Long term trends in abundance of humpback whales in Hervey Bay, Australia

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ABSTRACT

Seasonal abundance estimates of humpback whales resident during the austral winter in Hervey Bay, Queensland, Australia between 1987 and 2007 were obtained from a capture-mark-recapture study using photo-identification images of 3,155 individual whales. Hervey Bay is a major southbound stopover site for Breeding Stock E humpback whales returning to Antarctic waters from over-wintering in the vicinity of the Great Barrier Reef. Annual survival, recapture and abundance estimates were derived using a Cormack-Jolly-Seber modelling approach and a Horwitz-Thompson type abundance estimator. The best-fit model was a 2-ageclass Brownie-Robson type model that estimated apparent annual survival for the non-transient winter stopover ageclass at approximately 0.945 (95% confidence interval: 0.929–0.957). Apparent annual abundance of winter stopover humpback whales in Hervey Bay was estimated to have increased significantly over the past 21 years at *ca.* 13.4% per annum (95% CI 11.6–15.2). The most recent Hervey Bay winter stopover population (2007) was estimated to comprise *ca.* 6,246 post-yearlings (95% CI 5,011–7,482). This estimated rate of population increase is similar to estimates for other surveys along the east Australian coast but significantly higher than the intrinsic rate of increase (*rmax*) estimated recently for several recovering Southern Hemisphere humpback whale stocks based on the feeding ground sampling.

KEYWORDS: HUMPBACK WHALE; ABUNDANCE ESTIMATE; MARK-RECAPTURE; PHOTO-ID; AUSTRALIA; SOUTHERN HEMISPHERE; STATISTICS

INTRODUCTION

Humpback whales that migrate along the east coast of Australia are part of the Southern Hemisphere Breeding Stock E, which spend the austral summer in Antarctic Area V (130°E–170°W), and the austral winter breeding and calving in tropical waters in the vicinity of the Great Barrier Reef (Chittleborough, 1965; Dawbin, 1966; Kaufman *et al.*, 1990). Like stocks of humpback whales in other parts of the world, East Australia humpback whales were severely depleted by commercial whaling. By 1962, the entire Stock E was estimated to be between 200 and 500 animals (Allen, 1980; Chittleborough, 1965). The original 'pre-exploitation' population has traditionally been estimated at 10,000 (Chapman, 1974; Chittleborough, 1965), although doubt has been cast on the reliability of such estimates and subsequent population trend estimates by the revelation that the Soviets took some 40,000 unreported humpback whales in the Southern Hemisphere 1957–68 (Mikhalev, 2000). Nonetheless, since their protection from commercial whaling in 1963, there has been evidence that the number of humpback whales migrating along the east coast of Australia are increasing at a substantial annual rate, based on shore-based observations in Southern Queensland waters (Bryden *et al.*, 1990; Noad *et al.*, 2011; Paterson *et al.*, 2001), aerial surveys of the Great Barrier Reef Marine Park (Chaloupka and Osmond, 1998), and analysis of photo-identification data (Chaloupka *et al.*, 1999; Forestell *et al.*, 2003).

Despite favourable evidence of a general increase in the number of humpback whales observed along the east coast of Australia following cessation of commercial whaling, more detailed analyses of annual changes in estimated abundance remain important for assessing the extent to which those changes represent a real increase to the overall breeding stock size (or overall population of Southern Hemisphere humpback whales), and the extent to which observed changes represent seasonal increases associated with temporary movement of whales between breeding stocks (e.g. between Breeding Stock D and E; Chittleborough, 1965) or within the sub-groups of a given breeding stock (e.g. between east coast Australia and areas throughout Oceania; Garrigue *et al.*, 2000). As the number of potential impacts of human-generated activities and long term global cycles on marine mammal species becomes increasingly lengthy (Burns and Wandesford-Smith, 2002; Chaloupka *et al.*, 1999; Clapham *et al.*, 1999; Dawbin and Gill, 1991; Reeves and Reijnders, 2002; Stachowitsch *et al.*, 2005), the need to incorporate likely effects of those impacts on long term changes in abundance becomes increasingly apparent.

