g. Olavarría *et al.,* 2007; Rosenbaum *et al.,* 2009), even though in some cases there is evidence that individual whales range across breeding grounds. One example comes from the neighbouring South Pacific breeding grounds of Tonga and the Cook Islands. Satellite tagging and mark recapture studies showed that a number of whales travel through the Cook Islands en route to Tonga (Constantine *et al.,* 2012; Hauser *et al.,* 2010), but significant F_{ST} genetic differentiation is found between the two (Olavarría *et al.,* 2007), suggesting that at least one of these populations is a genetically heterogeneous mixture, possibly as a consequence of these breeding populations having multiple migratory routes to high latitude feeding grounds.

Humpback whale migratory journeys are structured by sex and life-stage (Brown *et al.,* 1995; Chittleborough 1965; Dawbin 1966), which can be a further challenge for designing studies to capture 'true' population identity and genetic variation, as well as for mark recapture surveys on breeding grounds. For example, complex population structuring has been observed off the coast of west South Africa (Carvalho *et al.,* 2014) and east Australia (Valsecchi *et al.,* 2010). The causes of this have not yet been satisfactorily resolved but may be a consequence of both sex and life-stage segregation on migration, compounded with the possible feeding ground sub-structuring within populations using a common breeding ground.

The complex population structuring of humpback whales has posed a challenge for delimiting whale 'stocks' for assessment. The IWC Scientific Committee assessments

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[2] Deme: A subdivision of a stock/population consisting of closely related plants, animals, or people, typically breeding mainly within the group.

have focused on Southern Hemisphere breeding populations that occur in a discrete geographical area, *where* abundance of whales associated with that area have been calculated, *and where* there is genetic evidence for differentiation from neighbouring breeding grounds. In practice, genetic differentiation has nearly always been the case due to the complex structuring of these populations. Where measures of differentiation, re-sighting of individuals, satellite tagging or *Discovery* mark evidence suggested breeding grounds are closely connected and/or share a common feeding ground, some assessments were co-conducted on multiple breeding grounds (*i.e.* for multiple sub-stocks) simultaneously (multi-stock assessment). Table 2 summarizes our current understanding of population structure within each breeding ground. The coastal locations of each breeding stock (Figure 1) are as follows: BSA (Brazil), BSB1 (Gabon), BSB2 (feeds off West South Africa, breeding ground unknown), BSC1 (Mozambique), BSC2 (Comoros Archipelago), BSC3 (Madagascar), BSC4 (Mascarene Islands), BSD (West Australia), BSE1 (East Australia), BSE2, (New Caledonia), BSE3 (Tonga), BSF1 (Cook Islands), BSF2 (French Polynesia), BSG (Colombia, Costa Rica, Ecuador, Panama).

An additional challenge the Scientific Committee faced was how to accommodate occasional migratory movements between breeding sites that were genetically and geographically differentiated, and so naturally subject to separate assessment. While humpback whales have notable site fidelity to breeding sites (e.g. Baker *et al.,* 2013; Herman *et al.,* 2011), there is also evidence that they can migrate to different breeding grounds between years (Garrigue *et al.,* 2011a; Garrigue *et al.,* 2011b; Pomilla *et al.,* 2005; Stevick *et al.,* 2011), possibly as a result of following a different path north after the high latitude summer feeding season. These movements are likely to be more common for breeding grounds that are geographically close, or which share the same or closely located migratory streams, such as East Australia/New Caledonia and the sub-populations breeding off west and east Africa. Regular movements between sub-populations can bias population assessments that are based on abundance estimates computed with mark-recapture methods, because these estimates may include animals shared between both sub-populations- assuming no interchange can generate a positive bias on abundance estimates.

Consequently, a series of interchange models were developed (Butterworth *et al.,* 2009), to accommodate humpback whale movements between stocks and/or sub-stocks within the assessment model framework.

During the Comprehensive Assessment, the IWC Scientific Committee assumed that density-dependence operates on humpback abundance on their breeding grounds, rather than their feeding grounds. This was because trend and abundance data were relatively well known for breeding grounds, whereas population structuring of humpback whales on their feeding grounds is still poorly understood (though progress is being made, see Loo *et al.,* 2008). During the assessment, a seven-stock (BSA-BSG) population model was attempted assuming a single common Southern Ocean feeding ground, on which density dependence operated (Müller *et al.,* 2010). This concept may be more biologically realistic, since for example prey availability (as a consequence of habitat quality) in the Southern Ocean is likely to provide a stronger constraint on numbers than habitat quality on the breeding grounds. Attempts to develop this population model have to date been unsuccessful as the analyses have failed to achieve convergence (Müller *et al.,* 2010).

Humpback whale catches and allocations

Humpback whale catches have been documented for around 400 years in the Southern Hemisphere, with some net whaling off New Zealand, Basque whaling off Brazil, and American-style shore whaling off east Australia, Chile, Equatorial Guinea, Mozambique, New Zealand, Norfolk Island and Tonga (Reeves *et al.,* 2007). Southern Hemisphere humpback catches prior to the advent of modern whaling at the start of the 20th Century were relatively low (around 16,000 over the 100 year period, Smith *et al.,* 2006) and were assumed negligible in the Comprehensive Assessment (IWC 2001).

Between 1904 and the mid 1920s, modern whaling in the Southern Hemisphere was limited to land stations or floating factories moored in coastal waters at both low and high latitude waters, with one exception of a floating factory expedition operating with limited success at the ice edge south of the South Sandwich Islands. The coastal migrations and coastal breeding grounds in low latitudes and locations of feeding grounds in the proximity to the Falkland Dependencies meant that humpback whales were the first of the baleen whales to be decimated by modern whaling. The advent of pelagic floating factory fleets in the Ross Sea in the 1923/24 season opened new areas of the Antarctic coast to modern whaling. Despite Southern Hemisphere humpback whales being afforded global protection from whaling in October 1963, considerable Soviet illegal catches continued until 1973 with considerable underreporting of humpback whale catches over the 1948/1949 to 1973/72 seasons. However many of the Breeding Stocks had been decimated (at both the northern and southern limits of their migrations) well before this (Allison 2006). Findlay (2001) provides a review of the catches of humpback whales by modern whaling operations.

Figure 2 shows annual modern whaling catches across the Southern Hemisphere by breeding and feeding ground. During the pelagic whaling period the International Whaling Commission identified six Southern Ocean Management Areas (I-VI, Figure 1) based on regions where the greatest concentrations of baleen whales had been caught (Hjort *et al.,* 1932; Mackintosh 1965). These were considered more representative of fin and blue whale concentrations than of humpback whales, although six clear humpback feeding hotspots were evident by longitudinal band. A seventh feeding region was identified in Area IIIW (associated with BSB and BSC) once the locations of the illegal Soviet catches were identified in 1998, as such data were not available to the IWC prior to this (IWC 1998).

Allocations of high latitude catches to low latitude Breeding Stocks has remained problematic throughout the Comprehensive Assessment. Southern Ocean catches were initially divided across Breeding Stocks based on the location of catch aggregations and reports of mark returns (both *Discovery* type tags and natural marks including genetic marks) between breeding and feeding grounds. As with breeding ground delineation, the introduction of new natural mark return data resulted in some evolution in the high latitude catch allocations during the Comprehensive Assessment process.

From the early 2000s, the IWC have had sufficient data to allocate Southern Hemisphere humpback catches by 10° of longitude, with subsequent finalization of the catch series in 2006 allowing fine-scale analysis of the impact of catches on breeding populations (Figure 3, from IWC 2010a).

As increasing Southern Ocean mtDNA data became available from high latitude sampling, mixed stock analysis (e.g. Bowen *et al.,* 2007) was also used to inform likely population origins of whales across the Southern Ocean feeding grounds (Albertson *et al.,* In press; Pastene *et al.,* 2011). 'Mixed stock' analyses are used to determine, given a number of 'source' populations and one or more 'mixed' populations, what proportion of each of the source populations is found in each of the mixed populations (Bolker *et al.,* 2007). This is commonly conducted by looking at the frequencies of mtDNA haplotypes since mtDNA is maternally inherited and each mtDNA lineage represents a matriline; a related group of whales. Developments in mixed stock analysis using a Bayesian framework could now accommodate the effects of sampling error and population size differences among sources (Bolker *et al.,* 2003; Okuyama *et al.,* 2005). During multi-stock assessments (such as for BSD, BSE and BSO), mixed stock analysis was used to check whether the high latitude catch proportions that were allocated by the assessment model were a good fit to the mixing proportions estimated using mtDNA haplotype frequencies. Within the Bayesian framework it is also possible to incorporate the mixed stock results directly into the population model, placing a prior constraint on model-predicted relative abundance from the mixed stock analysis period so that relative abundances most similar to the mixed stock estimated proportions have higher likelihoods.

