Population growth of Australian East coast humpback whales, observed from Cape Byron, 1998 to 2004

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ABSTRACT

Humpback whales (*Megaptera novaeangliae*) that migrate past the east coast of Australia comprise part of Group V (E(i) breeding stock). From 1995 to 2004 an annual 16 day survey was conducted from Cape Byron (28°37'S, 153°38'E), the most easterly point on the Australian mainland, monitoring the peak of the humpback whale northern migration. The annual rate of increase between 1998 and 2004 of humpback whales observed off Cape Byron is 11.0% (95% CI 2.3–20.5%). This rate of increase is consistent with that recorded from other studies of the humpback whale population off the east coast of Australia. The large confidence intervals associated with this estimate are due to considerable inter-annual variation in counts. The most likely explanation for this being the short survey period, which may not have always coincided with the peak of migration, and in some years a large proportion of whales passed Cape Byron at a greater distance out to sea, making sightability more difficult.

KEYWORDS: HUMPBACK WHALE; SURVEY-SHORE-BASED; TRENDS; GROWTH; MIGRATION; SOUTHERN HEMISPHERE; PACIFIC OCEAN

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) migrate north from Antarctica, along the east and west coasts of Australia during the Austral winter, to breed and give birth in the warm waters of northern Australia. The humpback whales that pass the east coast of Australia are thought to comprise part of the group that feeds in Antarctic Area V (130°E to 170°W). This group is therefore identified as 'Group V whales'. Recent studies suggest that there is sub-stock structure on the tropical breeding grounds and that these sub-stocks intermingle to at least a small degree (Garrigue *et al.*, 2000). Group V humpback whales on their tropical breeding grounds have been divided into three sub-stocks known as: Breeding Stock E(i), those wintering off the Australian east coast; E(ii), those wintering around New Caledonia; and E(iii), those wintering around Tonga (Bannister, 2005; Olavarria *et al.*, 2006). Breeding Stock E(i), the Australian east coast population, is the largest.

Historically, the Group V population was hunted from both land- and vessel-based operations throughout its migratory range, including the East Australian coastline and the Antarctic. Land-based whaling was conducted from several locations on the east coast of Australia, commencing in 1952. These locations included Twofold Bay, Jervis Bay, Byron Bay and Tangalooma on Moreton Island. Other locations where whaling activities occurred in the South Pacific include Norfolk Island, Cook Strait in New Zealand and Tonga. Small numbers of whales were also taken in Fiji and Vanuatu. Considerable illegal hunting of humpback whales was undertaken in Antarctic waters from 1959 to 1961 by the Soviet Union (Clapham *et al.*, 2005; Paterson *et al.*, 2001).

Prior to the 1950s there was little exploitation of the E(i) sub-stock. At this time the population size of the entire Group V population was estimated to be between 10,000 and 26,000

whales (Bannister and Hedley, 2001; Chittleborough, 1965). These figures are potentially an underestimate of the pre-exploitation population for Group V as the total number of 20th century humpback whale catches in Area V and in breeding area (E) was 102,398 whales (Clapham *et al.*, 2005; Clapham and Zerbini, 2006). Given the large number of whales killed and recent population modelling, it is now thought that the pre-exploitation population of the Group V whales was considerably larger than previously thought, potentially in the range of 30,000 to 40,000 humpback whales (Jackson *et al.*, 2006).

The industrial shore-based whaling and large scale illegal pelagic whaling in the Southern Ocean resulted in a population collapse by 1962 (Chittleborough, 1965). Estimates for the remaining population vary in size from 104 for all of Group V (Bannister and Hedley, 2001) to 500 for the east Australian and New Zealand populations (Chapman, 1974; Chittleborough, 1965). These estimates are less than 5% of the pre-exploitation size. In the 45 years since 1963, the east Australian population of humpback whales is one of a number of populations that has shown strong recovery (Brown *et al.*, 2003; Paterson *et al.*, 2001). The apparent lack of recovery of whales migrating past New Zealand (Childerhouse and Gibbs, 2006; Gibbs and Childerhouse, 2000), and low numbers recorded in some regions of the South Pacific (Garrigue *et al.*, 2002; Gibbs *et al.*, 2003), indicate that the strong increases seen in East Australia have not been seen across other parts of the South Pacific.

