

Progress on a two-stock catch allocation model for reconstructing population histories of east Australia and Oceania

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ABSTRACT

Humpback whales breeding along the coast of east Australia (E1) and near the islands of Oceania, South Pacific (E2, E3 and F) are thought to feed primarily in Antarctic Areas V and VI (120E to 110W). These breeding stocks were subject to intensive exploitation by pelagic and coastal whaling operations throughout much of the 20th century and have shown apparently variable levels of recovery. While east Australia has shown high rates of population increase, breeding stocks of Oceania, including those around Fiji and those that migrate past New Zealand, virtually disappeared and have yet to show signs of strong recovery. Reconstructing the history, and subsequent recovery of these populations is hampered by the difficulty of allocating historical feeding ground catch to each breeding ground population. Here we present progress on a two-stock Bayesian density-dependent logistic population model, developed to explore the influence of different catch allocations on the recovery of east Australia and Oceania. Probability distributions of carrying capacity (K), growth rate (r_{max}) and current abundance (N_{2009}) were determined for all whales breeding within east Australia (E1) and Oceania (E2, E3, F). Estimates of current abundance were provided by capture-recapture modeling, using individual identification photographs collected from 1999-2004. Sensitivity of the population model estimates to prior distribution choice, catch allocation (Naïve and Fringe 'maximum') and minimum past abundance (N_{min}) were investigated. Median posterior estimates of carrying capacity for east Australia and Oceania were 22,000-25,700 and 17,800-20,600 respectively. Median recovery estimates (N_{2009}/K) for the two-stock model with ranged from 44-46% (east Australia) and 23-30% (Oceania).

INTRODUCTION

Within the south Pacific, several breeding sub-populations of humpback whales (*Megaptera novaeangliae*) are recognized. These breeding populations migrate south annually to feeding grounds in Antarctic Areas V and VI (120E to 110W). Breeding stock E encompasses whales breeding off the coasts of east Australia (E1), New Caledonia (E2) and Tonga (E3) while breeding stock F encompasses whales breeding in French Polynesia and the Cook Islands. Population subdivisions within E and F are supported by analyses of maternal genetic differentiation (Olavarria *et al.* 2006). Discovery marks and photo-identification have linked eastern Australia stock E1 with Antarctic Area V (Chittleborough 1959; Dawbin 1964; Franklin *et al.* 2007)). Within Oceania, satellite tagging has connected Cook Islands whales with Area VI (Hauser *et al.* 2007), while genotype matching has confirmed connections between New Caledonia and Area V and Tonga and Areas VI and I (Steel *et al.* 2008).

Commercial fleets have been hunting humpbacks in the southern ocean since the start of the 20th century. Within Area V and VI, over 44,000 animals were killed between 1900 and 1978. Coastal whaling was also active in New Zealand, Norfolk Islands, east Australia and locally across a number of the Pacific islands. While whaling officially ceased in 1966, the Soviet Union continued illegal whaling throughout the Southern Ocean until 1973 (Yablokov *et al.* 1998). Many of the regional populations of south Pacific humpbacks underwent a severe decline in abundance, marked by the collapse of coastal fisheries throughout the Pacific and Australia in 1963.

Within the south Pacific, matching of humpback fluke photographs suggests that there is a more substantial sub-division between humpbacks wintering off east Australia (breeding population E1) and within Oceania (breeding populations E2, E3 and F). Photo-ID comparisons among the islands of Oceania ($n=679$ individuals) have documented 20 incidents of interchange (Garrigue *et al.* 2007a). However, recent comparison between this Oceania catalogue and a substantial catalogue from east Australia (Harvey Bay and Byron bay, $n=1,242$) found only four incidents of interchange (Garrigue *et al.* 2007b). The low level of interchange both within and between these regions supports the genetic data in suggesting that movement of humpbacks between these breeding populations is restricted.

Further evidence for demographic isolation between breeding populations in the south Pacific is provided by large differences in apparent recovery between populations. Comparisons of historical sightings data and whaling records (Dawbin 1956; Dawbin 1959; 1964) with recent sightings surveys from Fiji, New Zealand and Norfolk Island (Childerhouse and Gibbs 2006; Gibbs *et al.* 2006; Paton *et al.* 2006) suggest a lack of recovery and very slow return of humpbacks to these regions, while in east Australia the population is increasing at the rate of 10-11% per annum (Noad *et al.* 2008).

Conducting an assessment of the status of humpback populations in the south Pacific region is complicated by the challenge of catch allocation; all humpbacks share feeding grounds in Areas V and VI, where the substantial proportion of catches were taken. The division between Areas V and VI is directly due south of the Tongan (E3) population, one of the most abundant populations in the region (Baker *et al.* 2006). Microsatellite genotyping has connected animals from Tonga with three feeding Areas (Steel *et al.* 2008), illustrating the difficulty of allocating feeding Area catches to individual breeding populations with accuracy. Previous population assessments of humpbacks wintering in the south Pacific have focused on population E1 (Johnston and Butterworth 2005) and stocks E and F combined (Jackson *et al.* 2006). We present here progress on a two-stock model for assessing the status of south Pacific humpbacks. In this model, the two 'stocks' considered are east Australia (E1) and Oceania (E2, E3 and F).