A summary of catch allocations of Southern Hemisphere humpback whales in all breeding grounds, migratory routes and feeding grounds is provided in Figure 3. High latitude catches could sometimes be unequivocally allocated to a particular breeding ground, but in marginal areas where catches could be shared between breeding grounds, they were either divided equally between neighbouring breeding grounds or shared in proportion to annual estimates of abundance on each breeding ground. Model sensitivities were conducted by adding 'marginal' (neighbouring) area catches to core assessments, in order to gauge the impact of extra catch allocations on assessment outcomes (e.g. Figure 3). Where whaling occurred on migratory routes shared by whales from multiple breeding grounds (*e.g.,* west Africa, New Zealand, Norfolk Island), those catches were allocated as described for high latitude catches above.

Population abundance and growth

Breeding ground abundance and trend

Trends and abundance were directly calculated from sightings surveys for BSA, BSD, BSC1 and BSE1. Sightings survey data were not available for BSG, BSC3, BSB1, BSB2 and Oceania (BSE2, BSE3, BSF1, BSF2, also referred to as BSO). During each assessment, a biologically realistic prior on the intrinsic humpback whale population growth rate was selected based on the available life history information for the species. In 2007, the Scientific Committee reviewed this evidence and agreed to impose an upper boundary of 10.6% on the maximum intrinsic rate of population growth (r_{max}) for humpbacks (IWC 2007). Subsequent to this, higher plausible rates of population growth (11% and 11.8%) were proposed; the latter based on Monte Carlo simulations using life history parameter estimates (IWC 2009; Zerbini *et al.,* 2010). To date the 10.6% upper boundary for r_{max} has been kept throughout the assessment process, for consistency between individual population assessments. Since the 2007 assessment of BSG, updated estimates of abundance became available (Félix *et al.,* 2011a) and were used in a subsequent re-assessment of BSG (Johnston *et al.,* 2011) but no new trend and abundance data are available for any other breeding ground, to our knowledge.

Mark recapture data from photo-identifications and biopsy sampling of these populations was available from most populations as an alternative measure of abundance and inferred trend. BSG was one of the first populations to be assessed, and this assessment was conducted by fitting the abundance estimate from a photo-identification mark recapture study into the assessment model. Subsequent assessments were conducted by incorporating mark recapture data directly into the likelihood function of the population model, following a 2009 intersessional workshop on population modelling (IWC 2010b). Mark recapture data were used to weight the model-predicted abundance and trends in the likelihood function, using a binomial capture-recapture formulation of similar construction to the Pradel open population model. A fixed survival rate of 0.97 was used (see '*Model Constructions'*). With this development, trend and abundance information contained within the re-sightings directly informs the model likelihood, *e.g.* model trajectories better fitting to the mark re-sight data incur higher likelihoods. For the BSB assessment, a further correction was added to account for error, reflecting the percentages of true duplicates likely to be missed due to sequencing or human detection error

Genetic and whaling evidence indicates that humpback whales are at parity on the feeding grounds. However, genetic studies on some breeding grounds have sampled males much more often than females (ratio 2.1-2.4:1, Brown *et al.,* 1995; Pomilla *et al.,* 2006). This is possibly because males remain on the breeding grounds longer than females, or a greater proportion of females may remain in the Southern Ocean through the winter. As a consequence of this sampling bias towards males, mark recapture estimates of abundance from breeding grounds based on photo-identification are likely to be downwardly biased, as females are under-sampled. Therefore, whenever available, genetic mark recapture datasets were used in population assessments of some breeding stocks, including BSB, BSE1 and Oceania (BSO), as sex-specific recaptures could be obtained. For these assessments, male-only recaptures were incorporated into each population model and these were doubled to account for females, assuming parity. If males and females use the breeding grounds differently, this may influence estimates of abundance derived from line transect surveys also, since the resulting abundance estimate may not represent all whales in the population, rather the (possibly male biased) component present on the breeding ground during the survey period.

Assessments using mark recapture data alone can be downwardly biased, since humpbacks exhibit strong patterns of temporal and spatial residency across their breeding grounds, and unless the area is comprehensively sampled both spatially and throughout the breeding season, recaptures may reflect local density and recruitment rather than population abundance as a whole. In their study of Oceania, Constantine *et al.* (2012) included multiple breeding grounds and assessed the sensitivity of resulting abundance estimates to inclusion of less frequently sampled survey areas. Interestingly the inclusion of these areas did not significantly increase sightings (in fact many of these additional sightings were of whales which had already been sighted in other breeding areas), suggesting that spatial sampling across Oceania is comprehensive. More genetic sampling within the range of the eastern South Atlantic and southwestern Indian Ocean will be required to similarly evaluate spatial structure off Gabon or Madagascar.

Sightings surveys of humpback whales were used to calculate absolute abundance for BSA, BSC1, BSD and BSE1. Surveys of Brazil (BSA) and Mozambique (BSC1) were conducted on those breeding grounds via ship-based and aerial surveys respectively (Andriolo *et al.,* 2010; Findlay *et al.,* 2011). Aerial and coastal surveys of west Australia (BSD) and east Australia (BSE1) respectively were conducted on the migratory streams of whales travelling northwards en route to their breeding grounds (Hedley *et al.,* 2011a; Noad *et al.,* 2011). Surveys for BSD and BSE1 were designed to span the period of peak humpback migration, running for 4 and 8 weeks respectively. Validation of and calibration of some elements of both surveys was conducted by concurrently counting whales with different survey methods at the same time, conducting land-based counts to complement aerial surveys for BSD and conducting aerial surveys to complement land-based surveys for BSE1. Counts of the migratory stream are applied to whales that are seen travelling northward; when whales are milling, or not moving in the northward direction, they may be double counted or discounted, depending on the style of survey. As population abundance increases, the ability of surveyors to distinguish these behaviours also diminishes, which may increase this bias.

Migratory route surveys may be downwardly biased by whales missed because they migrated north outside the survey areas, or if they travelled north very early or late in the season. Similarly, breeding ground surveys may be downwardly biased if they do not encompass the entire breeding range of the population, or if whales are still on migration during the survey period. For example high encounter rates in the northern survey transects of BSC1 suggest the breeding ground may extend north of the survey edge (Findlay *et al.,* 2011).

For all line transect surveys, negative bias may also be introduced by uncounted whales that were present but underwater during the observation period, and whales that were observed but not conclusively identified as humpbacks. Correction factors for underwater whales are difficult to calculate. For BSE1, whales were double counted from two observation points in order to improve survey accuracy, and all assumed to be surface-available (Noad *et al.,* 2011). For BSD, an upward correction factor of 0.54 was used for the aerial surveys, derived from comparisons with parallel land-based counts (Hedley *et al.,* 2011a). For BSA, a correction of 0.67 was applied (Andriolo *et al.,* 2010). No correction factor was applied to the BSC1 Mozambique surveys, which assumed all whales were sighted from the trackline (Findlay *et al.,* 2011). These correction factors substantially influence final abundance estimates, so a good understanding of the sightability of whales ('g(0)') using each survey approach is extremely important.

While there are a number of elements possibly causing downward bias in visual surveys, visual surveys include all whales, while some mark recapture efforts exclude calves and/or juvenile whales from sampling and therefore only represent the adult or adult + sub-adult components of the population. It is common to exclude juvenile groups when surveying for abundance, since calf and juvenile survival rates are lower than those of adults, introducing capture heterogeneity which can bias mark recapture abundance estimates. However the junior component is a significant proportion of the population (a Leslie Matrix based analysis estimated 18-23%, IWC 2010b) so such mark recapture efforts will yield smaller estimates than visual surveys which include all animals.

Southern Ocean abundance and trend

Three circumpolar surveys south of 60°S were conducted by the IWC IDCR and SOWER programs from 1978 to 2004 to estimate abundance of whales (Branch 2011). Open ocean survey coverage and survey design varied between surveys, so Southern Ocean wide abundance estimates are not directly comparable over time. In all analyses g(0) was assumed as 1, with no upward correction for whales missed on the track-line. Abundance and trend calculated over the three surveys for comparable areas associated with BSA-BSG (Branch 2011) were used primarily in assessment sensitivity cases, since the feeding ground distributions associated with each breeding stock are not well known.

SCIENTIFIC CHALLENGES

Key scientific challenges associated with each assessment component are summarized in Table 1.

Model constructions used for the assessments

Model formulation

Population assessments were conducted using a density-dependent sex-aggregated generalized logistic model of the Pella-Tomlinson form (Pella *et al.,* 1969). Populations were assumed to be at pre-exploitation abundance (simplistically assumed to represent carrying capacity, parameter *K*) in 1900, prior to modern whaling. Single stock models were applied in the following form to breeding grounds BSA and BSG:

$$N_{t+1}^{i} = N_t^i + N_t^i \cdot r_{max}^i \cdot \left[1 - \left(\frac{N_t^i}{K^i}\right)^z\right] - C_t^i \qquad (1)$$

N_t^i is the stock abundance in year t for stock i

K^i is the stock carrying capacity in 1900 for stock i

Exponent z was fixed at 2.39, corresponding to a maximum sustainable yield of 0.6**K*, as conventionally set by the IWC.

r_{max}^i is the maximum population growth rate for stock i, which is estimated when fitting the model

C_t^i : catches allocated to stock i

A Bayesian statistical framework was used to estimate quantities of interest. The population was projected using the 'backwards' method developed by Butterworth and Punt (1995). With this approach prior distributions were imposed on the intrinsic growth rate (r_{max}) and the most recent abundance estimate ($N_{current}$). For single stock models, these priors were sampled and a bisection approach was used to find the unique value of K corresponding to each set of samples from the priors, given the catch history. For this reason, a formal prior is not required for K (Butterworth *et al.,* 1995).

