Humpback whale abundance south of 60°S from three complete circumpolar sets of surveys

T.A. BRANCH*

MARAM (Marine Research Assessment and Management Group), Department of Mathematics and Applied Mathematics, University of Cape Town, Rondebosch, 7701, South Africa
Contact e-mail: tbranch@uw.edu

ABSTRACT

Austral summer estimates of abundance are obtained for humpback whales (*Megaptera novaeangliae*) in the Southern Ocean from the IWC's IDCR and SOWER circumpolar programmes. These surveys have encircled the Antarctic three times: 1978/79–1983/84 (CPI), 1985/86–1990/91 (CPII) and 1991/92–2003/04 (CPIII), criss-crossing strata totalling respectively 64.3%, 79.5% and 99.7% of the open-ocean area south of 60°S. Humpback whales were absent from the Ross Sea, but were sighted in all other regions, and in particularly high densities around the Antarctic Peninsula, in Management Area IV and north of the Ross Sea. Abundance estimates are presented for each CP, for Management Areas, and for assumed summer feeding regions of each Breeding Stock. Abundance estimates are negatively biased because some whales on the trackline are missed and because some humpback whales are outside the survey region. Circumpolar estimates with approximate midpoints of 1980/81, 1987/88 and 1997/98 are 7,100 (CV = 0.36), 10,200 (CV = 0.30) and 41,500 (CV = 0.11). When these are adjusted simply for unsurveyed northern areas, the estimated annual rate of increase is 9.6% (95% CI 5.8–13.4%). All Breeding Stocks are estimated to be increasing but increase rates are significantly greater than zero only for those on the eastern and western coasts of Australia. Given the observed rates of increase, the current total Southern Hemisphere abundance is greater than 55,000, which is similar to the summed northern breeding ground estimates (~60,000 from 1999–2008). Some breeding ground abundance estimates are far greater, and others far lower, than the corresponding IDCR/SOWER estimates, in a pattern apparently related to the latitudinal position of the Antarctic Polar Front.

KEYWORDS: ABUNDANCE ESTIMATE; ANTARCTIC; BREEDING GROUNDS; DISTRIBUTION; FEEDING GROUNDS; MONITORING; SOUTHERN HEMISPHERE; SOUTHERN OCEAN; SOWER; SURVEY–VESSEL; TRENDS

INTRODUCTION

The International Whaling Commission (IWC) is engaged in a multi-year in-depth assessment of the current status of Southern Hemisphere humpback whales (*Megaptera novaeangliae*). Assessments of the individual Breeding Stocks rely heavily on current estimates of abundance from both their northern breeding grounds and their southern feeding grounds in the Antarctic (Johnston *et al.*, 2011; Zerbini *et al.*, 2011). The IWC currently recognises seven stocks of humpbacks in the Southern Hemisphere that migrate between northerly winter breeding grounds and summer Antarctic feeding grounds, and one (Breeding Stock X) that inhabits the northern Indian Ocean year-round for both breeding and feeding. The simplest way of assigning each Breeding Stock to an Antarctic summer feeding ground is given by the IWC's Naïve model, which assumes that there is no overlap between Breeding Stocks when they are in the Antarctic (IWC, 1998; 2006). The seven Breeding Stocks and their assumed longitudinal range in the Antarctic according to this Naïve model are:

(a) Brazil, especially the Abrolhos Bank (Antarctic: 50°W–20°W);
(b) Central west Africa particularly Gabon (B1) and a separate substock off western Namibia and South Africa (B2) (Antarctic: 20°W–10°E);
(c) Coastal waters of Mozambique (C1), central Mozambique Channel islands (C2) and coastal waters of north and east Madagascar (C3) (Antarctic: 10°E–60°E);
(d) Coastal western Australia, especially 15–16°S (Antarctic: 60°E–120°E);
(e) Coastal eastern Australia, particularly 18–21°S (E1), New Caledonia (E2), and Tonga (E3) (Antarctic: 120°E–170°W);
(f) Cook Islands and French Polynesia (Antarctic: 170°W–110°W);
(g) Coastal waters of western South America between southern Panama and northern Peru (Antarctic: 110°W–50°W).

Abundance estimates are available from most of the breeding grounds, but the only surveys covering the feeding grounds of all Breeding Stocks are the IWC's International Decade for Cetacean Research (IDCR) and Southern Ocean Whale Ecosystem Research (SOWER). The IDCR/SOWER surveys have completely encircled the Antarctic south of 60°S three times while completing circumpolar sets of surveys (CPs): in 1978/79–1983/84 (CPI), 1985/86–1990/91 (CPII) and 1991/92–2003/04 (CPIII). The survey and transit tracklines and positions of humpback sightings are shown in Fig. 1.

Previous humpback whale estimates from the IDCR/SOWER surveys have been based on an incomplete CPIII set of surveys. Branch and Butterworth (2001a) provided circumpolar estimates of 7,100 (CV = 0.36), 9,200 (CV = 0.29) and 9,300 (CV = 0.22) for the three CPs, but the CPIII estimate was based only on surveys up to 1997/98. Subsequent surveys filled in missing longitudinal coverage (140°W–110°W, 80°W–60°W and 80°E–130°E) and also more completely re-surveyed the 130°E–170°W region last surveyed in 1991/92. These recently surveyed longitudinal ranges cover the Antarctic regions where humpback whales are most abundant. Additionally, all

* Present address: *School of Aquatic and Fisheries Sciences, Box 355020, University of Washington, Seattle, WA 98195, USA.*

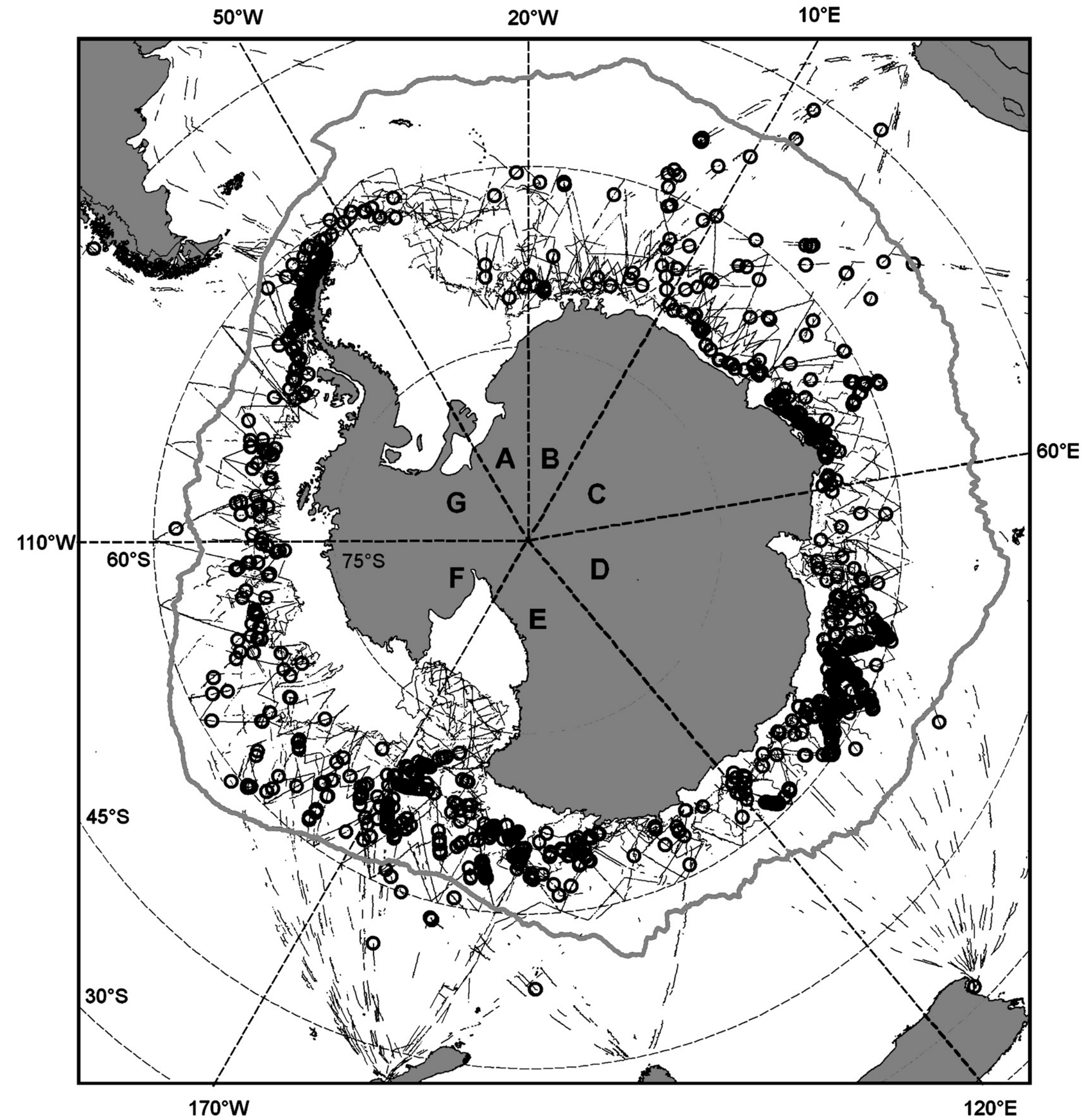

Fig. 1. Primary effort (thin grey lines) and associated sightings (black circles) from the IDCR/SOWER surveys from 1978/79 to 2004/05, including transits to and from the survey regions and survey years (1984/85, 2004/05) devoted primarily to experiments that are not included in the circumpolar estimates. Surveys (as opposed to transits) were normally conducted south of 60°S. The Antarctic Polar Front is represented by a thicker line and is based on data from Moore *et al*. (1999). Dashed lines extending from the South Pole and associated letters A–G represent the assumed Antarctic divisions between Breeding Stocks A–G based on the IWC's Naïve feeding model.

previous estimates were presented only at the circumpolar level and thus could not be used to assess the status of individual Breeding Stocks.

This paper presents updated circumpolar estimates of abundance and estimates for individual surveys, each Management Area (Donovan, 1991), and each of the Breeding Stocks divided according to the Naïve model feeding areas (IWC, 1998; 2006).

METHODS

The standard distance sampling methods used to analyse the IDCR/SOWER surveys have been described in detail in Branch and Butterworth (2001a). A broad overview is provided here together with particulars where methods have been updated from those in Branch and Butterworth (2001a); differences are also summarised in Table 1. Much of the process of data extraction and abundance estimation is automated in the IWC's Database Estimation System Software (DESS, Strindberg and Burt, 2004), although substantial post-DESS manipulation is needed to divide the estimates between Breeding Stocks and Management Areas. DESS version 3.42 dated April 2006 is used in these analyses.