Shore-based observation stations have been utilised to monitor trends in a number of populations of cetaceans (Bryden *et al.*, 1996; Buckland and Breiwick, 2002; Paterson *et al.*, 2004). Long term studies have been conducted on humpback whales in Cape Vidal, Natal (Findlay and Best, 1996b) and North Stradbroke Island, Australia (Brown, 1996; Bryden *et al.*, 1996; Noad *et al.*, 2011; Paterson *et al.*, 2004). Humpback whales migrate along the continental

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inshore waters along the east coast of Australia. Bryden (1985) demonstrated that the migratory corridor between Cape Byron and Cape Moreton, was particularly narrow, with 96% of humpback whales passing within 10km of headlands within this region. The width of the humpback whale migration corridor was reassessed in 1991 (Brown, 1996) and 2007 (Noad and Dunlop, 2007) and found to be consistent with the results of Bryden (1985).

The demonstrated effectiveness of using shore-based observations to monitor cetacean population trends combined with the fact that humpback whales are known to migrate close to the coast off northern New South Wales, make Cape Byron an ideal location for a long term assessment of the recovery of the E(i) Breeding Stock. This paper reports on land-based counts collected between 1998 and 2004 and the observed increase in humpback whales observed off Cape Byron during this period.

MATERIALS AND METHODS

Cape Byron is located at the most easterly point on the Australian mainland (28°38'S, 153°38'E). Early surveys were conducted from a location (28°38'19"S, 153°38'10"E) *ca*. 200m from the most easterly point on Cape Byron. This location has an altitude of 83m and unobstructed visibility from the south-southeast to the north-northeast (190º–346º). The Cape Byron Whale Research Project (CBWRP) operated at this location from 1995 until 1998. For the 1999 survey the CBWRP relocated to a location on the upper balcony of the Cape Byron Lighthouse. This location (28°38'19"S, 153°38'11"E) is 173m from the original land-based survey location and is 33m higher (total height is 116m above sea level). The new survey location has a slightly better outlook (south-southeast to the north-northwest) and has access to a reliable power supply for operating a computer. It also provides shelter during inclement weather and improved accuracy for distance determination because of the increased altitude.

The timing for the CBWRP was based upon historical whaling data collected at the Byron Bay station, which operated between 1954 and 1962 (Chittleborough, 1965). During this period 1,146 whales (primarily humpback whales) were taken near Byron Bay (Chittleborough, 1965). The survey period was chosen to coincide with the peak of the catches at the whaling station during the northern migration as it is assumed that this peak catch related to the peak in numbers of the northern migration. Observations were carried out from the land station during a 16-day period annually (i.e. last week of June and first week of July). Observations were carried out between the hours of 07:00 and 16:30 daily, weather permitting. Observations were suspended when rain made it impossible to undertake surveys; when wind strength reached a point making it impracticable to operate (25–30 knots) or lightning activity made it unsafe to be in the lighthouse. Two shifts operated each day with a 15 minute overlap, the first from 07:00 to 12:00 and the second from 11:45 to 16:30.

A software package named 'Cyclopes' was developed by staff and students from the University of Newcastle, Australia specifically for the CBWRP to improve and allow more reliable tracking of marine mammals and vessels. This real time tracking system uses an electronic theodolite interfaced to a laptop computer. The theodolite is used to acquire the location of the pod by measuring the horizontal and vertical angles to the pod, which are sent directly to the computer. Cyclopes then calculates the position of the pod

correcting for tides, earth curvature and refraction. The program determines which pod was observed and plots its position on a map shown on the computer screen. Cyclopes also has the capability to record information regarding the pod's make up, activity, speed, course, distance, direction and time of observation (Kniest and Paton, 2001).