All other Southern Hemisphere breeding stocks were assessed in a multi-stock framework. For multi-stock assessments of more than one population (for example the population assessments of BSB, BSC and BSE1/BSO), a downhill simplex minimization method was applied to derive K for each population. Once K was calculated, the likelihood of each prior set was measured using likelihood functions (see individual assessments for details) and the posterior distributions were derived with a sampling importance resampling (SIR) algorithm (Rubin 1988). The Bayesian implementation of this population assessment model for Southern Hemisphere humpback whales (Zerbini 2004) represented an improvement on the likelihood-based approach used in the initial assessments (e.g. Johnston *et al.,* 2002) and in previous IWC assessments, as it can accommodate prior information on parameters and better represents parameter uncertainty in the form of the posterior distributions, which are output.

N_{min} constraint on bottleneck abundance

An additional model-related element that was developed during the course of the Comprehensive Assessment was the use of parameter N_{min} to constrain the minimum abundance values of each trajectory. The minimum abundance point of a stock along the length of its trajectory ('N_{min}', Jackson *et al.,* 2006; Patenaude 2002) has been constrained by mitochondrial haplotype numbers during assessments, with the rationale that mtDNA diversity within the stock represents the minimum number of female lineages that survived whaling. This constraint was conceived to introduce independent biological information on bottleneck size into population assessment models, by extracting information from genetic data collected from current populations. In 2006 it was agreed that a 'hard' lower boundary ('N_{floor}') could be used to constrain these N_{min} estimates (p191-192, IWC 2007), set as 4 times the number of mitochondrial haplotypes (maternal lineages) in the stock in question.

When considering assessment of stocks with evident sub-structure (Table 2), the IWC (2011) agreed to count only private haplotypes in determining N_{floor}. Subsequently in discussion of humpback BSB, a breeding population which may contain more than one sub-stock, this boundary was set to 4 times the number of mitochondrial haplotypes that were 'private', *i.e.* counting haplotypes found in only one of the two putative stocks, with an additional downward correction factor to exclude low frequency private haplotypes that may have been shared but not detected due to their low frequencies (Appendix 2, IWC 2011). N_{floor} was subsequently revised down to 3 times the number of mtDNA haplotypes (IWC 2012b) to reflect a 1:1 sex ratio and an additional 1.5x for non-contributing females at the bottleneck. Since most assessments had been completed by this time, the 3x N_{floor} adjustment was only applied to the assessment of BSD, BSE1 and BSO.

For the assessment of all stocks, trajectories constructed by each unique prior combination were evaluated and if the minimum abundance fell below the N_{floor} value, they were not included in the posterior sample. An alternative implementation was also used where the total minimum abundance of the breeding grounds subject to multiple-stock assessment could not fall below 3 x the total haplotype diversity of those grounds combined (IWC 2012c). This approach relaxes constraints on smaller populations and acknowledges that exchange between populations is sufficiently good that the haplotype set in any one population may contain haplotypes contributed since the bottleneck by immigration from other breeding grounds included in the assessment.

Summary of modelling developments

A number of methodological developments took place from 2004-2014 to enhance the population assessments that took place. These have been described throughout the text and are summarized as follows:

- Population assessment models were implemented in a Bayesian framework rather than a likelihood framework from 2004 onward. This enabled specification of priors on biological parameters such as r_{max} and current abundance, rather than point values.
- N_{floor} was used as a constraint on minimum population abundance at the bottleneck point (IWC 2007).
- Upper boundary of 10.6% was imposed on r_{max}, the maximum intrinsic rate of population growth (IWC 2007).

- Mark recapture data was added directly into population model in order to integrate information on abundance, trend and interchange between populations (for multi-stock assessments) into the likelihood function. An error correction was also added to enable models to account for missed recaptures (IWC 2010b).
- A conditional-likelihood mixed stock analysis of mtDNA haplotype frequencies was used as an informative check on how to allocate high latitude catches to mixtures of low-latitude breeding grounds. However in-depth mixed stock analyses (some noted above) have yet to be applied to most of the assessments.

SUMMARY OF ASSESSMENT RESULTS

All of the Southern Hemisphere humpback whale Breeding Stock assessments (2007-2015) were collated, and assessments were re-run in order to project population abundance and recovery (relative to 1900 abundance, *K*) forward to 2040, including predictions of 2015 abundance and recovery. Population models chosen as the base case in each assessment and re-run for this exercise are shown in Table 3.

Trajectories differ markedly in terms of population recovery between oceans. Recovery levels of humpback whales in parts of the Indian Ocean look relatively strong (median recovery over 90% for humpback whales breeding along the east coast of Africa (BSC1 & BSC3) and west Australia respectively, BSD). However the probability intervals in recovery of the two east African populations span 50-100%, reflecting substantial uncertainty in the population identity and abundance of the BSC3 population. Recovery levels in the South Atlantic are much lower (<50% and <15% for humpbacks breeding off Brazil and the unknown breeding ground that predominantly feeds off west South Africa, respectively). The west African BSB1 and BSB2 population assessment contains the greatest level of uncertainty (Table 3), since the BSB2 breeding ground is unknown, and abundance and trend for either could only be inferred using mark recapture data. In the Pacific Ocean, the coastal breeding grounds off Colombia and Central America appear very close to recovery (>90%) and recovery off east Australia also appears good (>75%), while recovery in the offshore islands of Oceania is much weaker at <50%.

With these projections, it is also possible to predict the likely increase rates of individual populations, assuming the population assessment model is an appropriate representation of real dynamics of these populations. Annual increase rates from 2010-2015 were calculated using the median annual abundance from each population assessment. These were averaged over the 5-year period, in order measure model-predicted population increases over this time (Table 3). Estimates of current population growth ranged from 0.7-6.8%, reflecting a variety of population trajectories at a range of recovery levels.

The total abundance of Southern Hemisphere humpback whales in 2015 was estimated at around 98,000, with total pre-exploitation abundance of all breeding populations estimated at 137,000. A summary of the results is shown in Table 3 and plotted in Figures 4 and 5. These figures suggest current overall recovery levels to be around 70%, although this represents a very simplistic summary of a complex array of connected populations, with varying catch histories and different rates of recovery.

Areas remaining for future work and development

Each population assessment concluded with unresolved research questions and recommendations for future work, which are summarized in Table 4 and scored by potential impact on assessment outcomes.

Population structure and abundance
Some Southern Hemisphere breeding grounds are too poorly understood to be assessed as distinct populations, although genetic data suggest they are distinct from neighbouring populations and may therefore have distinct population trajectories (Olavarría *et al.,* 2007; Rosenbaum *et al.,* In review; Rosenbaum *et al.,* 2009).

For example the breeding ground BSC2 off east Africa (spanning the Comoros Archipelago, southern Seychelles and waters of West Madagascar) is genetically distinct from the breeding grounds off Mozambique, but not east Madagascar (Rosenbaum *et al.,* 2009). No abundance estimates are available from BSC2, so it was assumed to form part of the east Madagascar population BSC3 during assessment. This assumption was supported by photographic and genotypic matches (Ersts *et al.,* 2011) and recent satellite telemetry tracking of whales from the Comoros Archipelago and Antongil Bay (Cerchio *et al.,* 2013; Fossette *et al.,* 2014) During the Assessment process humpback whales also appeared to recolonise areas of the Mascarene Archipelago (BSC4, HR pers comm). The BSC4 breeding stock was assumed to be included within the BSC3 mark recapture abundance estimate. Subsequent to the completion of the Assessment for BSC, a number of photographic and genotypic matches between BSC3 and BSC4 (Ritter 2009) and satellite tracking has also confirmed recent movements within a single breeding season. (Dulau unpublished data).

In Oceania, genetic and mark recapture evidence suggests that breeding sites off New Caledonia, Tonga and French Polynesia are demographically independent, but available mark recapture data were not sufficient to provide robust abundance estimates for Tonga and French Polynesia, and so an assessment of each breeding ground could not be done. Instead, Oceania was assessed as a single unit (BSO), combining Tonga, French Polynesia and New Caledonia (IWC In press), since mark recapture data across all three study sites was available to calculate overall abundance (Constantine *et al.,* 2012). Assessment of these sites independently remains an important goal, since they are genetically distinct (Olavarría *et al.,* 2007) with inter-population interchange levels within Oceania the same as interchange levels between the western Oceania breeding ground (New Caledonia) and the neighbouring east Australian population BSE1 (Jackson *et al.,* 2012). Recent estimates of the annual population increase in New Caledonia, western Oceania are ~15% (Orgeret *et al.,* 2014), far too high to be a consequence of natural population recruitment and suggesting a likely influx from the much larger east Australian breeding ground to the west. Such information was beyond the scope of the present Comprehensive Assessment but suggests an avenue for future research and assessment of recovery in the South Pacific (see Table 4).