Survey design

Survey cruise tracks and strata have been presented for the earlier surveys (Branch and Butterworth, 2001b; Matsuoka *et al.*, 2003). Important features include that: the first five CPI surveys generally left an unsurveyed region between the northern and southern strata; surveys in CPI and CPII generally left an unsurveyed area between the northern boundary of the survey region and 60°S; in general the CPI tracklines were rectangular while later survey tracklines were zigzag in pattern; and CPI and CPII took six years each while CPIII took 13 years (Figs 2a–c). Finally, individual surveys within CPI and CPII were non-overlapping while in CPIII some longitudinal ranges were surveyed more than once. These features make it difficult to obtain comparable estimates from the three CPs.

Table 1
Summary of changes to the analyses compared to those in Branch and Butterworth (2001a).

Topic	Branch and Butterworth (2001a)	This paper	Implications
Activity codes	BA, BB, BC, BL, BR, SE, BH, BI, BO, BP, BQ, BU, BV	BB renamed to BK	None
Duplicates and triplicates	'Definite' and 'possible' duplicates and triplicates treated as multiple records of a single sighting	Only 'definite' duplicates and triplicates treated as multiple records of a single sighting	No effect on estimates based on surveys up to and including 1997/98 (Branch and Butterworth, 2001a)
Survey legs parallel to ice edge in 1988/89 and 1989/90	Included	Excluded	Increases CPII estimates by a moderate amount, because 1,535.3 n.miles of effort and associated sightings were excluded in 1988/89; and 30.1 n.miles in 1989/90
Area of ES stratum in 1996/97	67,072 n.mile^2	Corrected to 52,534 n.mile^2	Decreases CPIII estimate by 0.1%
EN2 stratum in 1997/98	Treated as if divided into two separate strata each surveyed by one vessel	Treated as one stratum surveyed by two vessels	Negligible effect
Estimated school size	Either regression method or mean within 1.5 n.miles	Regression method unless positive correlation or school size less than one, then mean within 0.5 n.miles	No effect since regression always positive for humpback whales

Data selected for analysis

Survey modes and activity codes

In CPI the surveys were conducted in closing mode only but in CPII and CPIII the vessel alternated between closing mode and independent observer (IO) mode. In closing mode, when a sighting is made the vessel leaves the trackline to confirm the species identity and school size of the sighting. In IO mode (which is a form of passing mode) the vessel does not leave the trackline when a sighting is made, and an additional observer is placed on the IO platform just below the barrel who operates independently from the barrel observers to provide information about the detectability of whales on the trackline. For minke whale analyses, closing mode and IO mode are treated separately (Branch and Butterworth, 2001b), but the paucity of sightings for other species renders this difficult so that closing mode and IO mode data are combined in this paper to obtain abundance estimates for humpback whales. In a sensitivity test conducted on the surveys up to 1997/98, estimates obtained separately from closing and IO mode were similar (Branch and Butterworth, 2001a).

A variety of activity codes have been used over the years in both closing and IO mode. The same codes used in Branch and Butterworth (2001a) are used here (Table 1) except that the 'BB' code has now been renamed 'BK' (and is included) while 'BB' now refers to blue whale research periods (and is excluded).

Species codes

Sightings recorded as code 07 ('humpback whale') are included and code 71 ('like humpback') excluded in obtaining abundance estimates. A sensitivity test conducted by Branch and Butterworth (2001a) revealed that including 'like humpback' sightings increased the abundance estimates by 0.0%, 0.6% and 1.6% for the three CPs respectively, up to 1997/98.

Duplicates and triplicates

During IO mode duplicate (or even triplicate) records can be made of the same sighting from different platforms. Duplicates and triplicates are coded as 'definite', 'possible' or 'remote'. The most recent analysis of humpback whale abundance from these surveys (Branch and Butterworth, 2001a) treated all 'definite' and 'possible' duplicates and triplicates as a single sighting, while 'remote' duplicates and triplicates were treated as sightings of multiple schools. In this paper only 'definite' duplicates and triplicates are treated as single sightings, bringing the methods in line with those used for minke whales (Branch, 2006; Branch and Butterworth, 2001b). A previous sensitivity test for this change for minke whales revealed that abundance estimates changed by less than 1% (Branch and Butterworth, 2001b); a similar minor impact is likely for humpback whales.

Abundance estimation

Abundance estimates were obtained using the standard distance sampling formula (e.g. Buckland *et al.*, 1993):

$$N = \frac{A \cdot \bar{s} \cdot n}{2 \cdot w_s \cdot L} \qquad (1)$$

where:
N = abundance estimate
A = area of stratum (n.miles^2)
$\bar{s}$ = mean school size
n = number of schools sighted during primary search effort
w_s = effective search half-width for schools (n.miles)
L = primary search effort (n.miles)
The CV for N is calculated from:

$$CV(N) = \sqrt{\left[CV\left(\frac{n}{L}\right)\right]^2 + \left[CV(\bar{s})\right]^2 + \left[CV(w_s)\right]^2} \qquad (2)$$

Effective search half-width

Recorded angle and forward distance data are often rounded, artificially introducing peaks in the distribution of perpendicular distances that do not reflect the true distribution of perpendicular distances. To account for this rounding error, sightings are assumed to be evenly 'smeared' across a particular sector of angles and distances before the distribution of perpendicular distances is calculated. Smearing is conducted using Method II of Buckland and Anganuzzi (1988). The resulting distribution of perpendicular distances is then grouped into 0.1 n.mile bins to the truncation distance of 2.4 n.miles as in Branch and Butterworth (2001a). The detection function is fitted to these data based on perpendicular distance *y*.

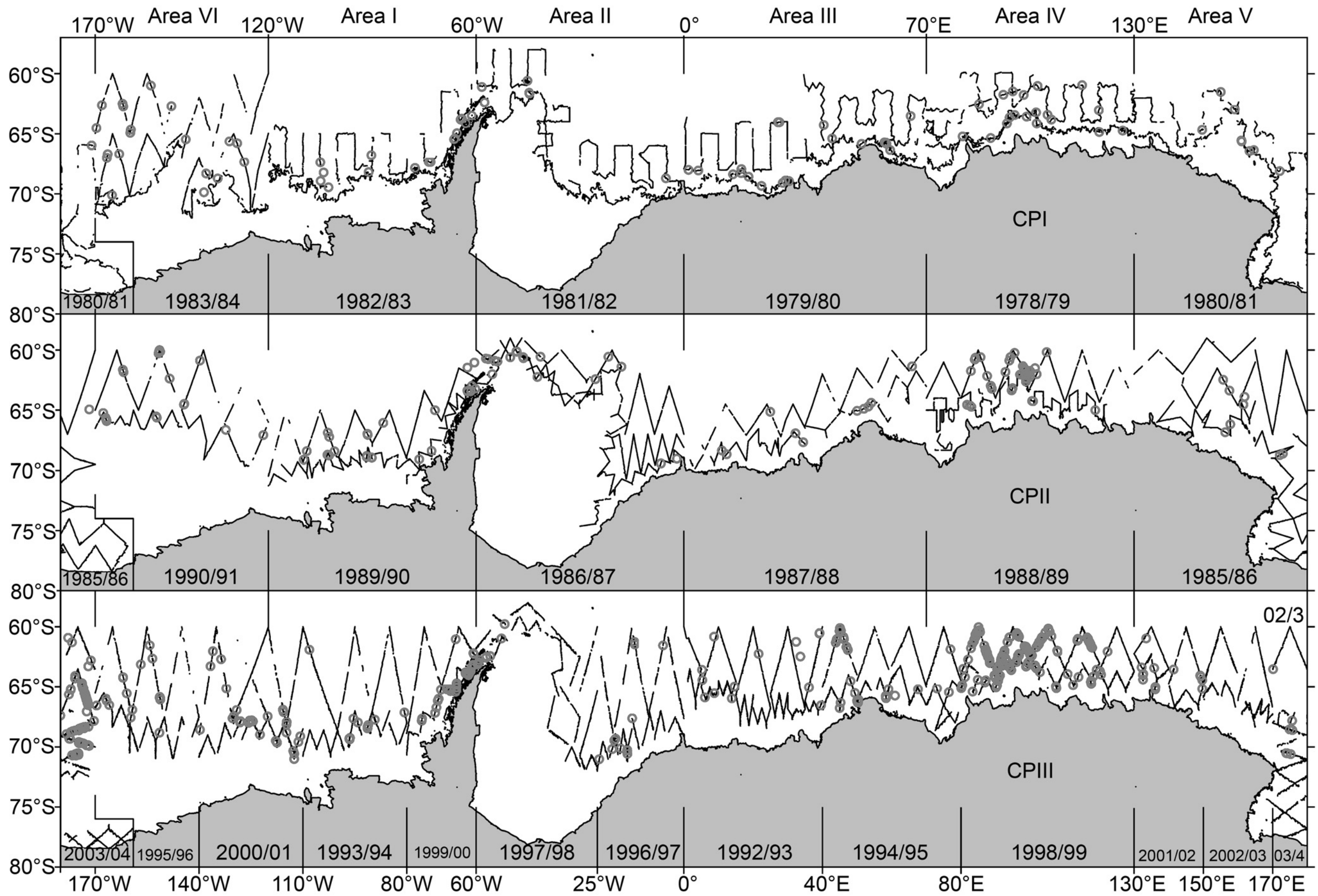

Fig. 2. Primary search effort (solid lines) and associated humpback whale sightings (circles) during each of the surveys included in the three circumpolar sets of surveys (CPI, CPII and CPIII). Vertical lines at the top of each panel show the longitudinal boundaries of the six IWC Management Areas, while vertical lines at the bottom of each panel show the divisions between each survey (six surveys in CPI and CPII, twelve in CPIII).

$$f(y) = f(0)g(y) = f(0)\left[1-\exp\left(-\left[\frac{y}{a}\right]^{-b}\right)\right] \qquad (3)$$

where *g(y)* is the probability that a school at a perpendicular distance *y* from the trackline will be sighted and $a \geq 0.0001$ n.miles and $b \geq 1$ are parameters to be estimated. It is assumed that $g(0) = 1$, i.e. that all schools on the trackline are sighted. It is possible in theory to estimate $g(0)$ for humpback whales using the duplicate sightings in IO mode data, but this has proven complicated even for minke whales (Okamura *et al.*, 2003; 2005; 2006) and is beyond the scope of this paper.

Mean school size

School size estimates are obtained from sightings with confirmed school sizes in closing mode only. Closing mode estimates are used because IO mode estimates of school size are negatively biased (IWC, 1987, p.70). Large schools are visible at greater distances than small schools and therefore estimates of school size were corrected for bias using the regression method proposed by Buckland *et al.* (1993), which accounts for changes in the detectability of different school sizes with distance from the vessel.

