Estimating seasonal abundance trends and survival rates
of humpback whales in Hervey Bay (east coast Australia)

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ABSTRACT

The seasonal abundance of east Australian Group V substock (EAGVS) humpback whales resident during winter in Hervey Bay was estimated from a 10 yr mark-resight study using photo-identification of 969 individual humpbacks sighted between 1987 and 1996. Hervey Bay is on the east coast of Australia and is the major southbound stop-over site for EAVGS humpbacks returning to Antarctic waters from overwintering in Great Barrier Reef (GBR) waters. Hervey Bay is also the major whale-watching centre in Australian waters. Annual seasonal abundance estimates were derived from the mark-resight profiles using a reduced form Cormack-Jolly-Seber model (constant survival, time-varying resight likelihood) that fitted the data well. The bootstrap mean CJS abundance estimate over the 9 yr period from 1988 to 1996 was 855 (95% CI: 750 to 936). Estimated seasonal humpback abundance in Hervey Bay showed significant temporal variability superimposed on an increasing linear trend estimated using times series regression model bootstrapping at 6.3% pa (95% CI: 2 to 11%). The seasonal Hervey Bay population comprised ca 30 to 50% of the EAGVS southbound to Antarctic feeding grounds. Estimated seasonal abundance increased from 554 post-yearling humpbacks in 1988 to a peak of 1040 in 1991 before declining to 921 by the mid-1990s. Standard errors of abundance estimates suggested good precision and were derived using a variance components approach that separated sampling error from ecologically relevant variation. The trends in temporal variability and annual rate of humpback abundance increase were consistent with findings from an aerial surveillance study (1982 to 1996) of monthly sightings of the EAGVS overwintering in GBR waters (Whitsunday Is). The concurrence of findings from an independent method of abundance estimation supports confidence in the CJS model used in this study to estimate abundance. Post-yearling survivorship was estimated from a 4 yr (1993 to 1996) photo-identification mark-resight study of 517 individual humpbacks sighted at 2 seasonally sequential overwintering sites (Hervey Bay, Whitsundays) using a robust design CJS modelling approach with estimators that account for bias due to temporary emigration. A reduced form CJS model (constant survival, time-varying resight likelihood) also fitted the data well with the mean annual survival rate for the EAGVS humpbacks estimated at 0.966 (95% CI: 0.87 to 1.00). The good fit of the robust design reduced form CJS survival rate model supports further confidence in the model used to estimate seasonal abundance in Hervey Bay, which suggests that the EAGVS has been recovering at a slow and variable rate.

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) migrate each year during the austral autumn along the east Australian coast from Antarctic summer feeding grounds to overwintering grounds in tropical waters (Kaufman et al 1990, Kaufman et al 1993). This stock was severely reduced by commercial whaling during the 1950s and early 1960s (Chittleborough 1965). With the cessation of commercial whaling in 1963 this stock was estimated to have been less than 5% of its original size (Chittleborough 1965).

Despite severe depletion, the east Australian Group V humpback stock (EAGVS) has maintained its annual migration along the east Australian coast to overwintering grounds in Great Barrier Reef waters (Kaufman et al 1993, Chaloupka & Osmond in press). The post-whaling recovery of the EAGVS has been documented in recent studies using shore-based observations in southern Queensland waters (Paterson et al 1994) and aerial surveillance sightings in the Great Barrier Reef Marine Park (Chaloupka & Osmond in press).

During the southbound return migration to feeding grounds in Antarctic waters a proportion of the EAGVS humpbacks enter Hervey Bay in southern Queensland waters (Fig 1). A major commercial whale-watching industry has developed recently in Hervey Bay and southern Queensland waters (Chaloupka 1990, 1996) creating a need for policies designed to ensure recovery of the EAGVS humpbacks. The development of management policies and recovery plans depends on a clear understanding of EAGVS population dynamics and reliable estimates of seasonal population abundance and overall Group V stock size.