Ideally, future regional assessments will accommodate smaller breeding sites such as those within Oceania and off the east coast of Africa explicitly, using data from local surveys either to model exchange with the larger breeding grounds, incorporating these whales into overall abundance estimates, or assessing these breeding grounds independently, if there is genetic or other biological evidence for demographic isolation.

There are still breeding grounds in the Southern Hemisphere which are either unidentified or only nominally known. Humpback whales breeding off the west coast of Africa (BSB1 and BSB2) posed significant challenges for population assessment for this reason. The breeding sub-stock off Gabon (BSB1) is significantly differentiated from the whales feeding off west South Africa (Carvalho *et al.,* 2014). The breeding ground associated with the west South Africa feeding area is unknown, and referred to as BSB2. Significant further surveys of the continental coast, combined with satellite telemetry deployments, collection of fluke photographs and genetic samples for individual identification, are still required to characterize the breeding sub-stock associated with of this feeding ground, which is small in size and has high inter-annual re-sight rates (Barendse *et al.,* 2013; Barendse *et al.,* 2011). This significant gap in understanding has also been a challenge for catch allocation, as significant whaling was conducted along the western coastline of Africa (Figure 3), but the relative whaling impact on the two breeding sub-stocks is unknown. There are many additional examples (eastern French Polynesia, Pitcairn, Galapagos Islands, Fiji, Mascarene Islands) where data are sparse and population abundance, isolation and status is unknown (Félix *et al.,* 2011b; Gannier 2004; Horswill *et al.,* 2012; Poole 2006).

The extent of breeding ground distributions are still poorly known in some areas (such as within the BSB1 and BSB2 breeding range extent), and as populations recover, these distributions are likely to expand (as for the Mascarene BSC4 example above). Where geographical spread is very broad, population sub-structuring may also occur due to spatial fidelity of humpbacks to particular areas within the distribution. Monitoring the abundance and trend of these populations will become increasingly difficult due to the logistical and financial difficulty of conducting regular surveys that adequately capture the dynamics across the breeding grounds. While humpback populations were small in number following the end of commercial whaling, in some places it was possible to measure numbers via seasonal counts of the migratory stream from land-based survey points (*e.g.,* east and west Australia). However as populations increase, the number of whales migrating further from the shore may also increase, and become harder to count accurately. Such monitoring approaches are therefore likely to become negatively biased, as observers are less able to adequately track and differentiate among large numbers of whale groups, and the migratory stream widens to include whales travelling a much greater distance from shore. The use of line transect surveys or mark recapture sampling regimes that can cover the entire breeding range therefore becomes increasingly important.

Improving abundance estimates from breeding grounds where they are currently imprecise is an important goal for future assessments. Highest priority are those for which current estimates yield the broadest coefficients of variance, including BSD (west Australia), sub-stocks BSE3 (Tonga) and BSF2 (French Polynesia) in Oceania, BSB1 (Gabon) and BSB2 (west South Africa) and BSC3 (Madagascar).

A number of breeding stocks are also lacking trend data (BSB1, BSB2, BSG and Oceania, including BSE3 and BSF2), a core model component which will enhance the precision of future assessments. Continued relative abundance surveys from other breeding grounds are also important to provide up-to-date measurements of regional population growth as populations recover.

Catches

Throughout the Comprehensive Assessment, only modern whaling catches of humpback whales were considered, although there is evidence of pre-modern humpback whaling stretching back centuries (Reeves *et al.,* 2007). In the 19th century alone, at least 15,000 humpback whales were killed according to records from

Townsend (Smith *et al.,* 2006; Townsend 1935). Further analyses of logbooks, landings and export records in order to estimate regional catches would be useful to enable future assessments to take pre-modern whaling impacts into account.

Model development

Proposed future modelling work to consider for future humpback whale assessments is listed below, along with the likely impact of this future work on assessment outcomes:

1. To date the humpback whale assessments have been conducted with an age and sex aggregated density-dependent logistic model. It may be possible to disaggregate some of the populations by sex, since ~44% of all catches are known by sex (Allison 2006). Since humpbacks have differential availability by sex on their breeding grounds, a sex-disaggregated population model could be a better fit to the data, and can better incorporate available sex-specific mark recapture data. It would also be useful to investigate age-disaggregated models (either age- or stage- structured) in future assessments.

   Impact: unknown.

2. Assess populations by feeding ground rather than breeding ground. Humpback whales have a breeding ground preference for shallow coastal waters and bays, so density dependence may act on breeding grounds where this habitat is limited. However resource limitation due to availability of the species' primary prey, Antarctic krill, may drive density dependence on feeding grounds. This could be particularly relevant to consider for areas where breeding populations mix on a common feeding ground, since density dependence on the feeding ground would then act commonly on both breeding populations (rather than each having a separate density dependence as is currently assumed). In this case, breeding ground populations do not necessarily recover to the same level as their pre-exploitation abundance, since only feeding ground carrying capacity is constant. There have been some efforts to conduct feeding ground assessments during the Comprehensive Assessment (e.g. Leaper *et al.,* 2011; Müller *et al.,* 2010). Leaper et al. (2011) conducted a simulation test using the population parameters and assessment of BSD and BSE as a framework, and calculated how much population trajectories would differ, if breeding ground density dependence is assumed but in reality feeding ground density dependence is operating. They found substantial differences between the population trajectories under these two scenarios, demonstrating that the impact of such model mis-specification on estimated population recovery can be significant, at least for breeding populations which mix on common feeding grounds. Since a key goal of conservation management is to restore species relative to a given baseline, future assessments considering feeding ground density dependence are recommended. Müller *et al.* (2010) attempted to develop a joint assessment model of all seven breeding stocks; however the work was not completed owing to convergence problems. An advantage of this approach is that feeding ground catches can be apportioned to the different stocks in proportion to the model-predicted abundances rather than allocated somewhat arbitrarily externally to the model. It would be worthwhile to consider the utility of such an all-stock model in investigating the assumption of feeding ground rather than breeding ground density dependence.
   Impact: potentially high.

3. Integrate mixed stock proportions into the population model, as this provides

information on the relative abundance of two populations sharing a common feeding ground in multi-stock assessments. Mixing proportions would be fitted onto the model-predicted abundances for the year/average of years over which the genetic samples were taken, and used to inform the posterior likelihood.
Impact: low?

4. Explore alternative maximum sustainable yield (MSYR) values for humpback whales. Throughout the assessment, humpback MSYR has been set at 0.6*K*, corresponding to the relative recovery point at which population productivity (MSYR_{1+}) is maximal. At the IWC assessment methodology workshop (IWC 2010b), the possibility of exploring MSY from 0.5-0.9 was suggested, and could be conducted to explore the sensitivity of assessment outcomes to different MSY levels (MSYL). More fundamentally, it would be useful to explore whether MSY=0.6 is an accurate representation of productivity levels for humpbacks, given real biological data. During recent attempts to estimate MSY with biological data, the Scientific Committee noted that when environmental effects are incorporated and when there is inter-annual variation in demographic rates, MSY is closer to 0.5 than 0.6 and agreed that $\text{MSYR}_{1+}= r_0/2$ should be implemented for future RMP trials (IWC 2014a).
   Impact: medium
5. Population models that explicitly incorporate environmental variability would be of great interest, and useful to nominate candidate SH humpback populations for such an exercise, particularly as significant progress has been made on this already during the MSY review.
   Impact: medium/high
6. With the standard density-dependent logistic model used in these assessments, population growth rates are maximal when the population is very small relative to carrying capacity, and decline as the population increases in size. However there is evidence that reducing population sizes can have the opposite effect on growth rates, with populations suffering inverse density dependence at very low levels. Depensation is likely to be driven by a mixture of local factors including loss of fitness due to inbreeding, reduction in benefits of sociality and demographic stochasticity (Courchamp *et al.,* 1999). Depensation could have an additional angle for whales if maternal traditions regarding migratory routes and habitat use are lost. If there is sufficient biological information to specify the extent of inverse density-dependence for whales, this could be incorporated into future assessment models. The impact of incorporating this metric is unknown.
   Impact: low/medium
7. Increase maximum bound on r_{max} in population models from 10.6% to 11.8%, as simulation analyses conducted by Zerbini *et al.* (2010) using available life history data suggest that this is a biologically realistic upper bound.
   Impact: low
8. Examine the impact of pre-1900 humpback whale catches on population assessment results. Impact on population assessment outcomes may be substantial for breeding grounds where >2000 humpback whales were killed (Smith *et al.,* 2006) and current abundance is not large, such as the breeding ground associated with west south Africa (BSB2), Tonga (BSE3) and Central America (BSG).
9. Re-run population assessment models for BSA, BSG, BSC1 and BSC3 with the

revised minimum abundance constraint N_{floor} of 3 x the number of mtDNA haplotypes, as implemented for BSB1, BSB2, BSD, BSE1 and Oceania, for consistency across assessments.
Impact: low. Estimated N_{min} values are shown in Table 3; preliminary runs suggest no impact from changing this parameter for the BSC1/BSC3 assessment. The lower 95%-ile for N_{min} of BSG is above the original N_{floor} constraint, suggesting that lowering this constraint will have a minimal effect. There may be some impact on BSA as the lower 95%-ile of N_{min} is below the 4 * N_{floor} constraint.