Pooling to estimate the search half-width and mean school size

Sample sizes were small in most of the surveys (especially CPI and CPII), and therefore search half-width and mean school size could not be estimated separately for each survey; instead, separate estimates for search half-width and mean school size were obtained for each CP set, as in Branch and Butterworth (2001a). Given the higher number of sightings in CPIII, it might be possible to obtain separate estimates of these quantities for the first and second halves of CPIII in future analyses.

Averaging for strata surveyed by two vessels

Where a stratum is surveyed by two vessels the resulting abundance estimates were combined by effort-weighted averaging.

Obtaining CVs for combined stratum estimates

When individual abundance estimates for each stratum (N_i) and associated CVs (CV_i) are combined, CVs are stratum-specific for each n_i/L_i component, but from data pooled over each CP for $\bar{s}$ and w_s. The following procedure is therefore needed to correctly obtain the overall CV for the sum of several strata:

$$X_i = \frac{N_i \cdot w_s}{\bar{s}} = \frac{A \cdot n_i}{2 \cdot L_i} \qquad CV(X_i) = \sqrt{CV(N_i)^2 - CV(\bar{s})^2 - CV(w_s)^2}$$

$$X = \sum_{i=1}^{n} X_i \qquad CV(X) = \sqrt{\sum_{i=1}^{n}\left[X_i \cdot CV(X_i)\right]^2} \Big/ X$$

$$N = \sum_{i=1}^{n} N_i \qquad CV(N) = \sqrt{CV(X)^2 - CV(\bar{s})^2 + CV(w_s)^2}$$

Combining estimates

Abundance estimates for individual strata need to be combined to obtain estimates applicable to the CPs, to Management Areas, to the Breeding Stocks and to each individual survey. Surveys in 1984/85, 2004/05 and 2005/06 are omitted when obtaining abundance estimates for the CPs as these were largely dedicated to experiments. Abundance estimates for CPI and CPII are comparatively easy to obtain because the individual surveys each covered one Management Area, but during CPIII some surveys overlapped, and CPIII surveys sometimes crossed the border between two Management Areas. In general these combinations require omitting some strata or surveys, and splitting other strata (and their associated effort and sightings) into substrata. Where strata are split it is also necessary to re-calculate the new stratum areas, the areas of the unsurveyed regions north of the new strata, and the unsurveyed areas between the northern and southern strata during the first five surveys. More detail is given below.

Stratum areas

When the strata are divided to obtain Management Area and Breeding Stock estimates, survey effort and sightings must be split into the two new strata. Additional calculations are needed to find the area of the two new strata and the area of the unsurveyed region (if any) between the northern strata and 60°S, and between the northern and southern strata in CPI. An *R* script provided by M.L. Burt (pers. comm.) is used to calculate these new survey areas.

Circumpolar abundance estimates

Circumpolar abundance estimates are obtained using the ‘survey-once’ method, i.e. the most recent and most complete survey is preferred when surveys overlap (Branch, 2005; Branch and Ensor, 2004). Key elements are: (1) The 1991/92 survey in Area V is omitted since Area V was re-surveyed more completely and more recently in 2001/02–2003/04; (2) *ad-hoc* strata ENA and ESA in 1999/00 and ESA in 2001/02 are omitted; (3) longitudinal bands are omitted from the 1993/94 (60°W–80°W) and 1996/97 (25°W–30°W) surveys; (4) the entire ES stratum and also EN east of 180° are omitted from the 2002/03 survey; (5) N1 west of 180° in 2003/04 is omitted; and (6) the 2004/05 and later surveys are excluded since these were devoted primarily to experiments and not to abundance estimation.

IWC Management Areas

Management Area estimates are obtained using the ‘survey-once’ method (Branch, 2005; Branch and Ensor, 2004). For CPI and CPII each individual survey covered a single Management Area, but for CPIII surveys exclusions were required as for circumpolar estimates. In addition the 1994/95 strata are split at 70°E, and the 2000/01 strata are split at 120°W. An additional abundance estimate is provided for Area V based on the 1991/92 survey estimate, which is denoted as CPIII* since this survey is excluded under the ‘survey-once’ circumpolar method. This additional estimate is included when estimating the rate of increase of humpbacks in Area V.

Breeding stocks

The assumption was made that the Naïve model used for allocating catches in the feeding areas to the Breeding Stocks (IWC, 1998; 2006) was also appropriate for dividing the abundance estimates among the Breeding Stocks. In addition to the deletions outlined for the circumpolar estimates, many strata had to be split to obtain abundance estimates for these longitudinal regions. Divisions were required at 20°W, 10°E, 60°E, 120°E, 170°W, 110°W and 50°W. It should be noted that under the Naïve model, the currently agreed division between Breeding Stock G and A is at 50°W south of 58°S and either at 50°W or 70°W north of 58°S, whereas other divisions do not change with latitude. An additional estimate (denoted CPIII*) is provided for Breeding Stock E based on the 1991/92 survey combined with a 10° longitudinal section from the 1998/99 survey. This 10° slice of the 1998/99 survey was also included in the other CPIII Breeding Stock E estimate, but contributes less than 200 whales to the total.

Individual surveys

Abundance estimates are provided for each survey used in the CPs and for 1991/92. No longitudinal slices are omitted except for the *ad-hoc* strata ENA and ESA in 1999/00 and ESA in 2001/02.

Comparable-area estimates

The differing nature of the three CPs poses several issues when comparing estimates. Major issues include the different survey design, survey modes, and unsurveyed central regions in CPI, the lack of survey effort northwards to 60°S in most of the CPI and CPII surveys, and the unknown proportion of humpback whales north of 60°S during the survey period. Only the unsurveyed northern areas are taken into account to obtain estimates from ‘comparable areas’. The simple assumption employed by Branch and Butterworth (2001a; 2001b) and Branch (2007) is used here: that the density in the unsurveyed northern areas is the same as in the strata adjacent and south of the unsurveyed strata. If instead the true density in the unsurveyed areas was lower than in the more southerly surveyed areas, this assumption would cause positive bias in estimated whale abundance for CPI and CPII, and negative bias in the estimated increase rate.

In most cases this is straightforward, but for the 1981/82 survey between 40°W and 30°W there was no northern stratum, only a southern stratum (W2S). As densities are expected to be higher near the ice edge in the southern stratum, it was deemed inappropriate to adjust the W2S estimates upwards, and instead the estimate from the adjacent EN stratum (or the western section of EN when EN is split to obtain Breeding Stock estimates) is adjusted upwards. This differs slightly from the methods used previously, where the W1N estimates were adjusted upwards for the unsurveyed region north of W2S in 1981/82 (Branch and Butterworth, 2001a; 2001b).

For this work the areas of the unsurveyed northern regions have been more accurately estimated from the stratum boundaries and these differ slightly from those in previous papers (Branch and Butterworth, 2001a; 2001b).

Estimating the annual rate of increase

To estimate the annual rate of increase for each series of abundance estimates (circumpolar, Management Areas etc), an exponential growth model was fitted to the log of the ‘comparable areas’ abundance estimates:

$$\ln \hat{N}_t = \ln N_0 + rt$$

where

N_0 is the first abundance estimate in the series;

$\hat{N}_t$ is the abundance estimate t years after the first abundance estimate;

r is the annual rate of increase.

The actual distribution of whales within each area is expected to change from year to year, and this variability would not be taken into account if the overall variance accounted only for the sampling variance reported from each individual survey. This missing variability is termed 'additional variability'. When fitting a growth model to interannual estimates, the overall variance comprises both the reported variance for each survey and the additional variance (which is assumed to be the same for all surveys). To obtain maximum likelihood estimates for r, the following negative log likelihood is minimised:

$$-\ln L = \sum_t \left[\ln \sqrt{CV_t^2 + CV_{\text{add}}^2} + \frac{\left(\ln N_t - \ln \hat{N}_t\right)^2}{2\left(CV_t^2 + CV_{\text{add}}^2\right)} \right]$$

where

CV_i is the reported coefficient of variation for the abundance estimate in year t;

CV_{add} is the coefficient of variation for the additional variance.

Likelihood profiling was used to find the 95% confidence intervals (e.g. Hilborn and Mangel, 1997), i.e. finding the two values of r for which the negative log likelihood is 1.92 units higher than the maximum likelihood estimate.

Comparison with breeding ground estimates

Surveys in both the Antarctic and the northern breeding grounds may only incompletely cover the entire Breeding Stocks (this would be indicated by any substantial differences between estimates from the two regions). Northern breeding ground estimates were collated by reviewing abundance estimates presented to the IWC at the Workshop on the Comprehensive Assessment of Southern Hemisphere Humpback Whales, 4–7 April 2006, Hobart Australia, and summarised in other papers (Bannister, 2005; Johnston and Butterworth, 2006; Zerbini *et al.*, 2011). These estimates are generally more recent than the mid-year of the IDCR/SOWER estimates, and it is likely that all Breeding Stocks are increasing. For comparisons, the IDCR/SOWER estimates from CPIII were either assumed to remain constant or projected to the mid-year of the breeding ground estimates by assuming an increase rate of 5% or 10%, which are reasonable rates of increase given a maximum upper bound from life history characteristics of 11.8% (Zerbini *et al.*, 2010).

RESULTS

The IDCR-SOWER surveys covered 64.3% (CPI), 79.5% (CPII) and 99.7% (CPIII) of the region between 60°S and the ice edge, based on updated estimates of the areas of the unsurveyed regions (Table 2). Plots of the primary survey effort and primary sightings during CPI, CPII and CPIII are given in Figs 2a–c. Of particular interest is the absence of humpback whale sightings in the Ross Sea south of 72°35'S despite extensive effort (Fig. 1).

Stratum-specific details of the components of the abundance estimates are presented in Table 3 and estimates of search half width and estimated school size are found in Table 4. Detection function fits to the smeared sightings are plotted in Figs 3a–c for each of the CPs. Search half-width increased substantially from 0.746 n.miles in CPI to 0.924 n.miles in CPII and 1.505 n.miles in CPIII. One further result to note is the high number of sightings recorded directly on the trackline in CPI (Fig. 3a).