The recent ability to identify individual whales through photographs of natural markings has provided the basis for long-term studies of humpback population dynamics (Baker et al 1986, Clapham & Mayo 1987, Katona and Beard 1990, Kaufman et al 1993). A major aim of such photo-identification studies is the estimation of population abundance and stock recovery rates using capture-recapture or mark-resight methods (Hammond 1986).

We present estimates of annual population abundance and long-term recovery rates for the EAGVS resident in Hervey Bay based on photo-identification of individual humpbacks sighted during the southbound migration between 1987 to 1996. We also present survival rate estimates for the EAGVS humpbacks using a robust sampling design (Pollock et al 1990) for photo-identification of whales at 2 overwintering sites and statistical estimators that account for potential parameter bias due to temporary emigration (Kendall et al 1997).

METHODS AND MATERIALS

Study site

Hervey Bay is a large shallow marine embayment located in Queensland on the east coast of Australia (Fig 1). It is bounded on the eastern side by Fraser Island, which protrudes across most of the continental shelf. Studies using aerial surveys have shown that a demographically random sample of the EAGVS humpbacks enter Hervey Bay during the southward migration only (August to October) and are concentrated in the eastern part of the Bay (Corkeron et al 1994). The eastern portion of Hervey Bay was declared a marine park in 1989 with a management framework implemented for the regulated development of a commercial whalewatching industry (Chaloupka 1990). In 1987 the Pacific Whale Foundation (PWF) began a mark-resight study in eastern Hervey Bay using photo-identification of individual EAGVS humpbacks sighted between August and October (Kaufman et al 1993). That program has been ongoing ever-since with support from the Queensland Department of Environment (Kaufman et al 1993).

Sampling approach

Depending on weather conditions, a PWF research team was deployed daily in Hervey Bay each season (August to October) from 1987 to 1996. Similar field sampling and photo-identification methods were used throughout the study with several of the field staff being involved for most of the 10 yr study period. Humpback pods (mainly 1 to 10 individuals) were observed by a research team (≥ 2 people) operating from a small outboard-driven vessel using a random search pattern. Hervey Bay is a large area (ca. 4000 km^2) but the seasonal concentration of humpbacks in the eastern portion of the Bay ensures a reasonable likelihood of sighting a whale that enters during the southbound migration.

Individual identification

EAGVS humpbacks have individually identifiable patterns on the ventral side of the tail flukes (Kaufman et al 1993). Many EAGVS humpbacks (ca 57%) also have a unique lateral body pigmentation pattern (Kaufman et al 1987). Photographs were taken of the ventral surface of the tail fluke of each whale sighted. Where possible, photographs were also taken of the left and right lateral body pigmentation pattern for individual recognition (Kaufman et al 1987) and of the genital area for sex determination (Glockner 1983). Each whale was photographed using a 35mm single-lens reflex camera, equipped with a motor drive and either a 300mm telephoto or an 80-200mm zoom lens. The cameras were loaded with either Kodak 64 or 100 ASA colour slide film. A photo-identification catalogue was compiled using tail fluke and lateral body pigmentation photographs that passed a standard quality acceptance test (Baker et al 1986, Kaufman et al 1993). The photo-identification catalogue enabled an annual resight history profile to be recorded for each of the 969 individual humpbacks sighted in Hervey Bay from 1987 to 1996.

Statistical modelling approach

Population abundance estimates of EAGVS humpbacks in Hervey Bay from 1987 to 1996 were derived using the annual resight histories for each of the 969 individually identified whales and the Cormack-Jolly-Seber (CJS) statistical modelling approach of Pollock et al 1990. The standard CJS approach does not assume demographic closure and so is suitable for estimation of population parameters where there is an underlying stochastic birth, death and permanent emigration process between sampling periods. The statistical assumptions and limitations of the CJS modelling approach for estimation of population abundance and demographic rates were discussed in detail elsewhere (Pollock et al 1990, Lebreton et al 1992, Kendall et al 1997). Hammond (1986) addresses some of these issues in relation to photo-identification based mark-resight studies of whale population abundance.