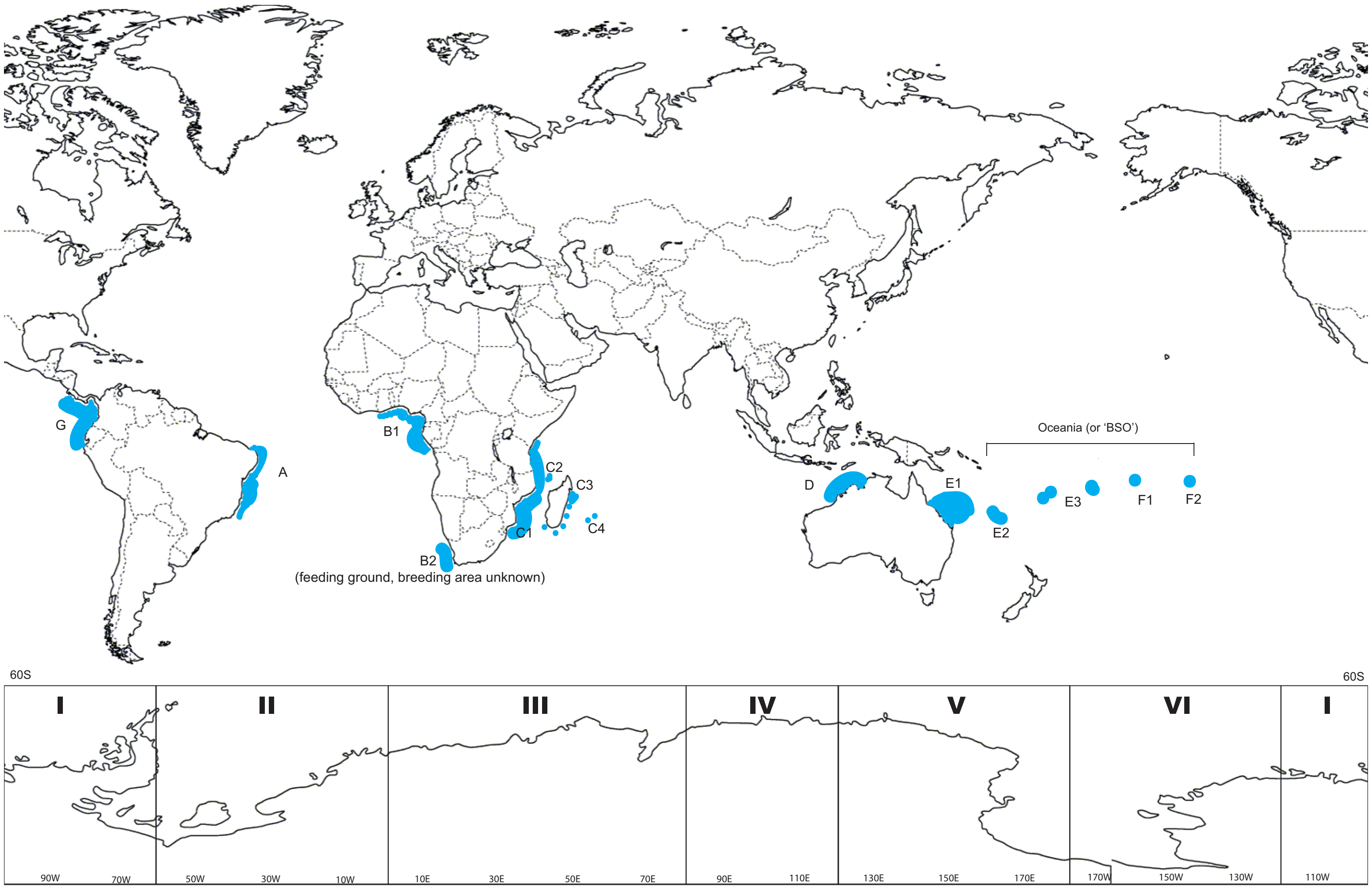

Figure 1. Southern hemisphere humpback whale breeding grounds for breeding stocks A-G, and Antarctic Feeding Areas I to VI.

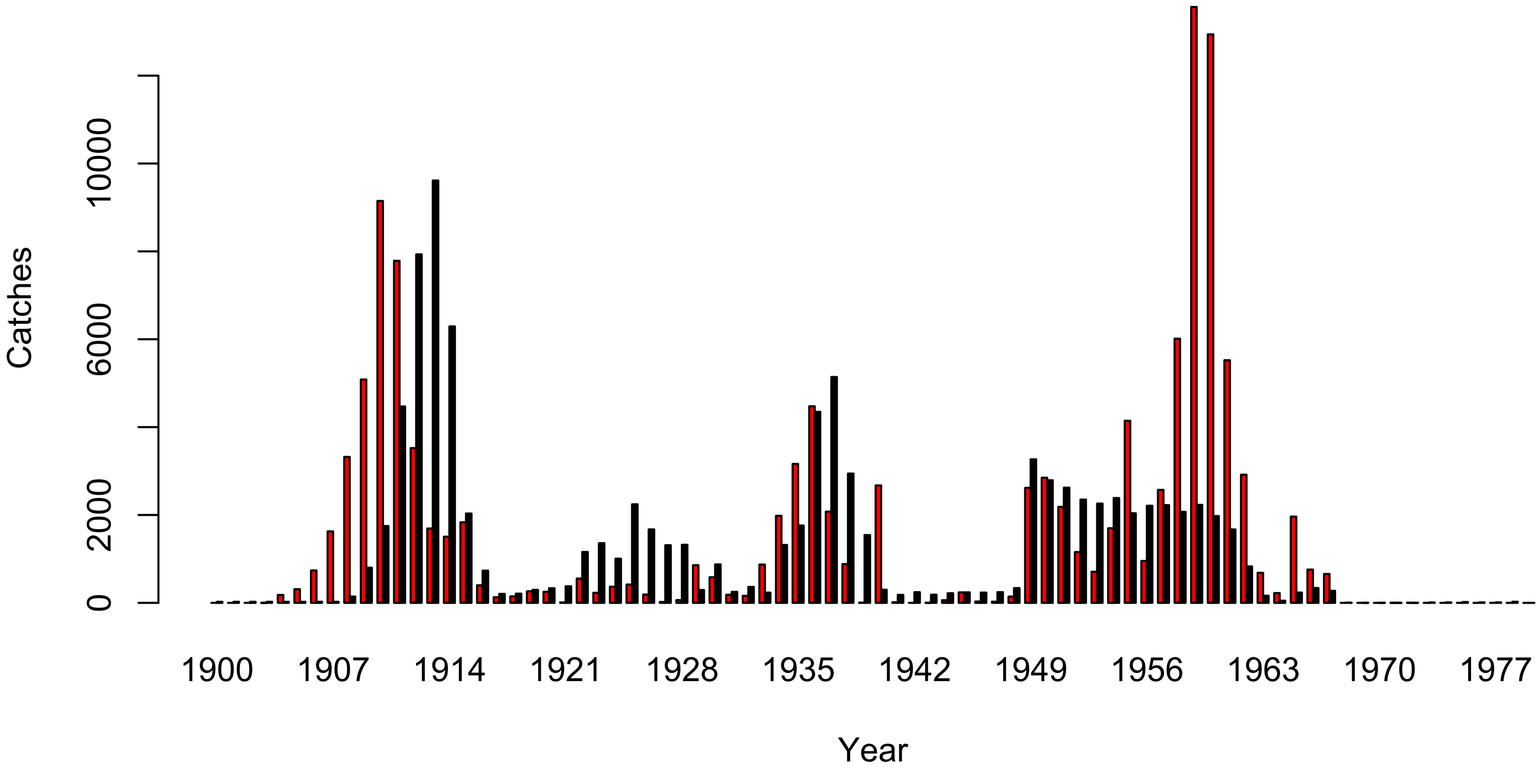

Figure 2. Annual Southern Hemisphere catches of humpback whales. Low latitude breeding ground catches are shown in black, high-latitude offshore catches in red