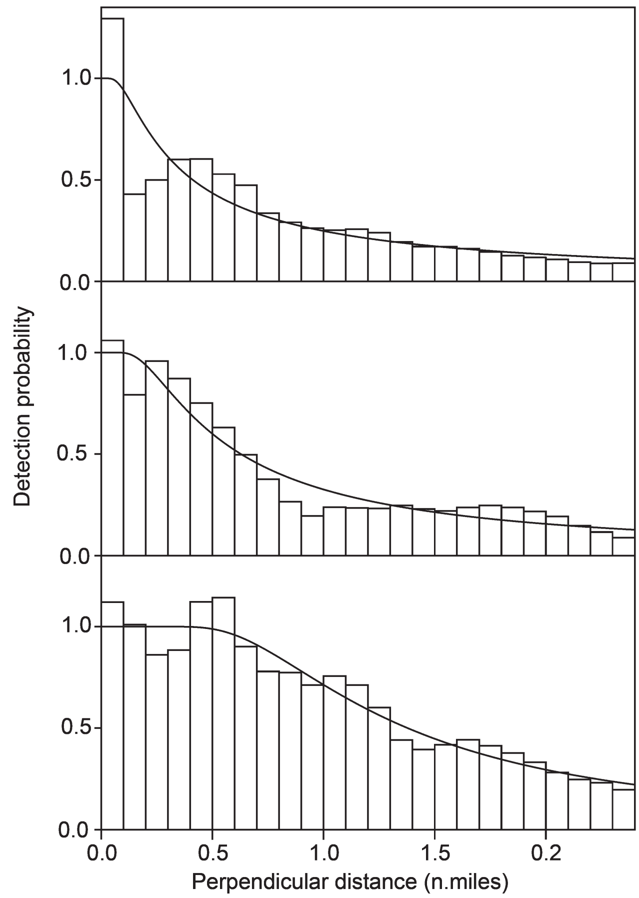

Fig. 3. Fit of the detection function to the smeared and truncated sightings recorded during CPI, CPII, and CPIII.

The crude sighting rate (total primary sightings divided by total primary search effort) for each CP is 1.8, 3.2 and 12.5 schools per 1000 n.miles for CPI, CPII and CPIII respectively. Estimated circumpolar abundance increased 45% from CPI to CPII and increased fourfold from CPII to CPIII (Table 5). The estimated abundance south of 60°S for CPIII is 41,500 (CV = 0.11). Most of this increase in the CPIII abundance comes from Management Areas IV (17,900) and V (13,200), although abundance estimates are also highest in CPIII in Areas I, II and III and similar to CPI and CPII in Area VI (Table 6). When separated into Breeding Stocks, stocks D (18,000) and E (13,300) are estimated to contain the majority of the CPIII abundance, and the CPIII estimates are also similar to or higher than CPI and CPII for all Breeding Stocks (Table 7). Estimates for individual surveys are provided in Table 8; the 1998/99 survey estimate of 17,700 (CV = 0.18) in Area IV accounts for 43% of the CPIII total. During the 1998/99 survey in Area IV alone, 208 primary sightings were recorded within 2.4 n.miles of the trackline, compared to 65 in total from CPI and 111 from CPII. More sightings were also recorded during the 2002/03 (87) and 2003/04 (93) surveys in Area V than from the CPI surveys.

The estimated circumpolar rate of increase is 9.6% per annum (95% CI 5.7%–13.3%), while point estimates ranged from –0.2% to 14.9% for Management Areas and from 1.6% to 14.4% for Breeding Stocks (Table 9). For most Management Areas and Breeding Stocks the confidence intervals were broad and ranged outside the [0%; 11.8%] interval (Zerbini *et al.*, 2010), although the estimated rate of increase was significantly greater than zero for Management

Areas IV and V, for Breeding Stocks D and E, and for the circumpolar estimates.

Abundance estimates from the northern breeding grounds (discussed in depth in the Discussion) varied greatly from the IDCR/SOWER estimates in CPIII (Table 10), even when the IDCR/SOWER estimates were extrapolated to the mid-year of the range of years to which the breeding ground estimates applied. For Breeding Stocks A, B and C, the IDCR/SOWER estimates were far smaller (3–44%) than the northern breeding grounds, for Breeding Stocks D, E and F, the IDCR/SOWER estimates were much higher (135–445%), and for Breeding Stock G the IDCR/SOWER estimates were similar (53%–124%).

DISCUSSION

Circumpolar abundance estimates for humpbacks presented here are the most recent and most complete to date, with strata coverage approaching 100% of the area south of 60°S in CPIII. The CPIII estimates should be adopted as the best available estimates for the summer abundance of humpback whales south of 60°S, and for certain Breeding Stocks arguably provide a better estimate of abundance than northern breeding ground surveys.

Although humpback whale sightings were recorded around the Antarctic, they were absent from the Ross Sea south of about 72°35'S, a pattern that has not previously

Table 2

Estimates of the unsurveyed areas between the northern boundaries of the surveys and 60°S, compared with those in Branch and Butterworth (2001b).

		This paper		Branch and Butterworth (2001b)	
Survey	Stratum	Unsurveyed south of 60°S	Surveyed north of 60°S	Unsurveyed south of 60°S	Surveyed north of 60°S
1978/79	EN	53,181		53,181	
1978/79	W1N	38,645		38,645	
1979/80	WN	255,938		255,938	
1979/80	EN	100,763		100,763	
1980/81	EN	263,267		263,267	
1980/81	WN	91,934		91,934	
1981/82	W1N		74,162	100,005	74,162
1981/82	EN	388,670		288,507	
1982/83	WN	243,507		243,506	
1982/83	EN	178,386		178,386	
1983/84	EN	35,088		35,088	
1985/86	WN		38,306		38,305
1986/87	WS2		12,060		11,992
1986/87	EN	74,342		74,341	
1986/87	WN		10,530		10,596
1987/88	WN	263,936		263,930	
1987/88	EN	58,824		54,823	
1988/89	EN	17,773		17,772	
1988/89	WN	17,773		17,772	
1989/90	WN	249,265		249,265	
1989/90	EN	167,243		167,243	
1990/91	EN	43,860		43,706	
1991/92*	WN	121,361		120,700	
1991/92*	EN	245,043		247,210	
1996/97	WNE	14,691		14,510	
1997/98	WS		13,670		14,040
1997/98	WN		32,548		32,722
CPI		1,649,379	74,162	1,649,220	74,162
CPII		893,015	60,896	888,852	60,893
CPIII excluding 1991/92		14,691	46,218	14,510	46,762

Table 3

Components of abundance estimates for each survey. Indicated for each stratum are the stratum name, vessel, area (A), number of transects (N_L), number of schools sighted after smearing and truncation (n_s), search effort (L), sighting rate (n_s/L), and estimates of abundance in each stratum (N). The strata that were surveyed by more than one vessel are indicated by the same number in the 'Ave' column; resulting abundance estimates are combined using effort-weighted averaging.

Stratum	IWC Area	Year	Vessel	Stratum	A (n.mile^2)	N_L	n_s	L (n.mile)	n_s/L*10^3	CV	N	CV	Ave
1	IV	1978/79	T16	EN	156,766	18	5.0	2,155.5	2.32	0.48	398	0.58	
2	IV	1978/79	T16	W1N	39,256	2	0.0	222.2	0.00	0.00	0	0.00	1
3	IV	1978/79	T16	W1S	20,389	5	0.0	200.6	0.00	0.00	0	0.00	
4	IV	1978/79	T16	W2N	153,914	3	1.0	384.7	2.60	0.86	438	0.33	2
5	IV	1978/79	T16	W2S	29,600	12	4.0	1,073.3	3.73	0.49	121	0.59	3
6	IV	1978/79	T18	ES	27,571	16	4.0	1,436.6	2.78	0.40	84	0.52	
7	IV	1978/79	T18	W1N	39,256	6	0.0	685.3	0.00	0.00	0	0.00	1
8	IV	1978/79	T18	W2N	153,914	11	2.4	1,212.5	1.98	0.54	327	0.64	2
9	IV	1978/79	T18	W2S	29,600	4	2.0	393.4	5.08	0.28	165	0.33	3

Cont.