The critical assumption of no temporary emigration is considered most likely to be violated in humpback demographic studies leading to biased estimates of abundance and survival rates (Buckland 1990). We evaluated this assumption in our study using the robust design extension to the standard CJS model (Pollock et al 1990) coupled with modified estimators that account for bias due to presence of temporary emigration (Kendall et al 1997). The robust design in the current study used a photo-identification sampling program of EAGVS humpbacks (n=517) resident in 2 overwintering locations (secondary samples) within each sampling year (primary samples). The primary samples spanned the 4 yr period from 1993 to 1996.

The 2 secondary sampling locations were the Whitsunday Is (southern Great Barrier Reef, sGBR) and Hervey Bay (Fig 1). The Whitsundays and sGBR lagoonal waters comprise the main calving and overwintering grounds for the EAGVS humpbacks (Chaloupka & Osmond in press). The Whitsunday Is program began in 1993 with sampling at the end of the northbound migration during June and July of each year prior to the research team relocating southward to Hervey Bay to continue sampling from August to October during the southbound migration (Fig 1). The robust design used here assumed that the EAGVS being sampled each year comprised a single superpopulation (see Kendall et al 1997) with demographic closure within a season during sequential sampling of the overwintering sites. Demographic closure was not assumed between primary sampling periods. The use of the robust design approach and modified CJS estimators provide not only an evaluation of the major assumption of no temporary emigration but also provided a robust estimate of the mean annual survival rate for post-yearling EAGVS humpbacks.

RESULTS

Mark-resight summary

There were 969 individual humpback whales identified photographically in Hervey Bay over the 10 yr sampling period between August 1987 and October 1996. All 969 resight history profiles used in the analysis were for post-yearlings comprising 156 subadults and 813 adults. Calves were not included in the photo-identification study because of the potential for substantial change in the pigmentation patterning in the first year of postnatal development (Carlson et al 1990). Sex was not considered because < 21% of the sample could be sexed and subadult males were 2 times more likely to be sexed than adult males due to frequent roll-over behaviour (odds ratio = 2.18, 95% CI: 1.01 to 4.68; see Fleiss 1981). The resight history profiles comprised 70% of the 969 whales sighted once only between sampling years, 21% sighted twice and 9% sighted ≥ 3 times. The mark-resight summary statistics for the 969 resight profiles required for Cormack-Jolly-Seber (CJS) population abundance estimation are shown in Table 1.

Initial goodness-of-fit tests

The full CJS model (time-varying survival, time-varying resight) comprising separate parameter estimates for the subadult and adult subgroups fitted the data set extremely well with no evidence for noncompliance with the standard CJS model assumptions (TEST 2+3 of Burnham et al 1987 as modified by Pradel 1993 to account for heterogeneity of resight likelihood: $\chi^2_{0.05} = 75.8$, df = 68, P > 0.20). Moreover, there was no evidence with any significant difference in survival or resight likelihood between the subadult and adult groups (TEST 1 of Burnham et al 1987: $\chi^2_{0.05} = 14.01$, df = 17, P > 0.65). Hence the subadult and adult subgroups were pooled into a data set of 969 resight profiles for the assessment of population abundance. Goodness-of-fit tests for mark-resight analyses are discussed in detail by Burnham et al (1987), Lebreton et al (1992) and Pradel (1993).

Population abundance estimates

The CJS model (time-varying survival, time-varying resight) and several reduced forms of the CJS model (Pollock et al 1990) were fit to the 969 resight profiles to estimate annual post-yearling population abundance. The best fit model was the CJS reduced form Model B (Pollock et al 1990), which assumes constant annual survival and time-varying resight likelihood. Seasonal resight likelihood was considered reasonable for such a mark-resight study with large population size (geometric mean = 16.8%, CV=15.6%). Model B fitted the data well ($\chi^2_{0.05} = 33.3$, df = 29, P > 0.27) with no evidence for noncompliance with standard CJS model assumptions. There was also no significant difference in fit between the full CJS model and the reduced form Model B ($\chi^2_{0.05} = 5.2$, df = 7, P > 0.64). Model B was therefore selected as the preferred model since it fitted the data as well as the full CJS model but was simpler requiring less model parameters. Model selection strategies for mark-resight analyses are discussed in detail by Burnham et al (1995).