In this preliminary population assessment we develop a Bayesian logistic 'HITTER' model to accommodate scenarios where the two stocks are subject to separate population growth rates (r), different levels of historical catch, different constraints on minimum past abundance (N_{min}) and recover towards different current abundances. We present results from an approach where feeding Area catches are proportionally allocated based on the yearly abundances of the two stocks. Key goals for future work to complete an assessment are identified in the discussion.

METHODS

A handful of population assessment scenarios were considered and explored for sensitivity to Antarctic catches (IWC Naïve and 'Fringe maximum' catch scenarios) and to the distribution of population growth rates (between 0 to 10.6%).

Catch Data

Catches south of 40°S

Pelagic catch data from the Soviet Antarctic whaling operation, detailing the magnitude and location of catches made in the 1960s, have been made available previously (Yablokov *et al.* 1998). The present updated catch series (Allison pers. comm.) represents the most comprehensive catch information covering 20th century whaling in the Antarctic so far. A Naïve catch allocation scenario was explored (IWC 2006a) in which all catches taken between 120E-110W were included in the population model. In order to reflect recent work showing that some humpbacks from within Oceania feed outside Feeding Areas V and VI {Hauser, 2007 #83; Steel, 2008 #89; Robbins, 2008 #384}, we also applied a maximal catch scenario ("Fringe maximum", as suggested in (IWC 2006b)) where all catches between 110E-100W were included in the population model (Table 1).

Catches north of 40°S

Recent evidence links New Zealand both to east Australia (Franklin *et al.* 2008) and Oceania stock E2 {Constantine, 2007 #93; Clapham, 2008 #385} but the strength of these connections has not yet been quantified. Allocation of New Zealand and Norfolk Island coastal catches (Allison pers. comm.) to the two stocks was therefore fixed at 50%, assuming equal use of these regions as a migratory corridor by both stocks.

Coastal catches from east Australia (E1) and Tonga (E3) were allocated to east Australia and Oceania stocks respectively.

Abundance Estimates

A number of capture-recapture analyses have been reported for Oceania both in combination and by region (Baker *et al.* 2006). The M_{th} closed capture-recapture estimate for the combined multi-year 1999-2004 abundance of E2, E3 and F ($n = 3,827$; C.V. = 0.12) was chosen from among the estimates reported because it was considered to be the most robust model for these data (Baker *et al.* 2006).

Abundance of the east Australian stock in 2004 was approximated by a recent shore count estimate $n = 7,090$ (95% confidence intervals ± 660) by Noad *et al.* (2006). This estimate was assumed to conform to a normal distribution in the logistic model.

Population Trends

Since 1978, land-based surveys have been carried out at Point Lookout, North Stradbroke Island (27°30'S) in east Australia (E1) during the peak of the northbound humpback migration (mid-June to mid-July). Two sets of surveys were conducted by independent teams working at this location between 1978 and 2000. One was initiated by Michael Bryden and continued by Miranda Brown until 2000 (Brown, 1997) while the other was conducted by Robert and Patricia Paterson with data analysis by Douglas Cato (Paterson *et al.* 2004). Both sets of surveys are now carried out by Michael Noad and his survey team. As formalized in Noad (2006, 2008), we shall refer to these data as the 'Bryden-Brown' surveys and the 'Paterson-Cato' surveys respectively. No formal trend data are presently available from Oceania.

Trend data from the Bryden-Brown surveys have been included in the current model. Trend data were incorporated into the model as described in Zerbini *et al.* (2006). The Bryden-Brown index of abundance (Brown, 1997) for stock E1 was scaled to the model predicted population size in each year i using a scale co-efficient, ' q ' and assuming a log-normal distribution for residuals (see Zerbini 2006, equation 3).

Population Dynamics Model

The logistic population dynamic 'HITTER' model used in this study is conceptually similar to that presented by Zerbini (2004). Integration of prior distributions on the parameters and the likelihood function was approximated using the Sampling-Importance-Resampling (SIR) algorithm of Rubin (1988), as described in Zerbini (2004), with trend data weighted as described in Zerbini 2006, equation 5). An initial sample of 2,000 parameter combinations from the data was re-sampled 100 times with the SIR algorithm. Posterior distributions were then summarized over these 100 re-samples. These numbers are low due to the computational time required to perform analyses.

The density-dependent age-aggregated generalized logistic equation used to model the dynamics of this population follows the standard form

$$N_{y+1} = N_y + r N_y \left(1 - \left(\frac{N_y}{K} \right)^z \right) - C_y$$

Where N_y represents the population abundance in year y , K the population initial carrying capacity (N_y in year 0), z the density dependent exponent (fixed at 2.39) and C_{yA} and C_{yB} the total catch in year y for stocks A (representing E1) and B (representing E2/E3/F) respectively. Parameter r represents the intrinsic growth rate of the population.

Catch is modelled as follows:

Stock A:

$$C_{y+I(A)} = C_{yCA} + C_{yP} \left(\frac{N_{yA}}{N_{yA} + N_{yB}} \right)$$

Stock B:

$$C_{y+I(B)} = C_{yCA} + C_{yP} \left(\frac{N_{yB}}{N_{yA} + N_{yB}} \right)$$

C_{yC} and C_{yP} represent annual coastal (north of 40°S) and pelagic (south of 40°S) catches respectively (Appendix 1).

The logistic equation was implemented in parallel for the two stocks. The best fitting K for any given parameter combination was found using the bisection method for stock A, while K for stock B was initially determined by choosing a random ratio (on a log scale between 0.01 and 100) of the initial K for stock A.