The project operated with a mean of six observers (range 2–8). Due to operational requirements, during lighthouse tours (about half an hour a couple of times a week), the survey team was reduced to two experienced observers for this short period. Survey effort was consistent over the period of the study (1998–2004). Normal survey operations included at least two observers scanning the ocean to the south and east of the Cape, and at least one scanning to the north of the Cape. For over 90% of the observation period, an experienced observer was present to confirm sightings of pods, species and composition. An observer was deemed to be experienced if they had already been involved with the project for two years, or if they had several seasons of prior field experience working with humpback whales. A research vessel worked in conjunction with the land station to undertake fluke photo-identification, confirmation of pod size, collection of behavioural data and to collect genetic samples.

Observers used both the naked eye and binoculars (7×50 Tasco compass binoculars and 10×50 Nikon binoculars) to detect whales. Once pods were sighted, a theodolite operator (who was in addition to the dedicated observers) using a Leica TC1105 (or similar) theodolite would take fixes on the location of the pod and track movement of the pod while within the field of view of the land station. When additional personnel were available a person was dedicated to operating Cyclopes and assisting the research vessel to locate pods. At all times at least one observer was scanning for new pods.

Records of effort and weather were kept during all observation periods. Weather information including wind speed and direction, cloud cover, sea state (Beaufort), swell, visibility (estimated in km) and any other factors such as smoke haze, were recorded using Cyclopes' weather recording function. In addition Cape Byron headland has a meteorological station with detailed weather information available for the site from the Australian Bureau of Meteorology.

When pods were first observed and an experienced observer confirmed the species, the observers would estimate pod composition and continually track each pod as it approached the Cape from the south. The pod composition would be adjusted (and confirmed by an experienced observer) when necessary. Careful notes were taken when pods split or joined, or there was a sudden change in behaviour. Pod composition was confirmed by the research vessel when the vessel intercepted the pod. The research vessel, under normal operating protocols, operated north of the Cape so as not to potentially disturb the movements of whales prior to passing the Cape.

Observers would monitor a pod's activity and direct the theodolite operator to the surfacing of pods. Where possible one event out of each surfacing cycle would be fixed using Cyclopes to monitor the movement pattern of the pod. Once a number of sightings of the pod were recorded, the program was able to predict the direction and speed of travel and any changes in course or speed. These data were plotted in real time on the computer screen showing the trackline of pods passing the land station. The program was extremely useful in eliminating duplicate counts of the same pod especially when pods were located close together or when a pod was lost for a period of time.

ANALYSIS

To determine the number of whales (and pods) migrating past the Cape during the survey period, all sighting data were converted to a standard 10hr day, consistent with the methodology used in other migratory humpback whale surveys (Brown, 1996; Bryden *et al.*, 1996; Findlay and Best, 1996b; Paterson *et al.*, 2004). The standard survey period was 9.5hr, therefore sighting rate was scaled pro-rate to a 10hr survey period. Due to the expansive field of view from the land station (over 180°), only pods that had crossed a line due east of the Cape during the survey period were included in the analysis. The time each pod passed the line extending east of the cape was calculated by projecting from the pod's closest observed position along a line representing its mean course and speed. These pods were included in the analysis if they were determined to have passed east of the Cape during the survey period. Only humpback whales observed travelling in a northerly direction were included in the analysis.

To avoid double counts or missing whales when pods split into separate groups or when other whales would join a previously tracked pod, the number of whales was only counted in the initial pod. After an affiliation or disaffiliation of a pod occurred, the new pods formed would be assigned new names. During analysis these pods would have the number of whales in the pod set to zero (although the pod composition is still noted). For example if pod 'D' (size = 1) joined pod 'H' (size = 2), the new pod formed would be called 'H/D' with composition noted as 3 but the pod size is assumed to be zero for the sake of determining whale counts; and the new pod is not included in the count as an extra pod.