Model B (constant survival, time-varying resight) enables abundance estimates to be derived for 9 yrs (1988 to 1996) of the 10 yr study (1987 to 1996). If the full CJS model (time-varying survival, time-varying resight) had been the best fit, rather than a reduced form model such as Model B, then abundance estimates would have been only possible for 8 yrs (1988 to 1995). The abundance estimates (N_i) derived from Model B and the approximate standard errors [se(N_i)] including non-sampling error terms are given in Table 1. Following the variance components approach of Link & Nichols (1995) it was possible to distinguish between variability in abundance estimation due to (1) sampling uncertainty and (2) ecologically relevant variation ([$se_{adj}(N_i)$], Table 1). Seasonal abundance estimates (1988 to 1996) and approximate 95% confidence curves are shown in Fig 2a based on the [se(N_i)] to reflect total variance since sampling uncertainty accounted for < 21% of the total variability in seasonal abundance. Standard errors of abundance estimates accounting for total variance suggested good precision (geometric mean CV=11.7%).

Sampling effort

Annual sampling effort measured as boat-days on water in Hervey Bay varied considerably from 1987 to 1996 (tse_i: Table 1). Model B does not take into account sampling effort nor any other study covariates (Pollock et al 1990). However, it can be shown graphically that annual abundance estimates derived from Model B (Table 1) were not a function of sampling effort (Fig 3a) nor were the resight likelihood estimates a function of sampling effort (resight/recapture probability ranged from 10 to 41%, geometric mean = 16.8%: Fig 3b). More comprehensive modelling of stage-specific survival rates (subadult, adult) between 1987 and 1996 using the parametric modelling approach of Lebreton et al (1992) found no linear or curvilinear functional relationship between either stage-specific survival or resight rate estimates and sampling effort (Chaloupka and Osmond unpublished).

Population recovery trend

A linear regression model with log link and second order moving average error (MA2: see Judge et al. 1985) was used to estimate the long-term linear trend in humpback abundance over time (1988 to 1996) shown in Fig 2a. The response variable (annual population estimate, Table 1) was in natural log form so that the parameter estimate for the independent variable (year; 1988 to 1996) was interpretable as proportional change or annual growth rate. The linear regression model with MA2 error fitted the data well (residual variance = 0.014, $R^2 = 0.68$, t-ratio (year) = 3.14, df = 7, $P < 0.01$) compared to a linear model with standard normal error (residual variance = 0.029, $R^2 = 0.32$, t-ratio (year) = 1.80, df = 7, $P > 0.05$), confirming that accounting for autocorrelated error in parameter estimation was needed. Statistical inference for the MA2 model was then derived from 1000 bootstrap samples (Efron and Tibshirani 1986) of the residuals drawn from the initial MA2 model with an empirical 95% confidence interval defined by the 2.5th and 97.5th percentiles of the 1000 bootstrap estimates of the year parameter estimate. Using this bootstrap procedure and the MA2 regression model, it was estimated that the Hervey Bay humpback population trend shown in Fig 2a has increased since 1987 at a mean annual growth rate of ca 6.3 % pa (95% empirical percentile CI: 2 to 11% pa).