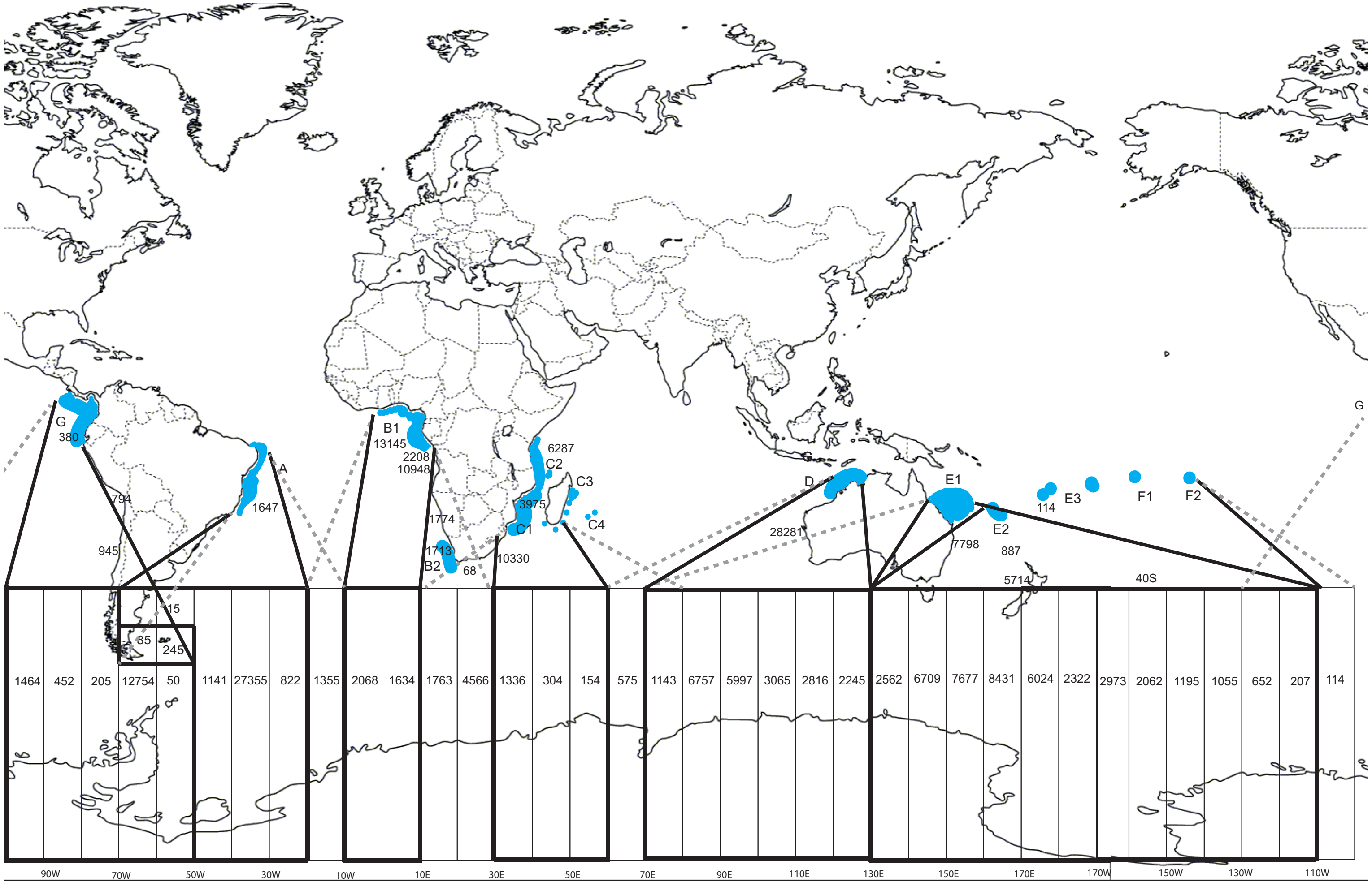

Figure 3. Humpback whale breeding grounds (BSA-G) and 20th century catches identified across the Southern Hemisphere. Catch allocations used in the reference case for each breeding ground population assessment are bordered with bold black lines. Allocations used in sensitivity analyses are shown with dotted lines.

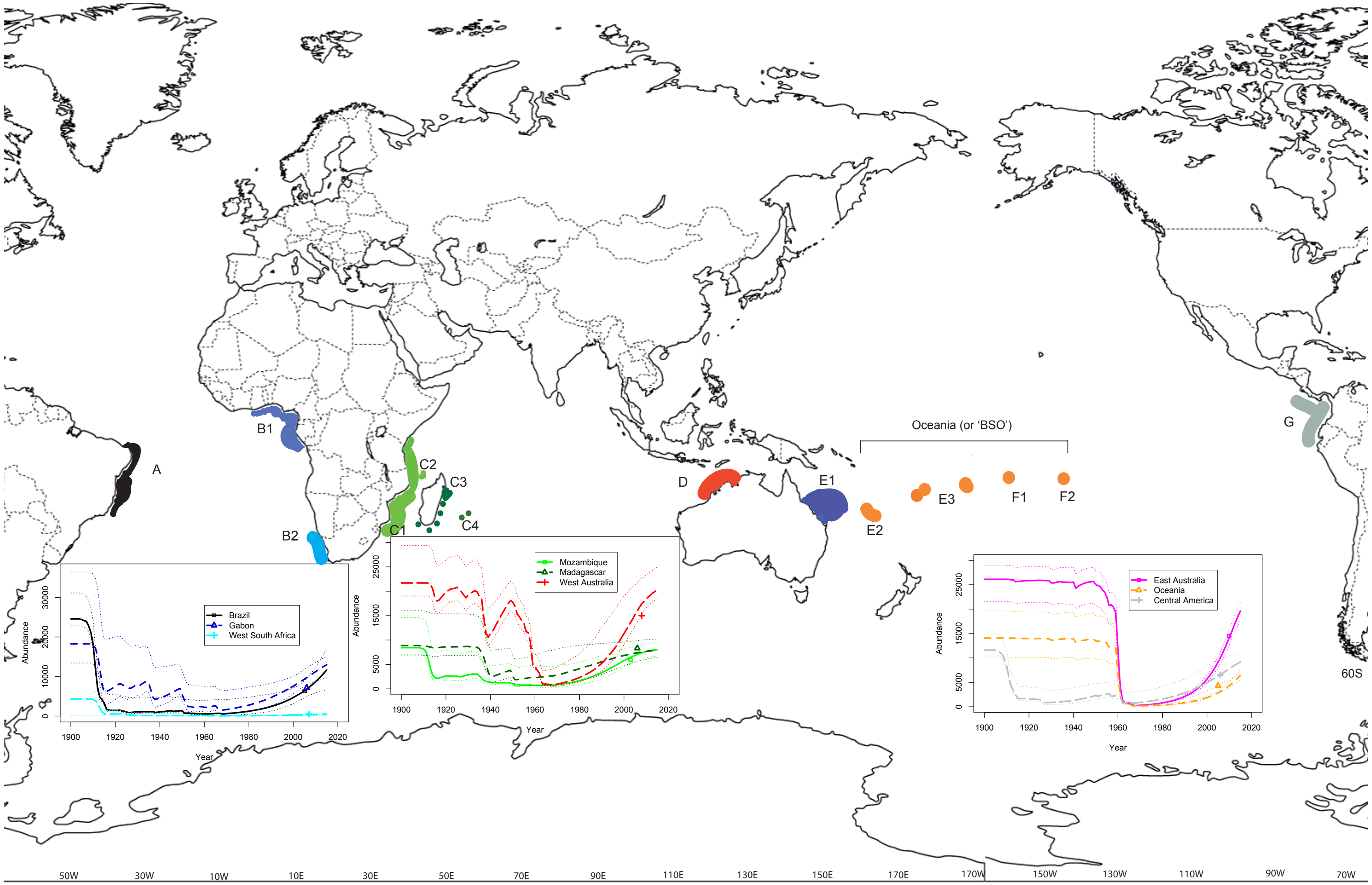

Figure 4. Southern Hemisphere humpback whale population abundance trajectories 1900-2020, plotted by ocean. Line transect estimates of abundance or estimates of abundance from mark recapture data used in the model fitting process are shown as points on the trajectory.