Determining which days should be excluded from the analysis due to adverse weather can be subjective. For the purposes of this analysis, the following protocol was used for the exclusion of days: (1) days with a mean sea state greater than Beaufort 3 and/or mean visibility less than 15km for extended periods; and (2) days on which fewer than five hours of survey were conducted.

Each day's count was converted to a standard 10hr count for that day, given by:

$$C_i = 10/h_i \times N_i$$

Where:

i is the ith day of the survey

h_i is number of hours of survey for the ith day (5hr < h_i < 10hr)

N_i is the number of whales that passed the survey point during the h_i hours.

The mean 10hr count (R_y) for each year was calculated from all the daily 10hr counts (C_i, where i = 1 to D_y, and D_y = the number of days surveyed for year y). A simple linear regression was fitted to the natural log of the mean 10hr count for each year (R_y) over the survey period to determine the growth rate (percentage increase per year).

A growth model has also been fitted by generalised least squares. Full details of the growth model are shown in Appendix 1.

RESULTS

Between 1998 and 2004 a total of 105 days (897hr, 45min) of land-based surveys were conducted from Cape Byron. During this period a total of 1,768 pods, comprising 3,340
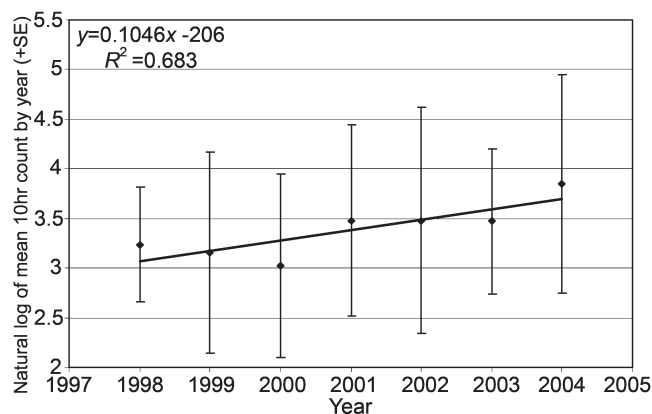

Fig. 1. Natural log of the mean 10hr count by year with standard errors show. A simple linear regression has been fitted.

humpback whales (including 19 neonate calves) were observed travelling north past the Cape. Nineteen pods of humpback whales (i.e. 1% of all pods seen), were observed to have a direction of travel other than in the general north direction (i.e. east, southeast or southwest). These pods were typically observed to be moving in a direction to interact with other pods of humpback whales. No pods were observed with a clear southerly migration direction during the survey. It is therefore assumed that, during the survey period all pods of humpback whales observed off Cape Byron have a clear northerly migration direction and therefore all pods were included in this analysis.

Most years of the CBWRP survey suffered from days with poor weather conditions and therefore not all days were surveyed. Other days were surveyed with below average conditions (such as rough seas) and have been eliminated from the analyses. Both 1999 and 2000 had a higher proportion of bad weather days than other years. Four days were lost due to rain in 1999 and another four days were removed because of rough seas or poor visibility.

Fig. 1 indicates the increase in the mean number of whales observed per 10hr for the seven years of the survey. Based on the fitting of a simple linear regression to the log of the mean 10hr counts for the 16-day survey period, the annual growth rate for the humpback population was estimated to be 11% (95% CI 2.3–20.5, see Appendix 1).

The seven-year survey had large variations in the mean distance offshore of pods as shown in Fig. 2. In 1998 and 2004, whales passed significantly closer to the Cape Byron survey station than other years except 2002 (p<0.05 ANOVA, post hoc Bonferroni Test). The overall mean number of humpback whales in each pod was 1.9±0.16 with slightly higher values in 1998 and 2004. The mean pod speed is reasonably consistent over years (Table 1). There was an increase in the number of newborn calves observed over the survey. The number of newborn calves observed annually, is approximately 0.5 to 1% of the total number of whales observed. Most pods had a composition of one (38%), two (43%) or three (12%) animals, while the rest of pods had between four to eight (7%) animals.