Stratum	IWC Area	Year	Vessel	Stratum	A (n.mile^2)	N_L	n_s	L (n.mile)	$n_s/L*10^3$	CV	N	CV	Ave
10	III	1979/80	K27	ES	41,772	20	4.0	1,346.5	2.97	0.54	135	0.63	
11	III	1979/80	K27	WN	200,724	16	4.0	2,014.9	1.99	0.65	436	0.73	
12	III	1979/80	T11	EN	217,865	20	2.0	2,636.7	0.76	0.60	181	0.69	
13	III	1979/80	T11	WS	33,619	19	7.0	968.2	7.23	0.30	266	0.45	
14	V	1980/81	K27	EN	208,159	14	2.0	877.3	2.28	0.57	519	0.66	
15	V	1980/81	K27	ES	98,766	5	0.0	439.6	0.00	0.00	0	0.00	4
16	V	1980/81	K27	WS	34,164	17	0.0	698.1	0.00	0.00	0	0.00	
17	V	1980/81	T11	ES	98,766	21	1.0	2,133.3	0.47	0.81	51	0.88	4
18	V	1980/81	T11	WN	139,191	15	3.0	1,151.6	2.61	0.75	397	0.82	
19	II	1981/82	SM1	ES	29,633	18	0.0	1,162.9	0.00	0.00	0	0.00	
20	II	1981/82	SM1	W1N	135,504	10	1.0	1,064.9	0.94	0.77	139	0.84	
21	II	1981/82	SM1	W2S	52,096	10	0.0	920.6	0.00	0.00	0	0.00	5
22	II	1981/82	SM2	EN	145,063	17	1.0	1,748.8	0.57	1.01	91	1.06	
23	II	1981/82	SM2	W1S	35,725	9	0.5	872.2	0.57	1.05	24	1.10	
24	II	1981/82	SM2	W2S	52,096	12	0.0	812.4	0.00	0.00	0	0.00	5
25	I	1982/83	SM1	ES	33,050	15	1.9	928.0	2.05	0.54	73	0.63	
26	I	1982/83	SM1	WN	163,926	15	1.0	1,426.1	0.70	0.81	126	0.88	
27	I	1982/83	SM2	EN	149,433	17	3.0	1,054.4	2.85	0.66	465	0.74	
28	I	1982/83	SM2	WS	25,596	19	0.0	1,414.8	0.00	0.00	0	0.00	
29	VI	1983/84	K27	EMS	158,893	5	4.0	1,094.4	3.65	0.59	635	0.68	
30	VI	1983/84	K27	WN	207,721	5	7.9	875.6	9.02	0.33	2,048	0.46	
31	VI	1983/84	SM1	EN	202,108	5	1.0	911.6	1.10	0.85	242	0.91	
32	VI	1983/84	SM2	WMS	156,457	5	2.1	1,309.0	1.60	0.46	273	0.57	
1	V	1985/86	K27	EN	279,611	16	0.0	1,757.7	0.00	0.00	0	0.00	
2	V	1985/86	K27	WS	104,814	28	2.0	1,596.8	1.25	0.53	117	0.57	
3	V	1985/86	SM1	EM	165,912	20	2.0	1,866.4	1.07	0.97	158	0.99	
4	V	1985/86	SM1	WM	166,349	8	2.0	850.0	2.35	0.61	347	0.64	
5	V	1985/86	SM2	ES	107,717	22	0.0	1,737.8	0.00	0.00	0	0.00	
6	V	1985/86	SM2	WN	139,065	10	0.0	1,121.5	0.00	0.00	0	0.00	
7	II	1986/87	K27	ES1	23,142	8	1.0	527.6	1.90	0.82	39	0.84	
8	II	1986/87	K27	WS1	10,270	4	2.0	185.5	10.78	0.65	98	0.20	
9	II	1986/87	K27	WS2	21,143	4	1.0	239.7	4.17	2.09	78	0.20	6
10	II	1986/87	K27	WS3	79,605	15	3.0	1,014.8	2.96	0.42	209	0.47	7
11	II	1986/87	K27	EN	124,057	7	0.0	965.9	0.00	0.00	0	0.00	
12	II	1986/87	SM1	EBAY	15,242	7	0.0	232.2	0.00	0.00	0	0.00	
13	II	1986/87	SM1	ES2	44,975	29	1.0	1,287.8	0.78	0.81	31	0.83	
14	II	1986/87	SM1	WBAY	11,505	3	0.0	166.4	0.00	0.00	0	0.00	
15	II	1986/87	SM1	WN	95,361	6	1.0	516.6	1.94	0.98	164	1.00	
16	II	1986/87	SM2	EM	69,908	9	0.0	1,445.6	0.00	0.00	0	0.00	
17	II	1986/87	SM2	WS2	21,143	3	2.0	234.6	8.53	0.96	160	0.20	6
18	II	1986/87	SM2	WS3	79,605	19	0.0	1,119.8	0.00	0.00	0	0.00	7
19	III	1987/88	SM1	ES	87,677	15	5.9	1,196.0	4.93	0.60	387	0.63	
20	III	1987/88	SM1	WN	148,821	13	1.0	857.3	1.17	1.22	154	1.24	
21	III	1987/88	SM2	EN	168,881	14	1.0	1,086.7	0.92	1.08	138	1.10	
22	III	1987/88	SM2	WS	74,351	21	4.0	1,247.3	3.21	0.52	212	0.56	
23	IV	1988/89	SM1	BS	6,520	4	0.0	231.9	0.00	0.00	0	0.00	
24	IV	1988/89	SM1	EN	181,166	12	2.0	1,116.3	1.79	0.70	288	0.73	
25	IV	1988/89	SM1	WS	58,693	10	5.0	483.5	10.34	0.87	539	0.89	
26	IV	1988/89	SM2	BN	17,486	15	0.0	627.7	0.00	0.00	0	0.00	
27	IV	1988/89	SM2	ES	52,441	9	1.0	554.3	1.80	0.93	84	0.95	
28	IV	1988/89	SM2	WN	156,617	12	29.9	1,431.9	20.88	0.57	2,899	0.61	
29	I	1989/90	SM1	ESBAY	62,594	24	8.0	1,386.7	5.77	0.54	321	0.57	
30	I	1989/90	SM1	WN	168,761	13	7.0	1,167.1	6.00	0.41	899	0.46	
31	I	1989/90	SM2	EN	153,029	14	1.5	1,429.8	1.05	0.73	146	0.76	
32	I	1989/90	SM2	WS	45,128	30	7.0	1,433.1	4.88	0.43	196	0.47	
33	VI	1990/91	SM1	EN	191,954	7	3.0	666.6	4.50	0.49	767	0.53	
34	VI	1990/91	SM1	WS	45,414	14	7.3	950.1	7.68	0.61	311	0.65	
35	VI	1990/91	SM2	ES	108,268	9	1.0	952.9	1.05	0.83	101	0.85	
36	VI	1990/91	SM2	WN	211,788	9	9.0	1,043.4	8.63	0.77	1,622	0.80	
1	V	1991/92	SM1	EN	165,429	17	7.5	1,008.8	7.43	0.26	827	0.26	
2	V	1991/92	SM1	WS	58,643	15	14.0	748.2	18.71	1.00	731	1.00	
3	V	1991/92	SM2	ES	82,039	22	0.0	1,416.4	0.00	0.00	0	0.00	
4	V	1991/92	SM2	WN	137,734	9	2.0	655.3	3.05	1.25	281	1.25	

Cont.

Stratum	IWC Area	Year	Vessel	Stratum	A (n.mile^2)	N_L	n_s	L (n.mile)	$n_s/L*10^3$	CV	N	CV	Ave
5	III	1992/93	SM1	ES	23,207	23	1.0	893.4	1.12	0.85	17	0.85	
6	III	1992/93	SM1	WN	210,035	15	0.0	1,404.5	0.00	0.00	0	0.00	8
7	III	1992/93	SM1	WS	61,527	3	1.0	143.0	6.99	0.67	288	0.06	9
8	III	1992/93	SM2	EN	150,547	9	1.0	1,101.2	0.91	0.97	91	0.97	
9	III	1992/93	SM2	WS	61,527	31	3.0	1,774.6	1.69	0.79	70	0.79	9
10	III	1992/93	SM2	WN	210,035	1	0.0	134.2	0.00	0.00	0	0.00	8
11	I	1993/94	SM1	WS	50,596	23	10.0	1,068.3	9.36	0.49	316	0.49	
12	I	1993/94	SM1	EN	293,196	22	2.0	1,581.8	1.26	0.70	248	0.70	
13	I	1993/94	SM2	WN	251,735	16	1.0	1,134.0	0.88	0.85	148	0.85	
14	I	1993/94	SM2	ES	72,249	20	4.5	1,076.4	4.18	0.36	202	0.37	
15	III	1994/95	SM1	WS	51,938	23	14.0	919.6	15.22	0.49	528	0.50	
16	III	1994/95	SM1	EN	146,681	15	1.0	1,154.5	0.87	1.01	85	1.01	
17	III	1994/95	SM2	WN	148,803	14	16.0	921.6	17.36	0.54	1,726	0.54	
18	III	1994/95	SM2	ES	60,046	17	3.0	899.2	3.34	0.52	134	0.52	
19	III	1994/95	SM2	PRYD	21,096	8	0.0	414.2	0.00	0.00	0	0.00	
20	VI	1995/96	SM1	WS	34,051	19	4.0	738.9	5.41	0.56	123	0.56	
21	VI	1995/96	SM1	EN	242,073	21	7.5	1,045.3	7.17	0.60	1,162	0.60	
22	VI	1995/96	SM2	WN	97,945	9	2.0	528.5	3.78	0.84	248	0.84	
23	VI	1995/96	SM2	ES	72,349	19	1.0	1,068.5	0.94	0.94	45	0.94	
24	II	1996/97	SM1	ES	52,534	38	5.8	1,229.2	4.72	0.58	166	0.58	
25	II	1996/97	SM1	WN	113,687	10	2.9	463.9	6.25	1.62	469	1.63	
26	II	1996/97	SM2	EN	241,928	32	3.0	1,260.4	2.38	0.73	385	0.73	
27	II	1996/97	SM2	WS	23,028	15	2.0	384.5	5.20	0.37	80	0.37	
28	II	1997/98	SM1	WS	32,620	17	8.6	490.3	17.54	0.83	381	0.83	
29	II	1997/98	SM1	EN1	84,726	12	0.0	581.1	0.00	0.00	0	0.00	
30	II	1997/98	SM1	ES2	10,451	9	0.0	226.3	0.00	0.00	0	0.00	
31	II	1997/98	SM1	EN2	80,013	4	0.0	202.1	0.00	0.00	0	0.00	10
32	II	1997/98	SM2	WN	52,135	8	1.0	493.3	2.03	1.37	71	1.37	
33	II	1997/98	SM2	ES1	47,036	16	0.0	741.5	0.00	0.00	0	0.00	
34	II	1997/98	SM2	EN2	80,013	4	0.0	330.8	0.00	0.00	0	0.00	10
35	IV	1998/99	SM1	WS	42,605	26	46.9	850.0	55.18	0.25	1,571	0.26	
36	IV	1998/99	SM1	EN	169,387	25	44.5	1,136.1	39.17	0.41	4,433	0.42	
37	IV	1998/99	SM2	WN	105,396	18	100.4	637.2	157.56	0.19	11,095	0.20	
38	IV	1998/99	SM2	ES	70,193	50	16.0	1,241.6	12.89	0.19	604	0.20	
39	IV	1998/99	SM1	ES	70,193	2	0.0	52.5	0.00	0.00	0	0.00	
40	I	1999/00	SM1	WS	20,506	13	5.2	446.9	11.64	0.52	160	0.53	
41	I	1999/00	SM1	EN	57,309	11	3.0	417.7	7.18	0.67	275	0.67	
42	I	1999/00	SM2	WN	110,906	11	0.0	664.4	0.00	0.00	0	0.00	
43	I	1999/00	SM2	ES	23,632	11	32.2	298.0	108.05	0.30	1,704	0.31	
44	VI	2000/01	SM1	WN	252,078	12	2.0	514.0	3.89	0.67	655	0.67	11
45	VI	2000/01	SM1	WS	43,916	16	2.0	446.5	4.48	1.07	131	1.08	12
46	VI	2000/01	SM2	WN	252,078	21	7.0	710.3	9.85	0.22	1,660	0.23	11
47	VI	2000/01	SM2	WS	43,916	16	5.0	311.5	16.05	0.34	471	0.35	12
48	I	2000/01	SM1	EN	127,789	19	2.0	700.8	2.85	0.83	244	0.84	13
49	I	2000/01	SM2	EN	127,789	2	2.0	37.3	53.62	0.07	4,578	0.09	13
50	I	2000/01	SM2	ES	29,080	20	9.0	542.7	16.58	0.34	322	0.34	
51	V	2001/02	SM1	WS	34,886	21	9.0	550.4	16.35	0.29	381	0.29	
52	V	2001/02	SM1	ES	26,099	11	0.0	292.9	0.00	0.00	0	0.00	14
53	V	2001/02	SM2	WN	46,333	7	0.0	438.5	0.00	0.00	0	0.00	
54	V	2001/02	SM2	EN	83,082	8	3.0	486.4	6.17	0.84	342	0.84	
55	V	2001/02	SM2	ES	26,099	3	1.0	131.2	7.62	0.82	133	0.06	14
56	V	2002/03	SM1	ES	126,870	24	14.0	1,018.0	13.75	0.25	1,166	0.26	
57	V	2002/03	SM1	EN	135,038	6	1.0	183.9	5.44	0.60	491	0.61	15
58	V	2002/03	SM1	W2N	101,237	11	20.6	459.1	44.87	0.58	3,037	0.58	16
59	V	2002/03	SM1	W1S	22,128	12	11.0	352.0	31.25	0.30	462	0.31	
60	V	2002/03	SM2	EN	135,038	23	2.0	861.6	2.32	0.58	209	0.58	15
61	V	2002/03	SM2	W2S	21,327	27	29.8	526.0	56.65	0.29	807	0.30	
62	V	2002/03	SM2	W1N	75,395	13	5.0	466.0	10.73	0.41	541	0.41	
63	V	2002/03	SM2	W2N	101,237	4	4.0	43.8	91.32	0.27	6,181	0.06	16
64	V	2003/04	SM2	N1	123,227	13	1.0	489.1	2.04	0.65	168	0.66	
65	V	2003/04	SM1	N2	95,445	18	38.2	587.2	65.05	0.38	4,147	0.38	
66	V	2003/04	SM1	N3	14,598	4	0.0	153.0	0.00	0.00	0	0.00	
67	V	2003/04	SM1	ROSS	56,444	23	0.0	544.6	0.00	0.00	0	0.00	17
68	V	2003/04	SM2	ROSS	56,444	15	0.0	556.7	0.00	0.00	0	0.00	17
69	V	2003/04	SM1	MID	131,782	18	37.7	707.3	53.30	0.47	4,689	0.47	18
70	V	2003/04	SM2	MID	131,782	23	16.0	881.5	18.15	0.36	1,594	0.36	18