The east coast of Australia is an important area for studying humpback whales. It is relatively accessible along much of its length, and it lies along a major portion of the migratory route of Breeding Stock E humpback whales (Chaloupka and Osmond, 1998; Chittleborough, 1965; Dawbin, 1966). Shore-based and aerial observations near North Stradbroke Island indicate that most humpback whales migrating along the east coast of Australia move within 10km of shore (Bryden, 1985). During their southward migration towards the end of the austral winter, large numbers of humpback whales may be reliably observed in the protected waters of Hervey Bay, Queensland (approximately 25°S, 153°E), especially in Platypus Bay, along the northwestern shores of Fraser Island (Forestell *et al.*, 2003; Kaufman *et al.*, 1987). The data reported here are derived from a long term photo-identification-based capture-mark-recapture programme that commenced in Hervey Bay in 1987.

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MATERIALS AND METHODS

Study area and dataset

The study was conducted in the Hervey Bay Marine Park that comprises around 1,600km^2 in area (Chaloupka *et al.*, 1999). Hervey Bay is a large, shallow embayment on the east coast of Australia (25°00'S, 152°52'E) and is the major southbound stopover site for humpback whales returning to Antarctic waters from overwintering in the Great Barrier Reef (Chaloupka *et al.*, 1999). Boat-based observations were conducted on a daily basis during each field season, depending upon weather conditions, using a small (5–6m) inflatable vessel equipped with outboard motors. During each sampling day the survey team would opportunistically search for pods of humpback whales throughout the marine park area of the Bay. Radio communication with whalewatch boats in the area was also used on occasion to help locate pods. Photographs of the ventral surface of the tail flukes were obtained using 35mm film or digital cameras equipped with motor drives and 300mm lenses (Kaufman *et al.*, 1987). Date, time, location, sea state, wind speed, direction and degree of cloud cover, sea surface temperature, pod number, pod composition and image number and content of each photograph were recorded. Photographs were processed using previously described techniques (Forestell *et al.*, 2003; Kaufman *et al.*, 1993) and then used to create a photo-identification-based recapture history for each humpback whale encountered in the sampling area over the 21 year period from 1987 to 2007.

Statistical methods

The Cormack-Jolly-Seber (CJS) modelling approach (Lebreton *et al.*, 1992) was used to estimate recapture and survival probabilities from the 2,142 recapture histories. All models were fitted using MARK (White *et al.*, 2006) while model selection was based on the quasi-likelihood form of Akaike Information Criterion, which is corrected for sample size and possible overdispersion (QAICc; Anderson *et al.*, 1998). CJS model assumptions were evaluated using RELEASE and UCARE (Pradel *et al.*, 2005) while goodness-of-fit was assessed using a bootstrap approach implemented in MARK. The best-fit model was used to estimate recapture and survival probability estimates. Annual sampling effort measured as either boat-days or boat-hours was fairly constant in the study area over the 21 year period except for 2001 and 2003, when there was little or no sampling effort. Therefore, the recapture parameters for these two sampling occasions were fixed to zero in the model estimation. The best-fit model capture probabilities (and variance estimates) were then used to derive annual Horwitz-Thompson type abundance estimates ($N_i = (n_i/\rho_i)$) (McDonald and Amstrup, 2001) of the humpback whale population in the Hervey Bay sampling area between 1987 and 2007, where n_i is number of whales captured in the ith year, N_i is number of whales in the sampled population in the ith year and ρ_i is estimated recapture probability in the ith year. The appropriate variance formulae for this estimator are provided in detail by McDonald and Amstrup (2001). The expected population growth rate was derived using a generalised least squares regression of the CV^2-weighted annual abundance estimates with first order moving average (MA1) error structure, which was fitted using the *nlme* package in *R* (Pinheiro and Bates, 2000).