DISCUSSION

The annual rate of increase between 1998 and 2004 for humpback whales observed off Cape Byron is calculated to be 11.0% (95% CI 2.3–20.5). This annual rate of increase is consistent with results recorded at Point Lookout, North Stradbroke Island (134km north of Cape Byron) by two
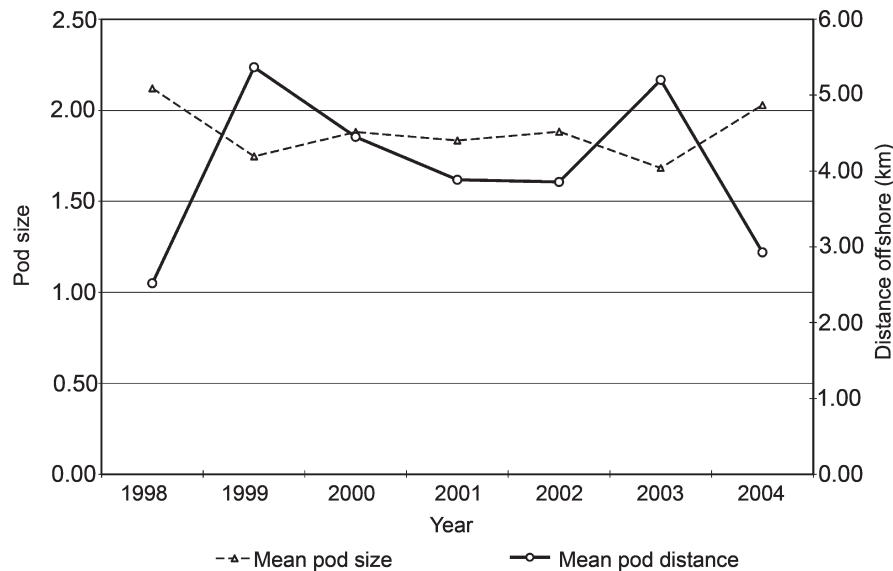
Fig. 2. Graph of the mean pod distance off shore and pod composition from 1998–2004.

independent land-based surveys. Surveys conducted by Paterson (Paterson *et al.*, 2004) estimate a growth rate of 10.5% per annum for the humpback whale population from 1984 to 2002. Other surveys conducted by Bryden *et al.* (1996) and Brown (1996) reported slightly higher annual rates of population recovery of about 12.3%. Brown *et al.* (2003) reassessed the Bryden/Brown data using more appropriate models and re-estimated the population increase (1981–2000) to be between 8.52% and 10.08%. However, Noad, continuing the Bryden/Brown surveys, reported a 10.6% (95% CI 10.1–11.1%) for the period 1987–2004 (Noad *et al.*, 2011) and an increase of 10.9% (95% CI 10.5–11.4%) for the period 1984–2007 (Noad *et al.*, 2008). While these population growth rates lie near or above the theoretical reproductive maximum of the species (Bannister and Hedley, 2001; Best, 1993; Brandao *et al.*, 1999; IWC, 2008), which on the whole, are based on life history estimates for Northern Hemisphere humpback whale stocks where estimates for population growth rates are lower than determined for the southern hemisphere, (IWC, 2008), they are remarkably consistent over time with a very tight correlation between log-transformed, normalised whale counts and year (Noad *et al.*, 2011).

While this survey provides a useful estimate of population growth rate for the E(i) breeding stock, there are several important considerations and some potential sources of bias that may influence the CBWRP estimate. There are several explanations for the observed variation in the number of whales counted per 10hr period over the survey period:

(1) there are large inter-annual variations in the number of humpback whales migrating up the east Australian coast;
(2) some of the surveys were influenced by bad weather or poor visibility conditions;
(3) the short (16 day) survey missed some of the peak migration period in some years; and
(4) large variations in the average pod distance out to sea may lead to differences in their sightability.