Prior Distributions

Two priors on population growth rates for Stock 'E2/E3/F' were used; one uninformative (U [0.00-0.106]) and one informative (N [0.067, 0.04]). The latter was bounded by the limits of the uninformative prior, recognizing that humpback growth rates over 10.6% are extremely unlikely (IWC 2007). The prior, N [0.067, 0.04], previously used by Zerbini (2004), is based on the average growth rate estimated from a hierarchical meta-analysis of growth rates of large baleen whales (Branch *et al.* 2004).

Initial prior distributions on N_{2004} were set at U [6,000-9,000] for east Australia and U [2,000-5,000] for Oceania. These were then subject to importance re-sampling against the normally-distributed abundance estimates provided in the *Abundance* section above.

Genetic Constraints for N_{min}

Humpbacks of the south Pacific have maintained substantial mitochondrial diversity despite a severe whaling history (Olavarria *et al.* 2007). A total of 42 haplotypes have been identified in east Australia (Olavarria *et al.* 2006) and a total of 78 in Oceania (Olavarria *et al.* 2007). In the preliminary assessment of this population, a hard lower boundary of 4 x haplotypes was used as a constraint on minimum past abundance (N_{min}). This is an underestimate of the N_{min} value that would be obtained by rarefaction and proper correction (see Branch and Jackson 2008; Jackson *et al.* 2008). Sensitivity of the model to each these boundaries was also explored by repeating analyses with and without each constraint.

RESULTS AND DISCUSSION

The assessment scenarios explored in this study are shown in Table 1 while a summary trajectory of the population history reconstructed under scenario 3 is shown in Figure 1. Posterior distributions of model parameters are shown in Table 2. This initial estimate of population parameters (100 re-samples) has been limited by the short computational time available. However the spread of the re-sample data (Table 1) is relatively narrow, suggesting that longer analyses will remain consistent with initial estimates.

Low estimates of population growth in Oceania are strongly favoured by the model (median estimates 5.1-6.4%), while much narrower growth rate estimates in east Australia mirrored that of the Bryden-Brown trend data (median estimates 10.4-10.5%). The model was insensitive to the effect of increased historical catches (~3,000 whales) provided by the 'Fringe maximum' scenario, and the choice of different growth rate priors (uninformative vs informative), although differences may not yet be discernable due to the low number of summarized re-samples. Estimates of pre-exploitation abundance were slightly higher for east Australia (median range 22,000-25,700) than for Oceania (median range 17,800-20,600). Similar median levels of pelagic catches were allocated to both populations (20-24,000 for east Australia, 20-23,000 for Oceania), while the initial catch ratio favoured by the model fell into a narrow range (medians 52-59%) across all scenarios explored.

Minimum past abundance

Posterior estimates of minimum abundance (N_{min}) for east Australia were significantly lower than those obtained for Oceania (median values 190-205 for east Australia, 550-680 for Oceania across all scenarios). The lower 95% confidence interval for east Australian minimum abundance across all scenarios is <10 greater than the genetic-based constraint on minimum abundance (168) for that stock, suggesting that the N_{min} constraint is exerting a strong influence on the allowable population trajectories for this population high growth rate.

Future directions

Population growth rates and trend information

We hope to shortly update this model with additional available historical trend information (Brown *et al.* 1997; Baker *et al.* 2006; Chittleborough 1965; Noad *et al.* 2008; Paterson *et al.* 2004) and a much increased sampling of the population model, to obtain up to 50,000 replicates and 2,500 re-samples for each scenario. Computational time may also be improved by re-coding the model in an alternative programming language.

Recent studies suggest that a proportion of females over-winter on feeding grounds, an effect which may explain the observed skew in humpback sex ratios towards males both on wintering grounds (Craig and Herman 1997; Pomilla and Rosenbaum 2006) and on migratory routes (Brown *et al.* 1995). In order to explore the effect of this bias on the population model, future modelling scenarios for Oceania should include a male-only population reconstruction, using sex-specific mark-recapture abundance estimates obtained from genetic markers.

Historical catches

The impact of the whaling industry in Tonga (E3) cannot be fully accounted for due to a lack of records (p37; IWC 2006). Additionally anecdotal information suggests that Soviet whalers may have hunted whales in Fiji and Tonga in the 1960s (Ivashchenko *et al.* 2007). The assumption that New Zealand catches took roughly 50% of each stock may also be erroneous. More information regarding location of capture and time of year might enable a more reasoned allocation to be made. For example Franklin *et al.* (2008) have suggested that humpbacks travelling toward or from different breeding populations adhere to geographically separate migratory streams as they pass through New Zealand.

In the current model all Area V and Area VI catches have been grouped and allocated among the two stocks. However there is very little evidence connecting east Australian whales with Antarctic Area VI. Sensitivity of the model to allocation of all Antarctic Area VI catches to the Oceania is yet to be explored. The allocation of Antarctic Area catches according to a mixed-stock analysis of current mtDNA distributions could be informative (Albertson-Gibb *et al.* 2008).

Effect of N_{min}

The N_{min} values used as lower boundaries in this model underestimate the values that would be obtained by rarefaction and proper correction (see Branch and Jackson (2008) and Jackson *et al.* (2008)). Future modeling should attempt to improve this, particularly in the context of east Australia, where model minimum abundance estimates fall very close to genetic based constraints on N_{min} .