been noted. No sightings were recorded despite extensive effort both on the IDCR/SOWER surveys (Fig. 1) and during JARPA surveys (Matsuoka *et al.*, 2011). A similar absence is evident for fin whales in the JARPA surveys, and contrasts with the presence of blue whales and high densities of minke whales in the Ross Sea (Branch, 2006; 2007; Branch *et al.*, 2007; Matsuoka *et al.*, 2005). The absence of humpbacks from the Ross Sea could be due either to extirpation from whaling, or because they never have inhabited the Ross Sea. The IWC catch database (provided by C. Allison, IWC) includes 21 expeditions listed as 'Ross Sea' during 1923–29. Catches from these expeditions included 9,330 blue whales, 1,451 fin whales and 890 humpback whales, i.e. humpback whales constituted about 8% of the total. These totals could, however, have come from the pack ice north of the entrance to the Ross Sea. A published account of the 1928/29 Larsen expedition to the Ross Sea reveals that all of the 13 humpback catches in the IWC catch database were taken in the pack ice outside the Ross Sea and not inside the Ross Sea (Marshall, 1930), thus it is possible that even during industrial whaling, humpback whales rarely entered the Ross Sea. Two hypotheses are proposed for the absence of

Table 4

Estimates of search half-width (w_s), estimated school size ($E[s]$) and their associated CVs for each circumpolar set. Estimates differ slightly for each category of the CPIII estimates due to slight changes in how the strata were divided and which strata were included to obtain the estimates.

Surveys	w_s	CV	$E[s]$	CV
CPI all	0.746	0.327	1.63	0.049
CPII all	0.924	0.193	1.64	0.067
CPIII circumpolar	1.504	0.055	2.02	0.031
CPIII IWC areas	1.504	0.055	2.02	0.031
CPIII breeding stocks	1.511	0.055	2.01	0.033
CPIII individual surveys	1.525	0.051	2.04	0.029

Table 5

Estimates of abundance obtained from each circumpolar set of surveys, and the associated CVs and 95% confidence intervals obtained using the method of Buckland (1992). CPIII estimates exclude the 1991/92 survey.

		Circumpolar estimates			Adjusted simply for equal areas		
Circumpolar set	Mid-year	N	CV	95% CI	N	CV	95% CI
CPI	1980/81	7,058	0.36	(3,500; 14,100)	9,701	0.36	(4,900; 19,300)
CPII	1987/88	10,233	0.30	(5,700; 18,300)	12,488	0.30	(7,000; 22,300)
CPIII	1997/98	41,505	0.12	(33,000; 52,200)	41,344	0.11	(33,000; 51,700)

Table 6

Estimates of abundance for each IWC Management Area. Estimates from Area V in CPIII were obtained from complete coverage south of 60°S in 2001/02–2003/04 but incomplete coverage in 1991/92 (denoted by CPIII*).

					Estimates		Comparable areas	
IWC Area	CP set	Seasons	Long. range	Mid-year	*N*	CV	*N*	CV
Area I	CPI	1982/83	60	1982/83	663	0.64	1,405	0.66
(120°W–60°W)	CPII	1989/90	60	1989/90	1,561	0.37	3,048	0.41
	CPIII	1993/94	30					
		1999/00	20					
		2000/01	10	1997/98	3,549	0.20	3,549	0.20
Area II	CPI	1981/82	60	1981/82	254	0.69	421	0.92
(60°W–0°)	CPII	1986/87	60	1986/87	550	0.38	464	0.40
	CPIII	1996/97	25					
		1997/98	35	1997/98	1,178	0.39	1,005	0.38
Area III	CPI	1979/80	70	1979/80	1,017	0.49	1,657	0.56
(0°–70°E)	CPII	1987/88	70	1987/88	890	0.46	1,212	0.56
	CPIII	1992/93	40					
		1994/95	30	1993/94	2,504	0.40	2,504	0.40
Area IV	CPI	1978/79	60	1978/79	968	0.45	1,102	0.46
(70°E–130°E)	CPII	1988/89	60	1988/89	3,809	0.52	4,167	0.53
	CPIII	1994/95	10					
		1998/99	50	1997/98	17,938	0.18	17,938	0.18
Area V	CPI	1980/81	60	1980/81	957	0.59	1,876	0.60
(130°E–170°W)	CPII	1985/86	60	1985/86	622	0.50	622	0.50
	CPIII*	1991/92	60	1991/92	1,838	0.46	3310	0.34
	CPIII	2001/02	20					
		2002/03	20					
		2003/04	20	2002/03	13,246	0.20	13,246	0.20
Area VI	CPI	1983/84	50	1983/84	3,198	0.47	3,240	0.47
(170°W–120°W)	CPII	1990/91	50	1990/91	2,801	0.53	2,976	0.51
	CPIII	1996/96	30					
		2000/01	20	1998/99	3,098	0.27	3,098	0.27

Table 7

Estimates of abundance for each breeding group of humpback whales, obtained from the feeding areas by assuming that the Naïve model is correct. Estimates of abundance for CPIII* include a 10 degree longitudinal section from the 1998/99 survey that is also included in the CPIII estimate.

					Estimate		Comparable areas	
Breeding group	CP	Seasons	Long. range	Mid-year	*N*	CV	*N*	CV
A (50°W–20°W)	CPI	1981/82	30	1981/82	98	0.96	45	0.88
	CPII	1986/87	30	1986/87	336	0.55	259	0.62
	CPIII	1996/97	5					
		1997/98	25	1997/98	168	0.61	200	0.64
B (20°W–10°E)	CPI	1979/80	10					
		1981/82	20	1980/81	246	0.85	692	0.84
	CPII	1986/87	20					
		1987/88	10	1986/87	70	0.63	70	0.63
	CPIII	1992/93	10					
		1996/97	20	1995/96	595	0.51	595	0.51
C (10°E–60°E)	CPI	1979/80	50	1979/80	720	0.53	1,043	0.62
	CPII	1987/88	50	1987/88	700	0.46	926	0.57
	CPIII	1992/93	30					
		1994/95	20	1993/94	2,391	0.41	2,391	0.41
D (60°E–120°E)	CPI	1978/79	50					
		1979/80	10	1978/79	1,033	0.44	1,219	0.46
	CPII	1987/88	10					
		1988/89	50	1988/89	3,869	0.52	4,202	0.52
	CPIII	1994/95	20					
		1998/99	40	1997/98	17,959	0.17	17,959	0.17
E (120°E–170°W)	CPI	1978/79	10					
		1980/81	60	1980/81	995	0.58	1,913	0.60
	CPII	1985/86	60					
		1988/89	10	1985/86	622	0.50	622	0.50
	CPIII*	1991/92	60					
		1998/99	10	1992/93	2,012	0.43	3,484	0.33
	CPIII	1998/99	10					
		2001/02	20					
		2002/03	20					
		2003/04	20	2001/02	13,300	0.20	13,300	0.20
F (170°W–110°W)	CPI	1982/83	10					
		1983/84	50	1983/84	3,198	0.47	3,240	0.47
	CPII	1989/90	10					
		1990/91	50	1990/91	2,801	0.53	2,976	0.51
	CPIII	1995/96	30					
		2000/01	30	1997/98	3,852	0.22	3,852	0.22
G (110°W–50°W)	CPI	1981/82	10					
		1982/83	50	1982/83	683	0.63	1,452	0.65
	CPII	1986/87	10					
		1989/90	50	1989/90	1,505	0.34	2,817	0.38
	CPIII	1993/94	30					
		1997/98	10					
		1999/00	20	1996/97	3,337	0.21	3,310	0.21

humpback whales from the Ross Sea. First, their body shape with long flippers may be unsuited for heavy pack ice concentrations, unlike the more ice-adapted minke whales (e.g. Ainley *et al.*, 2007), and they tend to avoid regions where they could encounter high ice concentrations. Second, the dominant krill species north of about 73°S in the Ross Sea is Antarctic krill (*Euphausia superba*), but south of 73°S, ice krill (*E. crystallorophias*) is dominant (Sala *et al.*, 2002). Perhaps humpback whales have an aversion to ice krill.

The pattern of an increase in search half-width from CPI to CPII to CPIII is a general feature of the IDCR-SOWER surveys and has been previously noted for blue, fin, minke, sperm, humpback, killer and southern bottlenose whales (Branch and Butterworth, 2001a). This change is reflected in a wider shoulder in the hazard-rate model fit to the sightings of these species (Branch and Butterworth, 2001a) and appears to reflect a real change in the searching pattern of observers, with less effort directed to searching directly ahead of the vessel over time. The pronounced peak in sightings in CPI that were exactly on the trackline, and slightly lower sightings at small distances from the trackline, likely reflects substantial rounding of small sighting angles to zero degrees in those earlier surveys, as was evident for other species in CPI (Branch and Butterworth, 2001a).

Previous analyses have shown that humpback estimates from the IDCR-SOWER surveys are relatively insensitive to the following analytical choices: choice of truncation distance; inclusion of like humpback sightings; excluding mixed schools; treating possible and definite duplicates and triplicates as a single sighting; and obtaining separate abundance estimates from closing and IO mode (Branch and Butterworth, 2001a).

Table 8

Estimates of abundance for each IWC survey.