A degree of inter-annual variation is expected when monitoring a natural system. Forestell *et al.* (2003) suggested that El Niño-Southern Oscillation (ENSO) events may have a significant impact on fluctuations in whale numbers on the east coast of Australia. They suggested that humpback whales might migrate to other foraging areas in the high-latitude feeding grounds as a result of ENSO-related effects on food stocks. The whales might then migrate from there to different low latitude breeding grounds leading to variation in the number of whales observed between years. However, the long term survey conducted by Paterson from North Stradbroke Island shows little variation in the overall humpback whale population count over the years (Noad *et al.*, 2011; Paterson *et al.*, 1994; 2001; 2004); there is no indication of large fluctuations in the migrating population from year to year. Clapham and Zerbini (2006) have also suggested that the rapid growth rate of the E(i) breeding stock may be a result of immigration from other populations. While these theories are plausible, the South Pacific Whale Research Consortium recently tested this hypothesis by undertaking an assessment of fluke identification

Table 1

Yearly summary of data collected from CBWRP, 1998-2004. The average pod distance is the estimated distance from the coastline to the pod. The average pod speed is given in km/h, and distances are in kilometres.

Year	Raw count	10hr count ± SE	Average pod size	Average distance	Average speed	No. of calves	Max. pod size	Max. distance
1998	375	25.47 (±1.79)	2.12	2.52	6.49	0	5 (4 pods)	8.5
1999	229	23.38 (±2.75)	1.75	5.37	6.11	1	7 (1 pod)	13.6
2000	302	20.52 (±2.52)	1.88	4.45	5.88	0	5 (4 pods)	15.2
2001	522	32.33 (±2.62)	1.83	3.88	6.16	3	5 (1 pod)	18.4
2002	563	32.36 (±3.13)	1.88	3.85	5.70	3	8 (1 pod)	15.3
2003	505	32.12 (±2.09)	1.68	5.20	5.39	5	5 (2 pods)	16.6
2004	814	47.02 (±3.01)	2.03	2.93	6.20	7	8 (1 pod)	15.8

photographs collected throughout Oceania (Breeding Stocks E(ii), E(iii) and F) and eastern Australia (Breeding Stock E(i)). This analysis, coupled with the recovery of Discovery marks from this region, indicates a very low level of interchange between eastern Australia and the Oceania region, which does not support this theory (Garrigue *et al.*, 2011a; Garrigue *et al.*, 2011b; Paton and Clapham, 2006).

Brown *et al.* (1995) report a bias in the sex ratio of humpback whales sampled off the east coast of Australia. They suggest that not all animals migrate every year as there is little reason for females who are not calving or mating to make the long migration. This may mean that, depending on environmental conditions, there may be inter-annual variation in the proportion of females undertaking migration, which in turn may lead to variation in survey counts. This issue remains unresolved with respect to eastern Australian humpback whales but has the potential to influence survey results between years.

Environmental conditions during surveys can have a significant impact on the sightability of whales. Some of the years appear to have been influenced by poorer than average weather conditions. In particular, 1999 and 2000 were badly affected by rain and poor weather and a large number of survey days were lost. Throughout the survey the average for the 10hr survey period was estimated only for those days with reasonable conditions. This should lead to an unbiased average from a smaller sample size but perhaps with a higher variance. Standardising effort between surveys in his manner should minimise any effect of environmental conditions on differences in whale counts between years.