RESULTS

The dataset comprised the recapture histories for 3,155 individual post-yearling humpback whales sampled over the 21 year period from 1987 to 2007. The mark-resight summary statistics for the 3,155 resight profiles are shown in Table 1. Calves were not included in this study because they rarely expose the ventral surface of their flukes needed for photo-identification (Kaufman *et al.*, 1993) and there can be significant change in pigmentation patterning during the first year of postnatal development (Carlson *et al.*, 1990). Sex was not considered because few whales in the sample could be sexed reliably and also because younger males are more likely to be sexed than adult males due to frequent roll-over behaviour (Chaloupka *et al.*, 1999).

All CJS models fitted are summarised in Table 2. The reference or global model was the fully time-dependent model shown as model 3 in Table 2. Several other CJS models were also fitted to compare with the global model (models 2,4,5: Table 2). The adequacy of the global model was assessed using variants of TESTS 2 and 3 in RELEASE and UCARE (Pradel *et al.*, 2005), which indicated failure only of test component 3.SR ($\chi^2 = 120.37$, df = 17, $p<0.001$) but not Test 2.CT or Test 3.SM. Failure of test component 3.SR is considered to be a consequence of the transient behaviour of individuals that were just passing through the study area and were not seen again (Pradel *et al.*, 2005). Consequently, we also fitted a simple age-specific survival model to account for apparent transient behaviour by separating into two ageclasses: newly marked; and previously marked whales. Ageclass is used here for convenience to refer to two groups that are based on time-since-first-marking, which is a form of quasi ageing although age is not strictly known. The two ageclasses might reflect differences in site fidelity between neophyte migrants and experienced migrants on the southbound migration back to Antarctic feeding grounds. The best-fit model of all the five models fitted was the 2-ageclass-specific Brownie-Robson type model (model 1 in Table 2) and a simple bootstrap goodness-of-fit assessment suggested an adequate model fit overall ($p = 0.47$).

The estimated annual survival probability derived from model 1 (Table 2) for the newly marked ageclass or 'transients' in the Brownie-Robson model was 0.631 (95% CI 0.576–0.682). Estimated annual apparent survival probability for the previously marked ageclass in the Brownie-Robson model was 0.945 (95% CI 0.929–0.956). The transients might be younger (neophyte migrant) whales with lower survival probability or whales just rapidly moving through the study area and never seen again, which in the latter case would strongly confound survival and permanent emigration. The survival estimate for the previously marked (and perhaps older and experienced migrants) whales is significantly higher than the estimate for the newly marked whales and is presumably far less biased by any permanent emigration effect. The survival estimate for the previously marked humpback whales is also consistent with the expected annual survival probability of highly mobile, long-lived, later maturing marine species such as bowhead whales (Zeh *et al.*, 2002), right whales (Caswell *et al.*, 1999), sea turtles (Troeng and Chaloupka, 2007) and manatees (Langtimm *et al.*, 1998).

The estimated annual recapture probabilities derived from the best-fit model were time-dependent and ranged from 0.04–0.43 with a geometric mean *ca*. 0.13. These recapture estimates derived from model 1 (Table 2) were then used to derive the Horwitz-Thompson type estimates of humpback whale abundance in the sampling area that are shown in Fig. 1a. The expected annual population growth rate trend in these annual abundance estimates is shown in Fig. 1b and was estimated to be *ca*. 13.4% per annum (95% CI 11.6–

Table 1

Mark-resight summary statistics for humpbacks resident in the Hervey Bay Marine Park sampling area during the annual southward migration (1987 to 2007). Summary notation as follows: n_i = total number of humpbacks (marked + unmarked) sighted in *i*th period, m_i = number of marked humpbacks sighted in *i*th period, R_i = number of n_i released after *i*th period, r_i = number of R_i sighted in *i*th period and resighted in a subsequent period, z_i = number sighted before and after *i*th period but not in *i*th period, effort_i = total sampling effort in boat-days in *i*th period.