Further modelling scenarios

We have also developed a second HITTER two-stock model scenario to explore catch allocation. In this model the ratio of Antarctic pelagic catch allocation between the two stocks in year n is provided by the ratio of breeding ground abundances in year $(n - 1)$. Yearly catches are described by

$$C_{y+1} = C_{yC} + C_{yP} \left(\frac{N_{yA}}{(N_{yA} + N_{yB})} \right)$$

Where catch parameters C_{yC} and C_{yP} represent annual coastal (north of 40°S) and pelagic (south of 40°S) catches respectively (Table 1) and N values represent abundances of stocks *A* and *B* in year y . This could be developed as a further means of testing the influence of catch allocation on the estimated recovery of these populations. This model also lends itself to further development as a multi-stock assessment where feeding ground catches cannot be easily determined.

Conclusions

A number of additional scenarios need to be explored in order to provide a fuller picture of the current status of the humpbacks of Oceania. A full assessment of each sub-stock is limited by the substantial uncertainty surrounding the historical catches attributable to each stock. However, some inter-annual interchange has been found among humpbacks wintering in Oceania, suggesting that an assessment of the combined region is plausible. We describe two modelling approaches by which an assessment of this region may be performed and identify those model parameters for which further exploration is necessary.

ACKNOWLEDGEMENTS

JAJ was supported by a grant to CSB and S. R. Palumbi from the Lenfest Oceans Program of the Pew Charitable Trust. We thank the many members of the South Pacific Whale Research Consortium for access to data and for advice on population dynamics of humpback whales in east Australia and Oceania.

REFERENCES

- Albertson-Gibb, R., C. Antolik, C. Olavarría, C. Garrigue, N. Hauser, M. Poole, M. Brasseur, D. Steel and C.S. Baker. 2008. Using mitochondrial DNA and mixed-stock analysis to describe migratory allocation of humpback whales from Antarctic feeding areas to South Pacific breeding grounds. Paper SC/60/SH15 presented to the IWC Scientific Committee, May 2008 (unpublished). XXpp. [Available from the office of this Journal].
- Baker, C.S., C. Garrigue, R. Constantine, B. Madon, M. Poole, N. Hauser, P. Clapham, M. Donoghue, K. Russell, T. O'Callahan, D. Paton and D. Mattila. 2006. Abundance of humpbacks in Oceania (South Pacific) 1999 to 2004. Paper SC/A06/HW51 submitted to the IWC southern hemisphere humpback workshop, Hobart, April 2006.
- Branch, T. and J.A. Jackson. 2008. Minimum bottleneck abundance of Antarctic blue whales based on current mtDNA diversity. Paper SC/60/SH10 presented to the IWC Scientific Committee, May 2008 (unpublished). 7pp. [Available from the office of this Journal].
- Branch, T.A., K. Matsuoka and T. Miyashita. 2004. Evidence for increases in Antarctic blue whales based on Bayesian modelling. *Marine Mammal Science* 20:726-754.
- Brown, M.R., P.J. Corkeron, P.T. Hale, K.W. Schultz and M.M. Bryden. 1995. Evidence for a sex-segregated migration in the humpback whale (*Megaptera novaeangliae*). *Proceedings of the Royal Society of London- Series B: Biological Sciences* 259:229-234.
- Brown, M.R., M.S. Field, E.D. Clarke, D.S. Butterworth and M.M. Bryden. 1997. Estimates of abundance and rate of increase for East Australian humpback whales from the 1996 Land-based survey at Point Lookout, North Stradbroke Island, Queensland. Paper SC/49/SH35 presented to the IWC Scientific Committee, May 1997 (unpublished). 15pp. [Available from the office of this Journal].

Childerhouse, S. and N. Gibbs. 2006. Preliminary report for the Cook Strait Humpback Whale Survey 2006. Unpublished report to the Department of Conservation, New Zealand: 6pp.

Chittleborough, R.G. 1959. Australian marking of humpback whales. *Norsk Hvalfangst Tidende* 48:47-55.

Chittleborough, R.G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Australian Journal of Marine Freshwater Research* 16:33-128.

Clapham, P., P. Wade and A. Zerbini. 2006. Plausible rates of population growth in humpback whales revisited. Paper SC/58/SH4 presented to the IWC Scientific Committee, May 2006 (unpublished). 12pp. [Available from the office of this Journal].

Constantine, R., K. Russell, N. Gibbs, S. Childerhouse and C.S. Baker. 2007. Photo-identification of humpback whales (*Megaptera novaeangliae*) in New Zealand waters and their migratory connections to breeding grounds of Oceania. *Marine Mammal Science* 23:715-720.

Craig, A.S. and L.M. Herman. 1997. Sex differences in the site fidelity and migration of humpback whales (*Megaptera novaeangliae*) to the Hawaiian islands. *Canadian Journal of Zoology* 75:1923-1933.

Dawbin, W.H. 1956. The migration of humpback whales as they pass the New Zealand Coast. *Transactions of the Royal Society of New Zealand* 84:147-196.

Dawbin, W.H. 1959. New Zealand and South Pacific whale marking and recoveries to the end of 1958. *Norsk Hvalfangsttid* 48.

Dawbin, W.H. 1964. Movements of humpback whales marked in the southwest Pacific Ocean 1952 to 1962. *Norsk Hvalfangsttid* 53.

Dawbin, W.H. 1997. Temporal segregation of humpback whales during migration in southern hemisphere waters. *Memoirs of the Queensland Museum* 42:105-138.