The population growth estimate from this study is based on a maximum survey period of 16 days in any one year and represents an incomplete survey of the total migration period. While the assumption is that the weeks surveyed are representative of the full migration period, the accuracy of this assumption remains unknown. The survey was undertaken at the same time each year and studies of the timing of the migration have provided good evidence that migratory patterns are reasonably consistent between years, but the peak in migration may vary by up to a couple of weeks (Dawbin, 1966; Paterson *et al.*, 2001). It is therefore

likely that the two-week survey period did not always capture the entire peak of the humpback migration each year. To investigate this, data from Cape Byron can be compared with data collected at North Stradbroke (134km north of Cape Byron), which are collected over a much longer period. It takes almost one day for the humpback whales to travel from Cape Byron to Stradbroke at an average speed of 6.0km hr^{-1}.

A comparison of 10hr counts averaged on a weekly basis for the equivalent two weeks (e.g. accounting for the one day travel time difference between the two sites) at Cape Byron and North Stradbroke Island can be seen in Fig. 3. While there are fluctuations between the two sets of data, the Byron count is generally less than the Stradbroke count for most years except for 2001 and 2004 where the data are very similar. Fig. 2 shows that the average pod distance is also much lower than most other years (except 1998). Because of the large variations in the Stradbroke weekly counts it is difficult to determine if the Cape Byron survey was conducted at the height of the peak migration period; it appears the peak migration often spans about a four-week period usually starting one week before the Byron survey starts.

The distance at which the humpback whales pass the Cape varies considerably within and between years. All years of the Cape Byron survey except 1998 had observations of pods more than 10km offshore and most years had observations of pods that were 15km or more offshore. The estimated average percentage of pods that travelled more than 10km offshore was 3.0% (range 0–16%); and the average for pods passing more than 5km out was 35.0% (range 13.4–53.0%). A preliminary vessel-based survey across the continental shelf off Cape Bryon conducted in 1996 (CBWRP, unpublished data) indicated that approximately 90% of humpback whales passing Cape Byron did so within 10km of the shoreline; the remainder travelling up to 23kms offshore. Had the CBWRP survey been conducted in 1998 or 2004 one would expect similar results to those of the present study; while quite different results would have most likely been obtained had the CBWRP study been completed in 1994 or 2003. Findlay and Best (Findlay and Best, 1996a)
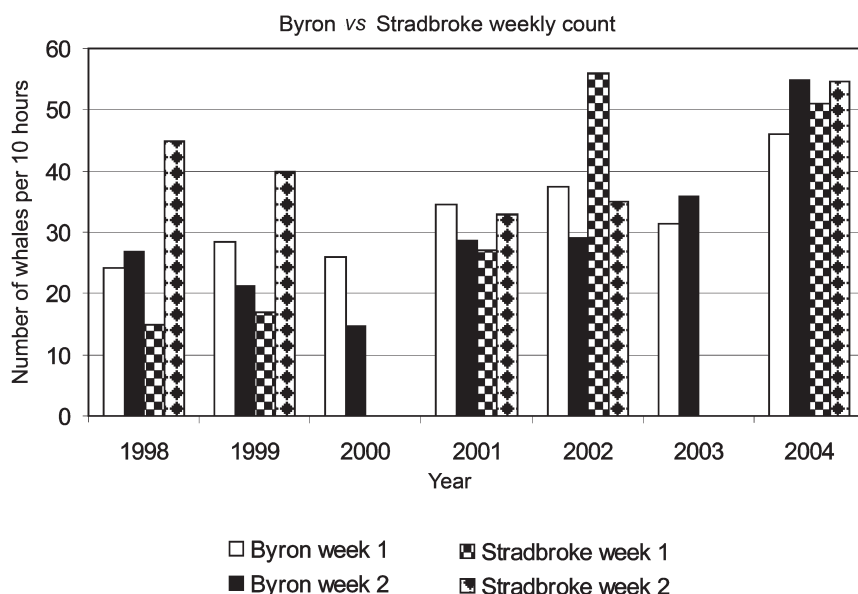

Fig. 3. Byron and North Stradbroke Island weekly 10 hours counts. The 1998 to 2002 Stradbroke Figures are from Paterson's surveys (Paterson *et al.*, 2001; 2004) and the 2004 Stradbroke Figures are from Noad *et al.* (2011).

found that between 40%–50% of whales travelling from 6–10km offshore can be missed during counts. About 37% of whales were measured further than 6km from the shoreline in 1999, 2000 and 2003. This implies there could be an error of about 18% in the counts for these years. Only ~10% of whales were observed more than 6km from the shoreline in 1999 and 2004.