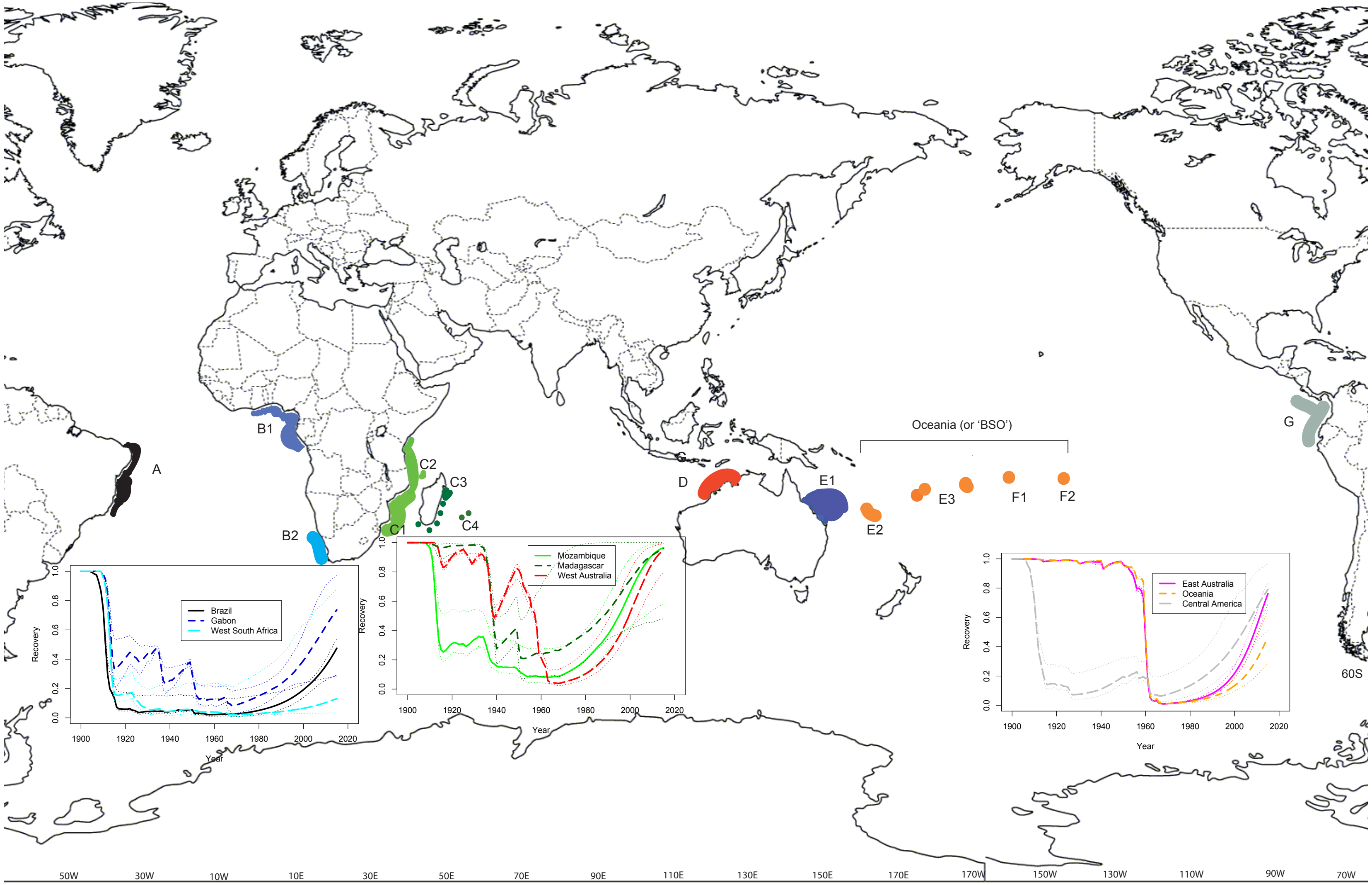

Figure 5. Southern Hemisphere humpback whale recovery levels (relative to 1900 abundance) plotted by ocean from 1900 to 2015.

Table 1. Key challenges undertaken during the Southern Hemisphere humpback whale Comprehensive Assessment

Key challenges	Complications	Causes	How met
Choosing the appropriate scale/s for assessment	Genetic differentiation seemingly at all geographic scales, including temporal and by sex (Carvalho *et al.,* 2014)	Long-term fidelity to different breeding/feeding grounds and sex/age stratification of the humpback migratory stream (Chittleborough 1965)	(1) Conduct assessments at multiple spatial scales to investigate the problem at all possible levels (2) Include exchange parameter to allow for population interchange
High latitude catch allocation to breeding grounds	High latitude feeding areas poorly known, limits unknown. Whales from multiple breeding grounds use common feeding grounds (e.g. Oceania), or migrate to distance breeding ground locations between seasons, suggesting long high-latitude movements.	Whales forage widely in the Southern Ocean (*Discovery* marks and later), feeding zones may shift.	(1) Catch database resolved at 10° longitude for fine scale resolution (2) Satellite tagging from breeding grounds informative about feeding areas (3) Multiple catch allocation scenarios (4) Mixed stock analysis to inform allocation scenarios
Measuring abundance/trend	Sighting surveys prohibitively expensive as populations increase, capture heterogeneity between males/females using low latitude grounds, challenge of surveying appropriate site to 'capture' the population.	Humpbacks have apparently strong temporal fidelity to particular areas and males have longer breeding ground residency times than females (depending on life stage)	(1) Careful survey design (2) Mark recapture modelling done by sex to account for sex-specific capture heterogeneity (3) Consider evidence from multiple independent surveys where possible
Population modelling	Population level data not sufficiently detailed for sex-age-disaggregated population model.	Catches not available to this resolution in most regions, and only from some present-day breeding grounds	Assessment recognizes simplified nature of humpback model but incorporates a number of modifications to improve the realism of the model, including N_{floor}, and incorporating mark recapture data directly.

Table 2. Assessment evidence for substructure within each breeding ground

Breeding ground	**Evidence for sub-structure**	**Divisions used for assessment**
BSA	None seen to date. Genetic studies of whales biopsy-sampled at Abrolhos Bank and Praia do Forte (13°S) found no genetic differentiation between the two regions (Cypriano-Souza *et al.,* 2010). Satellite telemetry shows whales moving freely through the breeding ground so there is not evidence for spatial separation of clusters of whales for either sex (Zerbini *et al.,* 2006).	BSA
BSB	Population structuring between Gabon (BSB1) and western South Africa (BSB2) revealed by mtDNA and microsatellite genotypes (Carvalho *et al.,* 2014; Rosenbaum *et al.,* 2009). There is some temporal heterogeneity among molecular markers for these two regions (Carvalho *et al.,* 2014). Significant haplotypic differentiation found between these regions for all samples (both sexes), and for females suggests that some portion of the whales in the Gulf of Guinea breeding ground do not feed in WSA (likely high latitudes instead, migrating offshore at Walvis Ridge, Rosenbaum *et al.,* 2014) and vice versa that some whales feeding in WSA do not winter in Gabon, indicating the possibility of a distinct breeding ground elsewhere on the west African coast. Inter-annual site fidelity to WSA is relatively high (~15%) and abundance low (~500 whales in 2007) (Barendse *et al.,* 2013; Barendse *et al.,* 2011).	BSB1 and BSB2 together, assuming Gabon abundance represents both sub-stocks. BSB1 and BSB2 separately, assuming Gabon abundance represents BSB1 and WSA abundance represents BSB2.
BSC	Significant mtDNA (F_{ST}) and nuclear (F_{ST} and R_{ST}) differentiation between Madagascar (BSC3 Antongil Bay) and eastern South Africa (BSC1 migratory stream travelling to Mozambique), suggesting restricted interchange between these regions (Rosenbaum *et al.,* 2009). Multi-strata mark recapture modeling of microsatellite genotypes collected from both regions resulted in estimates of exchange probability between mainland East Africa and Madagascar ranging from 0.07 (CI 0.01- 0.38) to 0.13 (CI 0.03 - 0.41) (IWC 2009).	BSC1, BSC3 ('Sabbatical' model as base case, with 'Resident' model as sensitivity)

Breeding ground	Evidence for sub-structure	Divisions used for assessment
BSD	No	BSD
BSE1 + Oceania (BSE2 + BSE3 + BSF2)	MtDNA population structuring between eastern Australia and neighboring breeding grounds in Western Australia, New Caledonia, Tonga, the Cook Islands and French Polynesia were all significant (Olavarría *et al.,* 2006b; Olavarría *et al.,* 2007; Valsecchi *et al.,* 2010), although the Cook Islands was subsequently found to be a migratory corridor for humpbacks travelling towards Tonga and American Samoa (Hauser *et al.,* 2010). Evidence of similar levels of interchange between the islands of Oceania (Garrigue *et al.,* 2011a; Garrigue *et al.,* 2011b) and with East Australia (BSE1, Jackson *et al.,* 2012), with interchange highest between neighbouring grounds, suggesting an isolation-by-distance pattern.	BSE1, Oceania ("BSO"=BSE2+BSE3+BSF2)
BSG	Re-sights in multiple breeding regions inter-annually have been recorded (Flórez-González *et al.,* 1998; Guzman *et al.,* 2014). Mark recapture and satellite telemetry data suggest that whales occupy a broad home range along the coastline (Guzman *et al.,* 2014), with short within-season residency to any one area , although Colombia has had a relatively high re-sight rate in the past (16 % of whales resighted inter-annually between 1986-1988, Flórez-González 1991). Genetic comparisons of individuals biopsy-sampled in Ecuador and Colombia also found significant differentiation between these regions (Félix *et al.,* 2012), suggesting that there may be some degree of breeding ground stratification. There is also a degree of breeding ground migratory preference exhibited by whales on their southern feeding grounds, suggesting that the population structuring within this region may be complex (between multiple breeding and feeding sites) and relatively subtle. BSG is connected to summer feeding grounds in the Magellan Strait (Acevedo *et al.,* 2007) and Antarctic Peninsula (Rasmussen *et al.,* 2007; Stevick *et al.,* 2004). Mark recapture and mtDNA genetic differentiation suggests limited interchange between these feeding grounds (Acevedo *et al.,* 2007; Olavarría *et al.,* 2006a). These data suggest the	BSG

Breeding ground	**Evidence for sub-structure**	**Divisions used for assessment**
	Magellan Strait feeding ground is primarily connected with breeding grounds off Panama and Costa Rica (Acevedo *et al.,* 2007; Capella *et al.,* 2008), while the Antarctic Peninsula feeding ground is primarily connected with breeding grounds off Costa Rica, Ecuador and Colombia (Félix *et al.,* 2012; Rasmussen *et al.,* 2007).	