Franklin, T., F. Smith, N. Gibbs, S. Childerhouse, D. Burns, D. Paton, W. Franklin, C.S. Baker and P. Clapham. 2007. Migratory movements of humpback whales (*Megaptera novaeangliae*) between eastern Australia and the Balleny Islands, Antarctica, confirmed by photo-identification. Paper SC/59/SH18 presented to the IWC Scientific Committee, May 2007 (unpublished). 5pp. [Available from the office of this Journal].

Franklin, W., T. Franklin, L. Brooks, N. Gibbs, S. Childerhouse, D. Burns, D. Paton, C. Garrigue, R. Constantine, M. Poole, N. Hauser, M. Donoghue, K. Russell, D.K. Mattila, J. Robbins, M. Anderson, C. Olavarria, J.A. Jackson, M. Noad, P. Harrison, P. Baverstock, R. Leaper, C.S. Baker and P. Clapham. 2008. Eastern Australia (E1 breeding grounds) may be a wintering destination for Area V Humpback Whales (*Megaptera novaeangliae*) migrating through New Zealand waters. Paper SC/60/SH3 presented to the IWC Scientific Committee, May 2008 (unpublished). 14pp. [Available from the office of this Journal].

Garrigue, C., C.S. Baker, R. Constantine, M. Poole, N. Hauser, P. Clapham, M. Donoghue, K. Russell, D. Paton, D.K. Mattila and J. Robbins. 2007a. Interchange of humpback whales in Oceania (South Pacific) 1999 to 2004 (revised SC/A06/HW55, March 2007). Paper SC/59/SH14 presented to the IWC Scientific Committee, May 2007 (unpublished). 10pp. [Available from the office of this Journal].

Garrigue, C., T. Franklin, K. Russell, D. Burns, M. Poole, D. Paton, N. Hauser, M. Oremus, R. Constantine, S. Childerhouse, D. Mattila, N. Gibbs, W. Franklin, J. Robbins, P. Clapham and C.S. Baker. 2007b. First assessment of interchange of humpback whales between Oceania and the east coast of Australia. Paper SC/59/SH15 presented to the IWC Scientific Committee, May 2007 (unpublished). 9pp. [Available from the office of this Journal].

Gibbs, N., D. Paton, S. Childerhouse and P. Clapham. 2006. Assessment of the current abundance of humpback whales in the Lomaiviti Island Group of Fiji and a comparison with historical data. Paper SC/A06/HW34 submitted to the IWC southern hemisphere humpback workshop, Hobart, April 2006.

Hauser, N., A. Zerbini, Y. Geyer, M.-P. Heide-Jørgensen and P. Clapham. 2007. Migratory destination of a humpback whale satellite-tagged in the Cook Islands. Paper SC/59/SH16 presented to the IWC Scientific Committee, May 2007 (unpublished). 4pp. [Available from the office of this Journal].

Ivashchenko, Y.V., P. Clapham, N.V. Doroshenko, D. Paton and R.L. Brownell Jr. 2007. Possible Soviet catches of humpback whales in Fiji and Tonga. Paper SC/59/SH20 presented to the IWC Scientific Committee, May 2007 (unpublished). 1pp. [Available from the office of this Journal].

IWC. 2006a. Annex H: Report of the sub-committee on the Other Southern Hemisphere Whale Stocks. Journal of Cetacean Research Management (Supplement) 8:151-176.

IWC. 2006b. Report of the Workshop on the Comprehensive Assessment of Southern Hemisphere Humpback Whales. Report SC/58/Rep5 to the International Whaling Commission, May 2006. [Available from the office of this Journal].

IWC. 2007. Annex H: Report of the sub-committee on the Other Southern Hemisphere Whale Stocks. Journal of Cetacean Research Management (Supplement)

Jackson, J.A., N.J. Patenaude, E.L. Carroll and C.S. Baker. 2008. How many whales were there after whaling? Inference from contemporary mtDNA diversity. Molecular Ecology 17:236-251.

Jackson, J.A., A. Zerbini, P. Clapham, C. Garrigue, N. Hauser, M. Poole and C.S. Baker. 2006. A Bayesian assessment of humpback whales on breeding grounds of eastern Australia and Oceania (IWC Stocks E1, E2, E3 and F). Paper SC/A06/HW52 submitted to the IWC southern hemisphere humpback workshop, Hobart, April 2006.

Johnston, S.J. and D.S. Butterworth. 2005. A Bayesian assessment of the west and east Australian breeding populations (stocks D and E) of Southern Hemisphere humpback whales. Paper SC/57/SH15 presented to the IWC Scientific Committee, May 2005 (unpublished). 25pp. [Available from the office of this Journal].

Noad, M., D.H. Cato and D. Paton. 2006. Absolute and relative abundance estimates of Australian east coast humpback whales. Paper SC/A06/HW27 submitted to the IWC southern hemisphere humpback workshop, Hobart, April 2006.

Noad, M. J., R. A. Dunlop, D. Paton, and D. H. Cato. 2008. An update of the east Australian humpback whale population (E1) rate of increase. Paper SC/60/SH31 presented to the IWC Scientific Committee, May 2008 (unpublished). 13pp. [Available from the office of this Journal].

Olavarría, C., M. Anderson, D. Paton, D. Burns, M. Brasseur, C. Garrigue, N. Hauser, M. Poole, S. Caballero, L. Flórez-González and C.S. Baker. 2006. Eastern Australia humpback whale genetic diversity and their relationship with Breeding Stocks D, E, F and G. Paper SC/58/SH25 presented to the IWC Scientific Committee, May 2006 (unpublished). 6pp. [Available from the office of this Journal].