Survival rate estimate

The full robust design CJS model (time-varying survival, time-varying resight: Kendall et al 1997) and several reduced model forms were fit to the 517 resight profiles for the 2 overwintering sites (Whitsunday Islands & Hervey Bay: see Fig 1) sampled concurrently between 1993 and 1996. The best fit model was Model 2 shown in Table 2 ($\chi^2_{0.05} = 21.8$, df = 17, $P > 0.19$, AIC = 124.9), which assumes constant survival, time-varying resight and permanent emigration. Burnham et al (1995) discuss the use of AIC for CJS model selection and goodness-of-fit testing (see also Lebreton et al 1992). There was no evidence for the presence of any significant temporary emigration using the 2-site sequential seasonal sampling design adopted during this 4 yr study (1993 to 1996) — compare Models 4 & 5 with Model 2 in Table 2. Model 2 is equivalent in terms of the survival, resight likelihood and emigration assumptions to the Pollock et al 1990 Model B used in this study to derive annual abundance estimates for the Hervey Bay humpback population (Table 1). The mean annual survival rate for post-yearling EAGVS humpbacks estimated from Model 2 in Table 2 was 0.966 (95% CI: 0.87 to 1.00). The asymmetric confidence interval results from the recommended lognormal-transformation with [0,1] constraint (Lebreton et al 1992).

DISCUSSION

Sampling issues

Four key sampling issues need to be considered to support confidence in the abundance estimates (Table 1) for post-yearling humpbacks derived from the mark-resight study using photo-identification — (1) reliability of individual recognition, (2) stock definition, (3) adequacy of seasonal and spatial sampling effort and (4) demographic representativeness.

The use of natural markings to support a photo-identification based mark-resight study is widely accepted for humpback populations (Baker et al 1986, Hammond 1986, Clapham & Mayo 1987, Buckland 1990, Katona & Beard 1990, Craig & Herman 1997). EAGVS humpbacks have individually identifiable patterns on the ventral side of the tail flukes (Kaufman et al 1993) and many have a unique lateral body pigmentation pattern (Kaufman et al 1987). The current photo-identification study was based on tail-fluke identification supplemented by lateral body markings where the latter was recorded. The use of these 2 natural marking schemes reduces the likelihood of mis-identification of those individual humpbacks that were effectively "double-marked".

The humpback stock that migrates annually between Antarctic Area V feeding grounds and various southwestern Pacific overwintering grounds is known as the Group V stock (Chittleborough 1965). The annual movement of Group V humpbacks between Antarctic Area V feeding grounds and east Australian coastal waters is well known from whaling records (Chittleborough 1965) and mark-resight studies based on photo-identification of individual humpbacks (Kaufman et al 1990). We refer to the Group V subset that migrates each year along the east Australian coast to overwinter in Great Barrier Reef waters as the east Australian Group V substock (EAGVS: Chaloupka and Osmond in press). The current study is based on EAGVS humpbacks that assemble for a short period each year in Hervey Bay during the southbound migration. Mean residence time of EAGVS humpbacks in Hervey Bay is ca 1 to 3 days (Corkeron et al 1994).

The seasonality of humpbacks in the overwintering grounds in southern Great Barrier Reef waters (Whitsundays to Capricorn-Bunkers: Fig 1) is known from a 14 yr study of aerial surveillance sightings (Chaloupka and Osmond in press). The historic seasonal peak for humpbacks in sGBR waters occurs in August with peak season in Hervey Bay occuring approximately 1 mo later during September (Corkeron et al 1994). The current photo-identification study in Hervey Bay commenced sampling each year from early August to late October during the southbound migration to ensure adequate seasonal sampling. The predominance of whales in the eastern portion of Hervey Bay (Corkeron et al 1994) reduced significantly the area that needed to be covered in order to locate whales in the sampling program. The sighting of humpbacks was also assisted by the commercial whale watching fleet that were in radio contact with the PWF research vessel. Annual sampling effort measured as boat-days on water in Hervey Bay varied considerably (Table 1) but recapture probability was adequate and not confounded with sampling effort (Fig 3b).

The demographic segregation of migratory humpbacks based on age and sex classes is well documented (Chittleborough 1965). Such nonrandom migratory behaviour could lead to sampling bias if Hervey Bay was also used disproportionately by a specific demographic group of the population on the southbound migration. There appears to be no demographic bias in the humpbacks sighted seasonally in Hervey Bay (personal observations, Corkeron et al 1994). Moreover, there appears to be no indication of population parameter bias due to either heterogeneity of resight or the possible presence of temporary emigration during the 4 yr span from 1993 to 1996 (Table 2). It is reasonable then to assume that the post-yearling humpbacks sighted in Hervey Bay each season between 1987 and 1996 were a representative sample of the EAGVS population during the southbound migration.