Table 3. Predicted median abundance, recovery and population growth estimates for all Southern Hemisphere humpback populations projected to 2015, with 2015 recovery levels calculated relative to pre-exploitation abundance in 1900.

Breeding stock	**Median K**	**Median N_{min}**	**Median projected abundance 2015**	**Recovery N2015/K**	**Population growth 2010-2015**	**Assessment model type**	**Reference**
BSA	24,558 (22,791-31,118)	502 (232-3,951)	11,672 (6,649-16,864)	0.47 (0.22-0.73)	6.1%	Single stock	IWC (2007)
BSB1	18,282 (13,435-36,452)	1510 (366-6,363)	12,973 (9,709-15,096)	0.74 (0.29-0.97)	2.9%	Model IIa	IWC (2012a)
BSB2	4,351 (244-6,573)	72 (26-183)	484 (138-860)	0.13 (0.03-0.88)	4.1%	Model IIa	IWC (2012a)
BSC1	8,440 (7,072-14,631)	688 (286-4,578)	8,045 (6,756-9,656)	0.97 (0.58-0.97)	1.1%	Sabbatical with BSC3	IWC (2010a)
BSC3	8,854 (6,906-16,106)	1885 (533-6,094)	7,972 (6,409-10,228)	0.96 (0.48-1.00)	0.7%	Sabbatical with BSC1	IWC (2010a)
BSD	21,686 (19,016-29,383)	824 (461-4,051)	20,337 (18,415-24,918)	0.95 (0.80-0.99)	2.0%	Three-stock, no exchange	IWC (In press)
BSE1	26,114 (21,590-29,011)	237 (203-272)	19,614 (17,644-21,454)	0.76 (0.69-0.84)	6.8%	Three-stock, no exchange	IWC IWC (In press)
BSO	14,103 (10,190-19,630)	132 (103-250)	6,404 (5,491-7,595)	0.47 (0.29-0.66)	8.2%	Three-stock, no exchange	IWC (In press)
BSG	11,584 (10,590-14,878)	732 (238-2960)	9,687 (8,520-10,202)	0.93 (0.74-0.98)	3.4%	Single stock	IWC (2007)
Total[1]	137,972 (111,833-197,781)		96,675 (78,041-117,527)	0.70	3.8%		

[1] Note: Totals are the sums of medians and 95% probability intervals calculated for individual breeding stocks.

Table 4. Unfinished elements of each breeding stock assessment. Key: C (catches), A (abundance), T (trend), PS (population structure), MS (model structure). Impact levels: H (high impact), L (low impact), U (unknown). Recommendations issued by the IWC are detailed.

Breeding stock	Unfinished elements	Impact of missing elements	Recommendations?	Reference
BSA	**C**: catches missing from northeastern Brazilian land station Costinha, 1910 and 1929-1946	**L/M**: likely <400 whales/year. Under-reported catch may cause negative bias in estimated *K*.	None	Zerbini et al. (2007; Zerbini *et al.,* 2011)
BSB1/BSB2	**PS:** Distribution of breeding ground, and boundary between BSB1 and BSB2 is unknown (possibly Walvis Ridge or the Angola/Benguela front). Therefore allocation of catches from coastal stations is uncertain, as is abundance and trend for both populations (see below).	**M**	1. Strategic implementation of satellite tagging effort to assess movements throughout the region and patterns of connectivity 2. Surveys and sampling of understudied areas where humpback whale concentrations are known or suspected, including range-wide sampling of humpback whales for genetics and photo-identification co-ordinated amongst regions. Principal areas: Angola, Namibia, Sao Tomé and Príncipe, Bight of Benin 3. Passive acoustic monitoring to characterise the distribution of humpback whales in less well-studied parts of their range. 4. Extension of coastal surveys and sampling into offshore areas (e.g. further offshore of	IWC (2012c)

Breeding stock	Unfinished elements	Impact of missing elements	Recommendations?	Reference
			the continental shelf). 5. A more comprehensive evaluation of the models and approaches to stock assessments (e.g. multi-stock assessments) that is: - informed by new data collected above; - considers a wider range of possibilities to ensure compatibility of models with data; - takes account of information on whales seen in more than one region.	
	A: Not known whether the feeding ground at WSA represents part or all of the BSB2 sub-population. WSA abundance as a proxy for BSB2 abundance has been assumed for this assessment.	**M**		
	T: there is no trend data for sub-population BSB2. BSB1 trend has been inferred from mark recapture data. These data are not strongly informative in the assessment model.	**H**: Posterior probability intervals very broad, and model fitting does not appear to update the r_{max} priors much.	Long-term study of BSB1 and BSB2 for estimates of trend.	IWC (2012c)

Breeding stock	Unfinished elements	Impact of missing elements	Recommendations?	Reference
	C: Approach to allocate catch between BSB1 and BSB2 is not clear so may be mis-specified in current 2-stock model. Mixed stock analysis from high latitudes not good fit with observed mixing proportions from model.	**H:** impact on the smaller stock (BSB2) likely significant.	Investigate mixed stock analysis further in order to provide more representative inputs for capture-recapture and genetic data. Further genetic sampling in the Antarctic to improve allocation of catches, dependent upon further understanding of the stock structure from low-latitude breeding grounds.	IWC (2012c)
BSB/BSC	**PS:** interchange between BSB and BSC has been documented, but existing assessment models do not take this into account.	**L/M:** level of interchange unknown.		Pomilla and Rosenbaum (2005)
BSC1/BSC3	**PS:** population structuring between BSC1/BSC3 uncertain, northern BSC1 has not been surveyed and may contain BSC3 animals.	**M**: Models have been assessed with different interchange levels assumed.		IWC (2010a)
	A: BSC3 abundance derived from mark recapture data collected from Antongil Bay only. This may be negatively biased if whales show spatial fidelity to other east Madagascar sites outside Antongil Bay.	**L:** Mark recapture data incorporated into model with large variance, so higher abundances accommodated		IWC (2010a)
BSD	**A**: Available data from aerial surveys are non-standard and difficult to convert to absolute abundance.	**H**: assessment models are sensitive to lower bound on abundance. Earlier assessment models were poorly fitting to abundance estimation of	Further refine estimate of BSD abundance.	IWC (In press)

Breeding stock	**Unfinished elements**	**Impact of missing elements**	**Recommendations?**	**Reference**
		28,000 whales in 2007. A		
BSE1	**C**: catch allocation of BSE1 whales, given population mixing with BSD and BSO on feeding grounds.	**L**: assessment model allowed high latitude catches from BSD and BSO to be allocated to BSE1.		IWC (In press)
BSO	**PS**: Significant population structuring within BSO suggests possible demographic independence or stepping stone isolation by distance across Oceania (Olavarría *et al.,* 2007). Assessment groups all Oceania breeding sites as one entity because individual trends/abundance estimates are not available for all sites.	**H**: Mark recapture suggests regular inter-population interchange but also equivalent levels of exchange with BSE1 (see **T** below). Assessment of BSO breeding grounds (in conjunction with BSE1) useful to measure regional recovery.		IWC (In press) Garrigue et al. (2011a) Jackson et al. (2012)
	T: no trend data available for BSO, though there is a recent trend available for New Caledonia with a very high 15% rate suggesting a recent influx of whales from BSE1.	**U**: impact unknown. Mark recapture estimates of trend over all of Oceania uninformative, with 95% CI over 1999-2005 spanning -10% to +18%.		Orgeret et al. (2014) Constantine et al. (2012).
	A: Abundance estimates/ mark recapture dataset sizes not sufficient e for all BSO breeding sites to enable individual assessment.	**U**		Constantine et al. (2012).
BSG	**T**: no trend data available, and IDCR/SOWER relative abundance from feeding grounds is likely a mixture of whales from BSG and BSA.	**H**: Assessment results highly sensitive to the trend and abundance indices used.		IWC (2007)
	A: A 2003/2004 abundance estimate was used in the original assessment. A much larger 2006 abundance estimate	**H**: New abundance estimate is double the size of the 2003/2004 estimate.	The Scientific Committee agreed that no firm conclusion could be drawn about recovery	IWC (2007) Félix et al. (2011a).

Breeding stock	Unfinished elements	Impact of missing elements	Recommendations?	Reference
	has since been published.		level, given the uncertainty surrounding both abundance and trend for BSG	
	PS: Significant mtDNA population structuring within BSG, and significant differentiation between Antarctic Peninsula and Magellan Strait feeding grounds. Population structuring may have analogies with BSB.	**U**		Félix et al. (2012) Acevedo et al. (2007) Olavarría et al. (2006a)

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