Olavarría, C., C.S. Baker, C. Garrigue, M. Poole, N. Hauser, S. Caballero, L. Flórez-González, M. Brasseur, J. Bannister, J. Capella, P.J. Clapham, R. Dodemont, M. Donoghue, C. Jenner, M.-N. Jenner, D. Moro, M. Oremus, D.A. Paton, H. Rosenbaum and R. K. 2007. Population Structure of South Pacific humpback whales and the origin of the eastern Polynesian breeding grounds. Marine Ecology Progress Series 330:257-268.

Paterson, R., P. Paterson and D.H. Cato. 2004. Continued increase in east Australian humpback whales in 2001, 2002. Memoirs of the Queensland Museum 49:712.

Paton, D., A. Oosterman, M. Whicker and I. Kenny. 2006. Preliminary assessment of sighting survey data of humpback whales, Norfolk Island, Australia. Paper SC/A06/HW36 submitted to the IWC southern hemisphere humpback workshop, Hobart, April 2006.

Pomilla, C. and H.C. Rosenbaum. 2006. Estimates of relatedness in groups of humpback whales (*Megaptera novaeangliae*) on two wintering grounds of the Southern Hemisphere. Molecular Ecology 15:2541-2555.

Rubin, D.B. 1988. Using the SIR algorithm to simulate posterior distributions. Page 805 in J.M. Bernardo, M.H. DeGroot, D.V. Lindley and A.F.M. Smith, eds. Bayesian Statistics 3: Proceedings of the Third Valencia International Meeting. Clarendon Press, Oxford.

Steel, D., C. Garrigue, M. Poole, N. Hauser, C. Olavarría, L. Flórez-González, R. Constantine, S. Caballero, D. Thiele, D. Paton, P. Clapham, M. Donoghue and C.S. Baker. 2008. Migratory connections between humpback whales from South Pacific breeding grounds and Antarctic feeding areas demonstrated by genotype matching. Paper SC/60/SH13 presented to the IWC Scientific Committee, May 2008 (unpublished). 9pp. [Available from the office of this Journal].

Yablokov, A.V., V.A. Zemsky, Y.A. Mikhalev, V.V. Tormosov and A.A. Berzin. 1998. Data on Soviet whaling in the Antarctic in 1947-1972 (population aspects). *Russian Journal of Ecology* 29:38-42.

Zerbini, A.N. 2004. Status of the Southern Hemisphere humpback whale breeding stock A: preliminary results from a Bayesian assessment. Paper SC/56/SH17 presented to the IWC Scientific Committee, May 2004 (unpublished). 18pp. [Available from the office of this Journal], Sorrento, Italy.

Zerbini, A. N. 2005. An updated Bayesian assessment of the Southern Hemisphere humpback whale Breeding Stock A. Paper SC/57/SH17 presented to the IWC Scientific Committee, May 2005 (unpublished). 7pp. [Available from the office of this Journal]

Zerbini, A. N., E. Ward, P. G. Kinas, M. H. Engel, A. Androlio, A. 2006. A Bayesian assessment of the conservation status of humpback whales (*Megaptera novaeangliae*) in the Western South Atlantic Ocean. Paper SC/58/SH2 presented to the IWC Scientific Committee, May 2004 (unpublished). 32pp. [Available from the office of this Journal]

TABLES

Table 1. Scenarios explored in a preliminary assessment of the two-stock model of catch allocation. Boundaries of Naïve and Fringe “max” catch allocation are shown in Appendix 1.

Scenario	E2/E3/F growth rates (r)	Antarctic catch allocation
1	Uniform [0-0.12]	Naïve (120E-110W)
2	Normal [0.067, 0.04]	Naïve (120E-110W)
3	Uniform [0-0.12]	Fringe max (110E-100W)
4	Normal [0.067, 0.04]	Fringe max (110E-100W)

Table 2. Posterior estimates of parameters of interest for stock E1 and combined stocks E2+E3+F. 95% posterior probability intervals are shown in square brackets.

Median posterior estimates						
East Australia (E1)						
Scenario	K	r_{max} (%)	N_{min}	N_{2004}	N_{2009}	$N_{2009} : K$
1	22,093 [20,062-26,673]	10.5 [10.2-10.6]	196 [168-243]	6,796 [6,007-8,239]	10,614 [9,630-12,773]	0.46 [0.38-0.54]
2	24,073 [16,457-25,435]	10.4 [10.2-10.6]	205 [175-235]	6,649 [6,238-7,951]	10,489 [9,629-12,264]	0.46 [0.41-0.60]
3	25,681 [22,008-27,499]	10.5 [10.3-10.5]	192 [175-242]	6,828 [6,196-7,957]	10,750 [9,937-12,496]	0.44 [0.37-0.52]
4	24,305 [16,282-25,804]	10.5 [10.4-10.6]	194 [178-220]	7,096 [6,519-8,246]	10,851 [10,191-12,915]	0.46 [0.41-0.65]
Oceania (E2, E3, F)						
Scenario	K	r_{max}	N_{min}	N_{2004}	N_{2009}	$N_{2009} : K$
1	20,576 [14,573-24,019]	5.1 [3.8-7.4]	676 [376-1,209]	3,805 [3,272-4,902]	4,801 [4,117-6,293]	0.23 [0.20-0.41]
2	17,818 [16,225-31,974]	5.6 [1.5-6.3]	529 [393-2,566]	4,016 [3,048-4,327]	5,129 [3,809-5,760]	0.27 [0.14-0.33]
3	17,939 [15,631-23,605]	6.4 [3.9-7.4]	445 [348-766]	3,935 [2,945-4,220]	5,290 [3,564-5,913]	0.30 [0.15-0.37]
4	19,734 [17,506-36,119]	5.8 [0.8-6.8]	553 [418-2,769]	4,190 [3,272-4,706]	5,472 [3,811-6,052]	0.26 [0.11-0.33]

Table 3. Posterior estimates of parameters common to both stocks and total catches allocated to each population. 95% posterior probability intervals are shown in square brackets.