Two factors affect precision of the rate of growth calculated from the Cape Byron surveys: (1) precision of R_y; and (2) number of survey years. Power calculations based on what is known about the migration patterns of this population could be conducted to determine whether annual surveys should be continued or whether a longer survey each second or third year would result in a greater improvement in precision per additional survey.

The 2004 count may be viewed as an outlier as it appears to be inflated compared to other years. However, it may in fact be a more reliable count than most years due to good weather conditions and the average pod distance offshore being less than other years. In addition, 2004 was the last year of the survey period and therefore will have the highest count for this study due to the population growth rate and this will further exaggerate this perceived bias. Some of the other years of the survey (2000 and 2003) have low counts of whales, which may have been a result of the greater average pod distance offshore and prevailing weather conditions. This may explain the difference between the growth rate calculated from the present study (11%, $R^2 = 0.683$) and the plausible IWC (2008) maximum biological increase of around 10.3%. A weighted least squares model can be used to improve the estimated growth rate of the humpback population by partly removing this bias. The weight (or variance) for each year's 10hr count (R_y) could be based on the standard error for each day's count (C_i) for that year. However the standard error generally increased with the increasing numbers of whales that passed each year, therefore the standard error for each year is divided by the average 10hr count for that year to determine the normalised weight. The weighted least squares linear regression produced a growth rate of 10.1% with a slightly improved solution ($R^2 = 0.713$).

The data collected by the CBWRP may be better suited for detailed studies of humpback behaviour patterns. The data may also be useful in studying the cause and effect of variables that influence observing conditions. A number of different relationships between pod behaviour and distribution patterns along with other factors that influence viewing conditions can be further studied.

ACKNOWLEDGEMENTS

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Appendix 1

GROWTH IN 10HR SIGHTING RATES IN BYRON BAY 1998–2004

The data analysed were:

Year	Rate	ln(rate)
1	25.471	3.238
2	23.375	3.152
3	20.518	3.021
4	32.331	3.476
5	32.357	3.477
6	32.118	3.469
7	47.020	3.851

A growth model was fitted by generalised least squares (REML)[1] according to the function:

$$\ln(rate)_{time} = \beta_0 + \beta_1 * time + \varepsilon_{time}.$$

[1] Using function GLS in package *nlme* (Pinheiro and Bates, 2000) in program *R* (*R Development Core Team*, 2006).

In terms of rate:

$$rate_{time} = e^{\beta_0} * e^{\beta_1 * time} * e^{\varepsilon_{time}}.$$

The parameter estimates on the log scale with 95% confidence intervals were:

$$\beta_0 = [2.598 < 2.965 < 3.332];$$
$$\beta_1 = [0.022 < 0.105 < 0.187]$$

The growth parameter on the rate scale with 95% confidence interval was (by back-transformation):

$$e^{\beta_1} = [1.02 < 1.11 < 1.21];$$

i.e. the estimated growth rate with 95% confidence interval was 2.3% < 11.0% < 20.5%.

This cannot be correctly stated as mean ± 95%CI because the interval was not symmetric about the estimate.

RSQ for the model was 0.683.

A plot of the autocorrelation function (ACF) on the residuals indicated little serial correlation structure and a second model which fitted an AR1 structure was found not to be a significantly better fit than the original model by the likelihood ratio test (p = 0.994). The estimate of the AR1 parameter with 95% confidence interval was:

$$phi(AR1) = [-0.864 < 0.006 < 0.868].$$

The estimated growth rate with 95% confidence interval from the AR1 model was

$$2.3\% < 11.0\% < 20.5\%.$$