Year	Area/s	Longitudes	*N*	CV
1978/79	IV	70°E–130°E	968	0.45
1979/80	III	0–70°E	1,017	0.49
1980/81	V	130°E–170°W	957	0.59
1981/82	II	60°W–0	254	0.69
1982/83	I	120°W–60°W	663	0.64
1983/84	VI	170°W–120°W	3,198	0.47
1985/86	V	130°E–170°W	622	0.50
1986/87	II	60°W–0	550	0.38
1987/88	III	0–70°E	890	0.46
1988/89	IV	70°E–130°E	3,809	0.52
1989/90	I	120°W–60°W	1,561	0.37
1990/91	VI	170°W–120°W	2,801	0.53
1991/92	V	130°E–170°W	1,838	0.46
1992/93	III	0°E–40°E	194	0.53
1993/94	I	110°W–60°W	915	0.31
1994/95	III+IV	40°E–80°E	2,473	0.40
1995/96	VI	170°W–140°W	1,579	0.47
1996/97	II	30°W–0	1,099	0.75
1997/98	II	60°W–25°W	451	0.73
1998/99	IV	80°E–130°E	17,703	0.18
1999/00	I	80°W–60°W	2,139	0.27
2000/01	VI+I	140°W–110°W	2,294	0.18
2001/02	V	130°E–150°E	764	0.41
2002/03	V	150°E–170°W	6,545	0.26
2003/04	V	170°E–170°W	7,288	0.27

Table 9

Estimates of the annual rate of increase for humpbacks in each Management Area, for each breeding stock and for the circumpolar estimates as a whole.

Region	Rate of increase	95% CI
Area I	0.046	(–0.029; 0.123)
Area II	0.065	(–0.026; 0.152)
Area III	0.033	(–0.072; 0.133)
Area IV	0.149	(0.100; 0.197)
Area V	0.128	(0.067; 0.174)
Area VI	–0.002	(–0.072; 0.068)
Breeding stock A	0.053	(–0.083; 0.214)
Breeding stock B	0.031	(–0.255; 0.285)
Breeding stock C	0.066	(–0.048; 0.171)
Breeding stock D	0.144	(0.096; 0.192)
Breeding stock E	0.137	(0.067; 0.185)
Breeding stock F	0.016	(–0.055; 0.086)
Breeding stock G	0.046	(–0.034; 0.129)
Circumpolar	0.096	(0.057; 0.133)

Circumpolar estimates for CPI and CPII are similar to previous estimates but the CPIII estimate of 41,500 is substantially greater than the previous estimate for CPIII (then incomplete) of 9,300 based on 1991/92–1997/98 (Branch and Butterworth, 2001a). This increase is explained by the high estimated abundance in Area IV, which was only surveyed in 1998/99, and by the re-surveying of Area V in 2001/02–2003/04. Most of the estimated abundance (75%) in CPIII is in Area IV and V. The Area IV estimate (17,938) is within the range of recent JARPA estimates (Matsuoka *et al.*, 2011) (Fig. 4). Although the Area V estimate (13,246) is above the highest reported JARPA estimate of 9,342, the confidence intervals around these estimates are wide and the differences are not statistically significant (Fig. 4).

The three CPs differ in substantial ways: survey design, primary effort mode, and unsurveyed regions all changed from one CP to the next. Previously, sensitivity analyses have shown that survey design and primary effort mode only had a minor impact on humpback abundance estimates (Branch and Butterworth, 2001a), but it is important to account for the unsurveyed area south of 60°S in CPI and CPII. To obtain comparable estimates from the CPs it was assumed that the density in the unsurveyed northern strata was the same as in the adjacent northern strata, an assumption that has been made for previous estimates based on the IDCR/SOWER data (Branch, 2006; Branch, 2007; Branch and Butterworth, 2001a; 2001b). Data from the IDCR/SOWER surveys provide some support for this assumption: humpback whale density is highest close to the pack ice, and lower further away, but density is fairly similar for distances of more than 60 n.miles from the ice edge (Kasamatsu *et al.*, 2000). If instead, density is lower in the northern unsurveyed areas, then the 'comparable areas' estimates for CPI and CPII will be too high compared to those for CPIII, and the estimated rate of increase will be negatively biased.

Estimated rates of increase are subject to the comparability of CPI, CPII and CPIII surveys, especially given that CPI and CPII surveys did not cover the most northerly areas. JARPA surveys in recent years have found high densities of humpback whales near 60°S in Area IV (Matsuoka *et al.*, 2011). However, given the magnitude of the increase from CPII to CPIII it is unlikely that a different method for comparability would alter the general conclusion that humpback whales have increased dramatically in numbers. According to the 'comparable-areas' estimates, circumpolar abundance estimates are increasing at 9.6% per annum (95%

Table 10

Comparison of abundance estimates for each breeding stock based on surveys and mark-recapture methods from the northern breeding grounds in austral winter (references provided in the text), and from the IDCR/SOWER CPIII surveys in the Antarctic in the austral summer. For comparability, the CPIII estimates are projected to the mid-year of the relevant breeding ground estimate by assuming an annual rate of increase (ROI) of either 0% (no increase), 5% or 10%. The ratio of the CPIII to breeding ground estimates is also given.

Breeding stock	Breeding ground estimates		CPIII projected estimates			Ratio of CPIII to breeding ground
	Year	Estimate	ROI = 0%	ROI = 5%	ROI = 10%	
A	2008	9,300	168	285	481	0.02–0.05
B	2004–06	7,600	595	956	1,538	0.08–0.20
C	2000–06	13,000	2,391	3,844	6,182	0.18–0.48
D	2005	12,800	17,959	26,131	38,020	1.40–2.97
E	1999–05	9,000	13,300	13,637	13,982	1.48–1.55
F	2003–07	1,350	3,852	5,071	6,676	2.85–4.95
G	2006	6,504	3,337	5,366	8,628	0.51–1.33
Total	1999–08	59,584	41,602	55,290	75,507	0.70–1.27

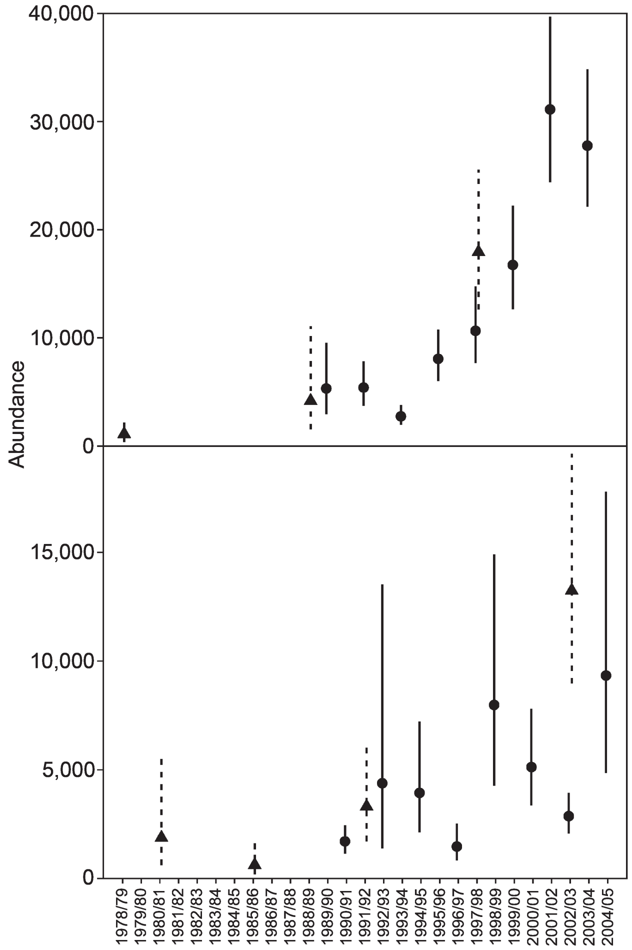

Fig. 4. Comparable-area IDCR/SOWER abundance estimates (triangles, dashed lines) and JARPA abundance estimates (circles, solid lines) for IWC management Area IV (top panel) and Area V (bottom panel). JARPA estimates were obtained from Table 3 of Matsuoka *et al*. (2011).

CI 5.8–13.4%), a rate that is significantly greater than zero. Estimated rates of increase for Area IV and V and Breeding Stocks E and F are at or greater than the estimated biological maximum of 11.8% (Zerbini *et al.*, 2010). JARPA surveys in Area IV also show an increasing trend at greater than 10.1% per year (Matsuoka *et al.*, 2005), mirroring the estimates here. An increasing rate is to be expected for large baleen whales recovering from depletion since intraspecific competition should be lower, and indeed this pattern has been observed in many other baleen whale populations (Best, 1993; Branch *et al.*, 2004), including humpback whales off the eastern and western coasts of Australia. Additionally, however, there is some variability around the circumpolar estimates and wide variation in the range of estimated rates of increase for different areas and Breeding Stocks, likely due to the small number of IDCR/SOWER abundance estimates for each group (3–4), high associated CVs, changes in the survey design between the circumpolar sets of surveys and year-to-year variability in the distribution of humpback whales.

No attempt was made to constrain either the point estimate or the confidence interval to a biological maximum of 11.8% (Zerbini *et al.*, 2010). Due to the limited number of abundance estimates in each area, and the wide confidence intervals associated with each abundance estimate, it is expected that some estimated rates of increase will be much smaller than the true rate, and others much larger, and that the confidence intervals around the estimated rates of increase will be broad.

Comparison of breeding ground and feeding ground estimates

Abundance estimates in the Antarctic differ greatly from those in the temperate breeding grounds. A suggested current abundance for each Breeding Stock is listed in this section, and compared with feeding ground estimates in Table 10.

Breeding stock A

For Breeding Stock A, a fixed-wing aircraft survey off Brazil estimated an abundance of 9,330 (CV = 0.16) for 2008 (Wedekin *et al.*, 2010). The projected CPIII estimate is only 2–5% of this estimate (Table 10). Satellite tagging data have demonstrated that humpback whales from this Breeding Stock travel to feeding grounds near South Georgia and the South Sandwich Islands, but no tracked whales have yet travelled south of 58°S (Zerbini *et al.*, 2006; Horton *et al.*, 2011), and high densities were also recorded north of 60°S in the JSV database between 25°W and 5°E during summer (Miyashita *et al.*, 1995), thus the IDCR/SOWER surveys likely cover only a very small fraction of the total stock. The IDCR/SOWER-estimated rate of increase of 5.3% (95% CI –8.3 to 21.4%) is accordingly not very applicable to this Breeding Stock. For Breeding Stock A, estimates of abundance and rates of increase should therefore be taken from the breeding grounds: abundance 9,330 (CV = 0.16) (Wedekin *et al.*, 2010); rate of increase: 7.4% (95% CI 0.6–14.5%) (Ward *et al.*, 2011).