Scenario	Initial Catch ratio O / EA	Median posterior estimates	
		Median total pelagic catch EA	Median total pelagic catch Oceania
1	0.518 [0.455-0.646]	20,136 [17,249-26,131]	22,982 [17,987-26,869]
2	0.575 [0.340-0.611]	22,872 [12,298-24,648]	21,246 [19,470-31,820]
3	0.589 [0.482-0.638]	25,067 [20,085-27,556]	21,981 [19,492-26,963]
4	0.552 [0.311-0.596]	23,276 [12,105-25,396]	23,772 [21,652-34,943]

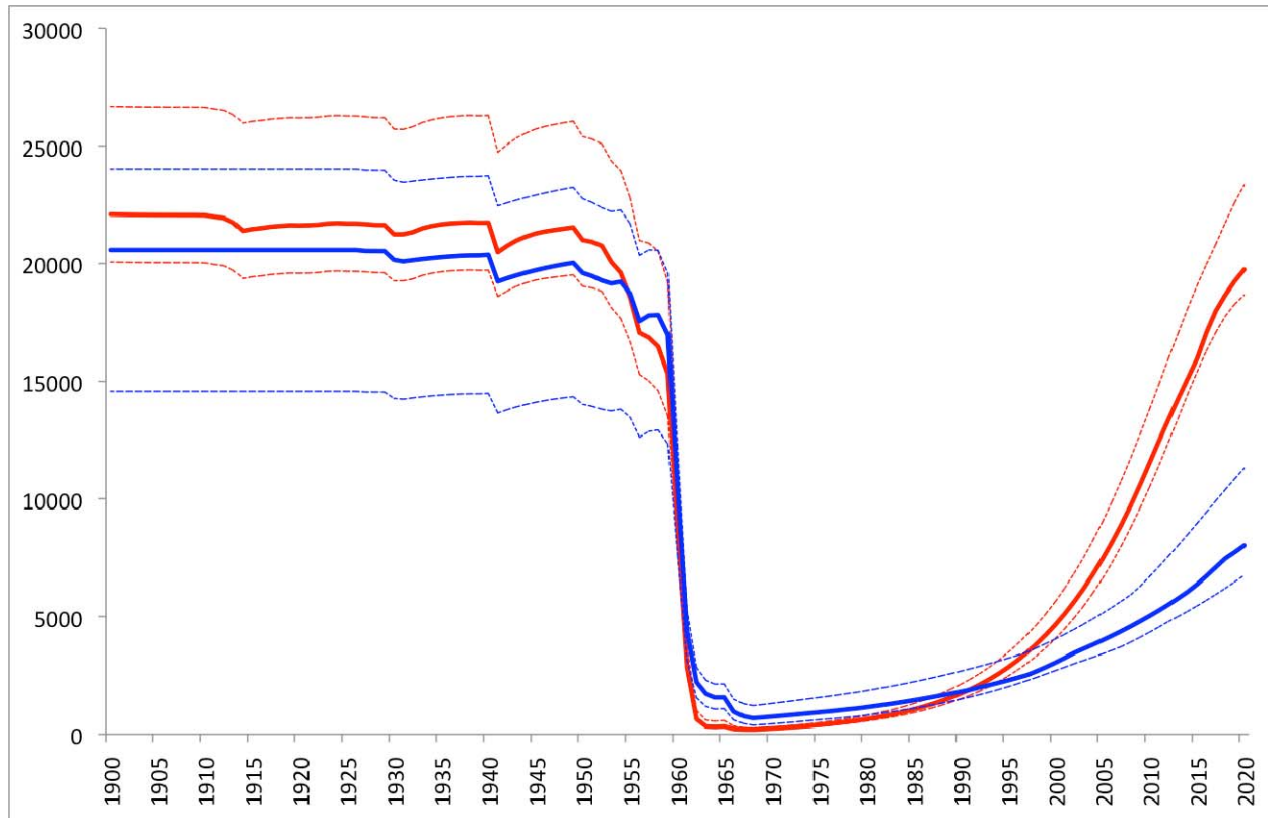


Figure 1. Population trajectories for Oceania and east Australia (Naïve model and uninformative growth rate prior r ; Scenario 1) showing changes in population abundance (N) over time. Median trajectory (solid line) and 95% posterior probability intervals (dashed lines) are shown in bold for Oceania and pale for east Australia.

APPENDIX

Appendix 1. Record of catches taken for southern hemisphere humpback whales feeding in Areas V and VI (south of 40°S) and coastally in this region (north of 40°S) between 1900-1978 (Allison pers. comm.). Naïve catches for the region encompassed 120E-110W and Fringe “maximum” catches for the region encompassed 110E-100W. Coastal catch from east Australia was allocated to E1, catch from New Zealand was divided 50% to E1 and 50% to E2+E3+F. All catches from Tonga (Dawbin 1997) were allocated to E2+E3+F.