Period	Year	n_i	m_i	R_i	r_i	z_i	Effort_i
1	1987	30	0	30	19		27
2	1988	179	9	179	106	10	59
3	1989	159	42	159	86	74	30
4	1990	105	31	105	48	129	30
5	1991	129	36	129	63	141	31
6	1992	119	39	119	58	165	37
7	1993	212	68	212	100	155	48
8	1994	172	81	172	78	174	57
9	1995	89	43	89	32	209	16
10	1996	126	50	126	49	191	22
11	1997	161	44	161	55	196	30
12	1998	236	79	236	66	172	31
13	1999	189	60	189	46	178	35
14	2000	219	64	219	45	160	44
15	2001	0	0	0	0	205	0
16	2002	174	51	174	46	154	49
17	2003	0	0	0	0	200	0
18	2004	235	30	235	45	170	53
19	2005	453	97	453	66	118	59
20	2006	587	118	587	54	66	56
21	2007	643	120	643			62

15.2). The highest winter stopover abundance estimate derived from this study to date was in 2007 (Fig. 1a) at *ca.* 6,246 post-yearling humpbacks (95% CI 5,011–7,482).

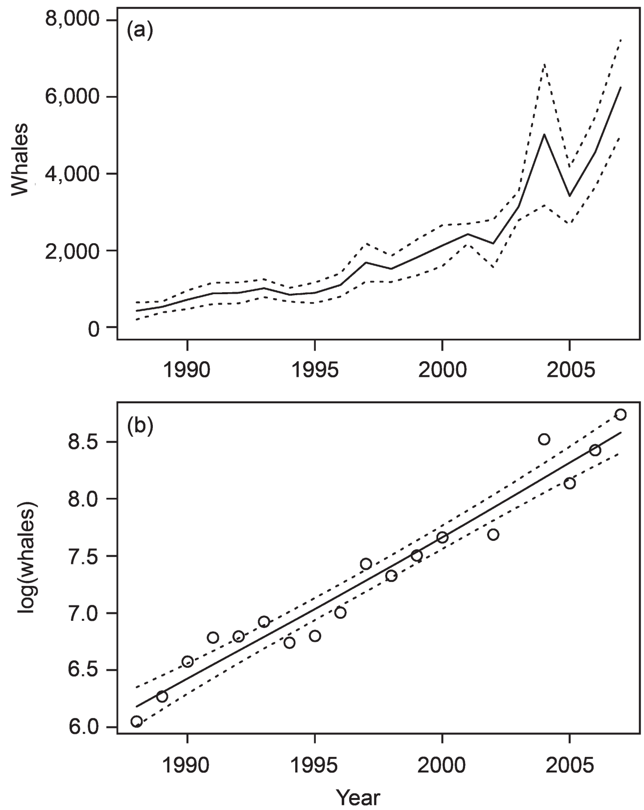

Fig. 1. Panel (a) shows Horwitz-Thompson annual abundance estimates (solid curve) and 95% confidence curves (dotted curves). Panel (b) shows on a log scale the Horwitz-Thompson annual abundance estimates (open dots) with the linear trend (solid curve) estimated by a linear regression model with MA(1) and 95% confidence bands (dotted lines) – model fitted using *nlme* package in *R*.

DISCUSSION

The Hervey Bay study area has shown a marked increase in the estimated number of humpback whales visiting there over the 21 years of this study. Fig. 1a demonstrates the increase was relatively minimal from 1987–95, moderate through to 2000, and remarkably high since then. This would explain the difference between the overall trend reported here up to 2005, and the earlier findings of Chaloupka *et al.* (1999), based on 10 years of Pacific Whale Foundation photo-identification data from Hervey Bay (1987–1996) and four years from the Whitsunday Islands, Queensland; and Forestell *et al.* (2003), based on a seven-year analysis of resights and exchange rates between Hervey Bay and the Whitsunday Islands. Those estimates suggested considerably lower overall rates of change in abundance, but they were based primarily on time periods prior to the onset of the rapid increases in more recent years demonstrated in the current findings. The overall increase in abundance estimates reported here is consistent with reports of increases in the number of humpback whales migrating along the east Australian coastline reported by others (Noad *et al.*, 2011; Paterson *et al.*, 2001), derived from shore-based counts of animals moving past North Stradbroke Island early in the season, during the northward phase of the annual migration.