Breeding stock B

For the B1 substock in Gabon, genotypic mark-recapture abundance was estimated to be 7,134 (CV = 0.23) in 2004–06 (Collins *et al.*, 2010). For the B2 substock, a photographic catalogue from 2001–05 contained 260 individuals with a high inter-annual resighting rate of 16.5% that suggested a small population (Barendse *et al.*, 2006). Assuming that the B2 substock was ~500, the total for Breeding Stock B was ~7,600 in 2004–06. The projected CPIII estimate is just 8–20% of this total (Table 10). During transits to and from the IDCR/SOWER surveys, relatively high numbers of humpback whale sightings were recorded (Fig. 1) north of 60°S in the 20°W to 10°E region. JSV data revealed high densities of humpback whales north of 60°S in the summer between 25°W and 5°E (Miyashita *et al.*, 1995). Finally, the 2005/06 IDCR/SOWER survey (not included in these abundance estimates), conducted fin whale research in the 55°S–61°S and 5°E–20°E region and recorded a large number (149) of humpback whale schools, nearly all north of 60°S (Ensor *et al.*, 2006). It is therefore likely that most humpback whales from this Breeding Stock do not migrate south far enough (to 60°S) to reach the region covered by the IDCR/SOWER surveys, and therefore the breeding ground abundance estimate of ~4,300 should be preferred. Rates of increase have not been estimated from the breeding grounds and the IDCR/SOWER estimate (3.1%) has broad 95% confidence intervals (–25.5% to 28.5%) and applies only to a portion of the population, thus current trends in Breeding Stock B are not well defined.

Breeding stock C

For the C1 substock, a ship-based line-transect survey estimated abundance to be 5,965 (CV = 0.17) in 2003 (Findlay *et al.*, 2011). For the C2 substock, a total of 250 individuals were photo-identified from the eastern Comoros Archipelago but no abundance estimate was calculated (Ersts *et al.*, 2006). For C3 at Antongil Bay, Madagascar, photographic and genetic mark-recapture techniques provided estimates ranging from 4,936 (CV = 0.44) to 8,169 (CV = 0.44) for 2000–2006 (Cerchio *et al.*, 2009). The total for Breeding Stock C was therefore approximately 13,000 in 2000–06. The extrapolated CPIII abundance estimate is only 18–48% of the total breeding ground estimate (Table 10). In the applicable Antarctic region (10°E–60°E), numerous sightings of humpback whales were made during transits north of 60°S (Fig. 1) and (as summarised above) during fin whale research on the 2005/06 IDCR/SOWER survey (Ensor *et al.*, 2006). It is therefore likely that the greatest portion of this Breeding Stock does not migrate south far enough to be included in the IDCR/SOWER surveys, and thus the breeding ground estimates summing to about 12,000 are more relevant for this stock than the IDCR/SOWER estimates. The best estimated rate of increase (9.0% or 12.3%) for this stock comes from shore-based counts at Cape Vidal, South Africa (Findlay and Best, 2006).

Breeding Stock D

In the breeding grounds, an aerial survey estimated that there were 12,800 humpback whales (95% CI 7,500–44,600) in Breeding Stock D in 2005 (Paxton *et al.*, 2011). This population has been increasing steadily at 10.15% (SE = 4.6%) per year (Bannister and Hedley, 2001). At this rate of increase, the CPIII estimates would have increased to about 38,000, i.e. 2.89 times the breeding ground estimate in 2005 (Table 10), only just below the upper confidence interval of the breeding ground estimate of 44,600. JARPA estimates for Management Area IV of 31,134 (CV = 0.123) in 2001/02 and 27,783 (CV = 0.115) in 2003/04 come from a similar longitudinal range (70–130°E vs. 60–120°E) and are also more than double the breeding ground estimates (Matsuoka *et al.*, 2011). Despite substantial effort during IDCR/SOWER transits, few humpback whales have been sighted north of the IDCR/SOWER survey region (Fig. 1), suggesting that the majority are inside the IDCR/SOWER survey region. If the feeding ground estimates provide a more complete survey of the entire Breeding Stock, this would imply that either the breeding ground survey does not cover the full distribution of this Breeding Stock or that a substantial portion of these humpback whales do not migrate to the west coast of Australia each year. An examination of the sightings from the breeding ground survey showed high numbers of sightings even in the northernmost survey leg (Paxton *et al.*, 2011), so it is possible that a portion of the breeding ground was not surveyed. Some support for non-migration comes from the male-biased sex ratio on the west coast of Australia: 194 males and only 64 females were sampled migrating past the North West Cape in 2002–03, and the authors suggested that the missing whales may overwinter near the feeding grounds instead of migrating (Jenner *et al.*, 2006). It is tentatively suggested that the feeding ground estimates from IDCR/SOWER and JARPA provide a more complete abundance estimate than the breeding ground survey, and hence the current abundance of Breeding Stock D is >30,000. Rates of increase from both IDCR/SOWER and JARPA surveys are above biologically plausible levels and have wide confidence intervals; therefore the more precise 10.15% annual rate of increase from the feeding grounds should be preferred for this Breeding Stock (Bannister and Hedley, 2001).

Breeding stock E

For substock E1 a shore-based survey at Point Lookout estimated abundance to be 7,090 (95% CI 6,459–7,782) in 2004 (Noad *et al.*, 2011), and a multi-point mark-recapture estimate of 7,041 (95% CI 4,075–10,008) was obtained for the east coast of Australia for 2005 (Paton *et al.*, 2011). Mark-recapture methods from 1999–2004 gave estimates of 383 (CV = 0.35) using photographs and 804 using genotypes for New Caledonia (substock E2); similar methods yield estimates of 1,168 (CV = 0.16) from photographs and 1,840 using genotypes for Tonga (substock E3) (Constantine *et al.*, 2010). The total breeding region abundance for Breeding Stock E is therefore ~9,000 during 1999–2005. The projected CPIII estimate is 1.48–1.55 times greater than this total (Table 10) and is also higher than the JARPA estimates in recent years (2,700–9,800 during 1998/99–2004/05) in Area V (Fig. 4). All sources have estimated a high rate of increase for this population, IDCR/SOWER: 13.7% (95% CI 6.7–18.5%), JARPA: 6.4% (CV = 0.71) (Matsuoka *et al.*, 2005), the Point Lookout shore survey: 10.6% (95% CI 10.1–11.1%) (Noad *et al.*, 2011), Byron Bay: 11.0% (95% CI 2.3–20.5%) (Paton and Kniest, 2011), and Hervey Bay: 13.4% (95% CI 11.6–15.2%) (Forestell *et al.*, 2011). The IDCR/SOWER and JARPA estimates probably include most of the Breeding Stock given that few humpback whales are sighted north of the survey region during IDCR/SOWER transits (Fig. 1). Humpback whales migrating past the east coast of Australia have a male-biased sex ratio of 2.4:1 (Brown *et al.*, 1995), suggesting that not all females leave the feeding grounds in winter (Paton and Kniest, 2011). It is not clear whether to prefer estimates from the breeding or feeding regions, although these estimates are broadly similar, suggesting that the total abundance of Breeding Stock C is probably in the range of 8,000–13,000. The Point Lookout survey provides the most precise estimate of the rate of increase: 10.6% (95% CI 10.1–11.1%) per year (Noad *et al.*, 2011).

Breeding Stock F

During 1998–2005, 93 individuals were identified (no interannual resightings) in the Cook Islands (substock F1), implying a small substock (Hauser and Clapham, 2006). In French Polynesia (substock F2), photographic mark-recapture methods provided breeding ground abundance estimates ranging from 853 (CV = 0.24) to 1,849 (CV = 0.16) during 2003–2007 (Albertson-Gibb *et al.*, 2009). The projected CPIII estimate is 2.84–4.94 times greater than the center of this range of breeding ground estimates (Table 10). There are several reasons to suspect that this estimate refers to only a portion of Breeding Stock F. First, no abundance estimate is available for the Cook Islands (Hauser and Clapham, 2006). Second, the French Polynesia estimate was based on two islands with the highest densities of humpback whales, but sightings have also been reported around 23 other islands (Poole, 2006). Third, the sex ratio in French Polynesia is male biased (1.5:1) (Poole, 2006), and therefore some females may remain near the feeding grounds in the winter. For these reasons, the IDCR/SOWER estimates (3,852, CV = 0.22) seem more appropriate for this Breeding Stock. The estimated rate of increase from the IDCR/SOWER is 1.6% (95% CI –5.5% to 8.6%), suggesting that this population could be increasing, stable or decreasing.

Breeding Stock G

A photographic mark-recapture study in Ecuador provides a breeding ground abundance estimate of 6,504 (95% CI 4,270–9,907) in 2006 (Félix *et al.*, 2011). The projected

CPIII estimate is similar (0.51–1.33) to this estimate (Table 10), and to an alternative feeding ground estimate from a CCAMLR survey in East Antarctica of 6,991 (CV = 0.32) in 2001 (Hedley *et al.*, 2001). The estimated rate of increase from IDCR/SOWER is 4.6% (95% CI –3.4% to 12.9%), while the breeding ground estimates are increasing rapidly during 1997–2006 (Félix *et al.*, 2011). It seems reasonable to conclude that Breeding Stock G numbers 5,000–8,000 and is increasing at 5–10% per year.

Summary of breeding stocks

Estimates for Breeding Stocks A, B and C are far lower than from the feeding grounds, while those for Breeding Stocks D, E and F are far higher. These differences may just be due to inherent uncertainty in the survey estimates. However, it is interesting to note that the ratio between the two appears linked to the position of the Antarctic Polar Front (Fig. 1). In regions where this front is far to the north, the breeding ground estimates are higher than the IDCR/SOWER estimates (suggesting that many humpback whales are further north and outside the IDCR/SOWER survey region), while in regions where the front is further south, breeding ground estimates are similar or lower than the IDCR/SOWER estimates. Differences in the estimates may also be due to the use of the Naïve model (IWC, 1998; 2006) to place longitudinal divisions between the Breeding Stocks in the Antarctic. In reality, the divisions between the Breeding Stocks are not fixed: there is some mixing of the Breeding Stocks in the Antarctic, but it is unlikely that most humpback whales from Breeding Stocks A, B and C actually migrate to the Antarctic regions assumed to be inhabited by Breeding Stocks D, E and F.

Total Southern Hemisphere abundance

The sum of all available abundance estimates from the northern breeding grounds is 60,000; whereas the corresponding totals for the IDCR/SOWER surveys are 42,000, 55,000 and 76,000 for assumed rates of increase of 0% (which is unlikely), 5% and 10% respectively (Table 10). Both IDCR/SOWER and feeding ground estimates are negatively biased. In the IDCR/SOWER surveys, some humpback whales on the trackline are missed (i.e. $g(0)<1$). Humpback whales produce very visible cues, thus this bias is probably small: an estimate of 10% was obtained from the eastern North Pacific (Calambokidis and Barlow, 2004). A more substantial negative bias comes because some humpbacks do not migrate southwards far enough to reach the IDCR/SOWER survey region. For Breeding Stocks A, B and C, where the Antarctic Polar Front is further north, the sum of the breeding region estimates is about 30,000 but the projected IDCR/SOWER estimates are only 3,000–8,000. The sum of the breeding ground estimates is probably also negatively biased because not all breeding grounds have been surveyed. For these reasons it is fairly safe to conclude that there are more than 55,000 humpback whales in the Southern Hemisphere.

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