Latitude	110E- 120E	120E- 130E	130E- 170W	Ross Sea	170W- 120W	120W- 110W	110W- 100W	East Australia	New Zealand	Tonga
Naïve Fringe	D DE	E DE	E E	E E	F F	F FG	G FG	E1	Both	Oceania
1900	0	0	0	0	0	0	0	0	8	0
1901	0	0	0	0	0	0	0	0	8	0
1902	0	0	0	0	0	0	0	0	8	0
1903	0	0	0	0	0	0	0	0	8	0
1904	0	0	0	0	0	0	0	0	8	0
1905	0	0	0	0	0	0	0	0	8	0
1906	0	0	0	0	0	0	0	0	8	0
1907	0	0	0	0	0	0	0	0	8	0
1908	0	0	0	0	0	0	0	0	8	0
1909	0	0	0	0	0	0	0	0	16	0
1910	0	0	0	0	0	0	0	0	77	0
1911	0	0	0	0	0	0	0	0	77	0
1912	0	0	0	0	0	0	0	27	197	0
1913	0	0	0	0	0	0	0	348	92	0
1914	0	0	0	0	0	0	0	0	93	0
1915	0	0	0	0	0	0	0	0	106	0
1916	0	0	0	0	0	0	0	0	82	0
1917	0	0	0	0	0	0	0	0	94	0
1918	0	0	0	0	0	0	0	0	90	0
1919	0	0	0	0	0	0	0	0	119	0
1920	0	0	0	0	0	0	0	0	107	0
1921	0	0	0	0	0	0	0	0	89	0
1922	0	0	0	0	0	0	0	0	57	0
1923	0	0	0	0	0	0	0	0	79	0
1924	0	0	0	0	0	0	0	0	107	0
1925	0	0	0	0	0	0	0	0	96	0
1926	0	0	0	82	0	0	0	0	78	0
1927	0	0	0	16	0	0	0	0	127	0
1928	0	0	0	17	0	0	0	0	105	0
1929	0	0	0	775	0	0	0	0	102	0
1930	0	1	234	0	0	0	0	0	78	0
1931	0	0	0	0	0	0	0	0	109	0
1932	0	0	0	0	0	0	0	0	18	0
1933	0	0	0	0	0	0	0	0	44	0
1934	0	0	0	0	0	0	0	0	52	0
1935	0	0	4	0	0	0	0	0	57	0
1936	0	0	0	0	0	0	0	0	69	0
1937	129	32	0	0	0	0	0	0	55	0
1938	180	24	24	0	0	0	0	0	75	0
1939	0	0	0	0	0	0	0	0	80	0
1940	0	0	2394	0	0	0	0	0	107	0
1941	0	0	0	0	0	0	0	0	86	0
1942	0	0	0	0	0	0	0	0	71	0
1943	0	0	0	0	0	0	0	0	90	0
1944	0	0	0	0	0	0	0	0	88	0
1945	0	0	0	0	0	0	0	0	107	0

Latitude	110E- 120E	120E- 130E	130E- 170W	Ross Sea	170W- 120W	120W- 110W	110W- 100W	East Australia	New Zealand	Tonga
Naïve Fringe	D DE	E DE	E E	E E	F F	F FG	G FG	E1	Both	Oceania
1946	0	0	0	0	0	0	0	0	110	0
1947	0	0	0	0	0	0	0	0	101	0
1948	0	0	0	0	0	0	0	0	92	0
1949	10	109	908	0	0	0	0	3	141	0
1950	0	0	171	0	317	0	0	0	79	0
1951	170	232	359	0	38	0	0	0	111	0
1952	0	0	517	0	13	0	0	600	121	0
1953	0	0	14	0	136	0	0	700	109	0
1954	0	0	940	0	340	0	0	718	180	0
1955	508	411	1962	0	334	0	0	720	112	0
1956	0	0	0	0	10	27	39	870	143	0
1957	12	0	220	0	167	31	0	841	184	16
1958	1276	882	1183	0	0	0	0	840	183	16
1959	41	44	12319	0	439	74	7	960	318	16
1960	171	71	9165	0	2758	0	0	980	361	16
1961	120	14	1557	0	2278	54	44	901	80	16
1962	118	58	415	0	285	18	24	177	32	0
1963	24	0	284	0	0	0	0	0	9	0
1964	17	1	85	0	0	0	0	0	0	0
1965	9	9	345	0	477	0	0	0	0	0
1966	26	7	49	0	237	0	0	0	0	0
1967	5	7	27	0	111	0	0	0	0	0
1968	0	0	1	0	0	0	0	0	0	0
1969	0	0	0	0	0	0	0	0	0	0
1970	0	0	0	0	0	0	0	0	0	0
1971	0	0	0	0	0	3	0	0	0	0
1972	0	0	2	0	0	0	0	0	0	0
1973	0	0	0	0	0	0	0	0	0	3
1974	0	0	0	0	0	0	0	0	0	4
1975	0	0	0	0	0	0	0	0	0	8
1976	0	0	0	0	0	0	0	0	0	4
1977	0	0	0	0	0	0	0	0	0	4
1978	0	0	0	0	0	0	0	0	0	11
Total	2816	1902	33179	890	7940	207	114	8685	5714	114