Population abundance

While there are many estimates of seasonal humpback abundance for short-term studies (< 5 yr) using individual photo-identification methods there have been very few studies that have presented long-term (ca 10 yr) abundance estimates considered essential for estimation of stock size and recovery trends (Hammond 1986). Buckland (1990) using a cohort-based CJS approach (Pollock et al 1990) to account for sampling bias due to resight heterogeneity estimated that seasonal abundance of western North Atlantic stock (WNAS) humpbacks in the Gulf of Maine feeding ground increased over a 9 yr period (1977 to 1985) from 99 (95% CI: 40 to 160) to 334 (95% CI: 300 to 360). While no indication of model fit was provided, the small apparent population size and very high resight likelihood in this study resulted in good precision of seasonal abundance estimates. However, Buckland (1990) attributed the trend in seasonal abundance to be a direct function of the increasing likelihood of resight over the 10 yr study period, which was probably a consequence of a temporal trend in sampling effort.

Katona & Beard (1990) estimated seasonal humpback abundance of the whole WNAS over an 8 yr period from 1979 and 1986 using a Lincoln-Petersen (LP) estimator that assumes demographic closure and constant resight likelihood. The annual abundance estimates displayed substantial inter-annual variability and comprised sightings pooled from many studies conducted in the breeding grounds and in the different feeding grounds with variable sampling effort and study duration. The estimated mean WNAS size between 1979 and 1986 was 5,505 (95% CI: 2,900 to 8,100), which was suggested by Palsboll et al (1997) to be an underestimate of WNAS abundance. Using a similar LP estimator and genetic-marker identification of individual humpbacks sighted in the West Indies breeding grounds, Palsboll et al (1997) estimated WNAS size in 1992 from a single year census as 7,698 (95% CI: 5,100 to 11,500). The confidence interval ranges in these 2 WNAS assessments suggest poor estimation precision probably due to failure of the LP estimator assumptions of demographic closure and constant resight likelihood (see Buckland 1990). Nonetheless, these estimates are the only recent whole-of-stock assessment estimates available for any humpback stock.

We present estimates of the abundance of EAGVS humpbacks resident during the late winter in Hervey Bay over the 9 yr period from 1988 to 1996 using a reduced form CJS model that fitted the data well. The good fit of the robust design CJS survival rate model (Table 2) supports confidence in the reduced form CJS model used to estimate EAGVS seasonal abundance in Hervey Bay. These estimates were based on a 10 yr mark-resight study using photo-identification of 969 individual humpbacks sighted in the Bay between 1987 and 1996 during the southbound migration to Antarctic waters. The estimated annual abundance of post-yearling humpbacks increased from 554 (95% CI: 329 to 779) in 1988 to a peak of 1040 (95% CI: 783 to 1297) in 1991 before declining to ca 921 (95% CI: 690 to 1152) by the mid-1990s (see Fig 2a).

It is important to note that these are estimates only of the seasonal abundance of EAGVS humpbacks in Hervey Bay (Table 1), which represents an unknown proportion of the EAGVS population that migrates each year along the east Australia coast. There are no long-term annual abundance estimates for the EAGVS humpbacks migrating along the east Australia coast concurrent with the same Hervey Bay photo-identification study period (1988 to 1996), let alone any estimates of Group V stock abundance. However, there are some point estimates of the EAGVS population size during this period.

For instance, using a shore-based observation study, Paterson et al (1994) estimated the size of the EAGVS population passing Moreton Bay (Fig 1) in 1992 to comprise 1836 post-yearlings (95% asymptotic normal CI: 1400 to 2392) compared to 1100 in 1987. The EAGVS population size in 1987 was estimated for the same location to be 1203 (95% Monte Carlo CI: 1134 to 1273) based on a 4 yr photo-identification study and Cormack's (1993) Poisson likelihood modelling approach (Chaloupka 1996).