Table 2

Summary of model fits.

φ = survival probability, ρ = recapture probability, (.) = constant, (t) = time-dependent, $a2$ = Brownie-Robson 2-ageclass structure to account for apparent transience, QAICc = sample size and overdispersion corrected Akaike Information Criterion, Pars = number of model parameters. Overdispersion parameter used to adjust AICc c-hat = 1.19.

Model	Description	QAICc	ΔQAICc	Model likelihood	Pars	Deviance
1	$\varphi(a2)\,\rho(t)$	6,465.93	0.00	1.000	20	1,451.30
2	$\varphi(.)\,\rho(t)$	6,525.62	59.69	0.000	19	1,513.01
3	$\varphi(t)\,\rho(t)$	6,541.55	75.61	0.000	32	1,502.55
4	$\varphi(t)\,\rho(.)$	6,777.36	311.42	0.000	10	1,782.89
5	$\varphi(.)\,\rho(.)$	6,865.96	400.03	0.000	2	1,887.56

Branch (2011) provides estimates of humpback whale abundance and rates of change based on three circumpolar surveys of Antarctic waters during the austral summer across the years 1978–2004. He reported a circumpolar annual rate of increase of 9.6% (95% CI 5.8–13.4), near the theoretical limit for humpback whales (Clapham *et al.*, 2006). Branch (2011) estimates annual rate of increase for Breeding Stock E at 14.4% (95% CI 9.6–19.2), similar to the Hervey Bay findings reported here. However, it is highly unlikely that the intrinsic rate of increase (*rmax*) for Breeding Stock E humpback whales could be so high (Clapham *et al.*, 2006). Branch (2011) notes that the small number of abundance estimates, high associated CVs, changes in survey design, and annual changes in humpback whale distribution severely limit the accuracy of the rate of change estimates for individual areas (stocks).

It is unlikely that the long term increase found for the Hervey Bay stopover population reflects the intrinsic rate of increase for Breeding Stock E humpback whales. The various estimated rates of increase of the population segment of the east Australian stock that migrates each year along the east Australia coast are all significantly higher than the intrinsic rate of increase (*rmax*) estimated recently for various recovering Southern Hemisphere humpback whale stocks based on the feeding ground sampling (Johnston and Butterworth, 2006).

The humpback whales entering Hervey Bay were found to comprise two major ageclasses that demonstrate significantly different survival rates: those captured once and not seen again (transients); and those re-captured following initial sighting. The transient portion of the Hervey Bay animals could represent a range of possibilities that reflect important demographic differences in lower ageclass-specific mortality, or ageclass-specific dispersal behaviour. A measure of transient behaviour that reflects temporary shifts in distribution between breeding stocks or between areas within breeding stocks would be important for improving the accuracy of stock assessment and estimates of change in abundance, particularly in light of recent estimates of population abundance and rate of increase that do not consider the effect of transients over extended time periods (Noad *et al.*, 2008; Noad *et al.*, 2011; Paterson *et al.*, 2001; Paton *et al.*, 2006). More accurate measures require the use of multi-state models (Pradel *et al.*, 2005). While there have been limited efforts to undertake such an analysis (Forestell *et al.*, 2003; Paton *et al.*, 2006), there is a pressing need to complete a comprehensive comparison of all available photo-identification images for this stock of whales.

Finally, it should be noted that whatever evidence there may be that whales behave differently in the presence or absence of whalewatching boats in Hervey Bay (Corkeron, 1995), these differences appear not to have had a deleterious long term effect on the number of whales that visit the area annually.

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