It was then estimated using a Monte Carlo simulation model that the EAGVS passing Moreton Bay in 1996 was ca 1928 post-yearlings (95% CI: 1645 to 2404), assuming that post-1987 population growth was a random variate sampled from an extreme value probability density function (mode = 5%, scale = 0.01%, range 3 to 11% pa; Chaloupka 1996). This annual growth rate sampling distribution is consistent with estimates based on aerial surveillance of EAGVS humpback sightings in the GBR (1982 to 1996; Chaloupka & Osmond in press), the current study for the seasonal abundance of EAGVS humpbacks in Hervey Bay (1988 to 1996) and with estimates for other humpback stocks (Volgenau et al 1995, Barlow & Clapham 1997). Assuming that the EAGVS abundance estimates for 1992 (Paterson et al 1994) and for 1996 (Chaloupka 1996) were reasonably accurate, then it was estimated that the seasonal abundance of humpbacks in Hervey Bay (Table 1) comprises ca 30-50% of the southbound EAGVS population.

Temporal variability

Brown et al (1995) suggested from a 1 yr biopsy sampling study of apparent sex ratios that a significant proportion of female EAGVS humpbacks in the Antarctic Area V feeding grounds did not migrate in 1992 to east Australian coastal waters and might have remained in Antarctic waters during that winter. Elsewhere, Craig & Herman (1997) have shown from a photo-identification sudy (1976 to 1991) that female North Pacific humpbacks were less likely to migrate in some years from high latitude feeding grounds to Hawaiian breeding grounds compared to male humpbacks. Such sex-specific differences in migration likelihood will be evident in significant aperiodic variability in the seasonal abundance of humpbacks in the breeding grounds.

The seasonal abundance in Hervey Bay between 1988 and 1996 was estimated with good precision (geometric mean CV = 11.7%) and displayed low frequency temporal variability (Fig 2a). It was estimated that the Hervey Bay population increased significantly during the 4 yr period from 1988 to 1991 and then declined significantly during the early-1990s before increasing towards the end of the study in 1996. This pattern of temporal variability is consistent with the findings of Brown et al (1995) and suggests that there is significant aperiodic variability in the demographic structure of the EAGVS that migrates each year along the east coast of Australia. The early 1990s comprises the most anomalous series of ENSO events this century (Wang 1995) and such ocean-climate effects might be implicated in the long-term temporal variability evident in the seasonal Hervey Bay population (Fig 2a). The ecological link with humpback migratory dynamics is unknown but could be a function of the complex relationship between climate, sea-ice extent and krill productivity in Antarctic waters (Loeb et al 1997).

The trend in temporal variability of the seasonal humpback abundance in Hervey Bay is consistent with findings from a 14 yr (1982 to 1996) aerial surveillance study of sightings of EAGVS overwintering in GBR waters (Chaloupka & Osmond in press). The relative abundance index for overwintering EAGVS humpbacks from Chaloupka & Osmond (in press) is compared with the CJS-estimates of seasonal abundance in Hervey Bay for the 9yr period between 1988 and 1996 (Fig 2b). The 2 seasonal abundance profiles derived from different and independent methods and data reflect similar temporal and growth trends providing confidence in the reduced form CJS model used in this study to estimate absolute abundance.

Population recovery trend

Chittleborough (1965) estimated that the entire Group V humpback stock was reduced from ca 10,000 in the pre-whaling period (1935 to 1939) to ca 500 individuals in 1962. It was estimated that 8,000 EAGVS humpbacks were caught in Australian coastal fisheries (1952 to 1962) while > 12,000 Group V humpbacks were caught in pelagic fisheries operating in Antarctic waters between 1949 and 1962 (Chittleborough 1965) — many of these would have been EAGVS humpbacks. Despite being reduced to near extinction in the 1960s, the EAGVS has shown no evidence of any major loss of genetic diversity (Baker et al 1993) and is undergoing significant population recovery.

The mean (9 yr) seasonal abundance of humpbacks in Hervey Bay derived in the current study from 1000 bootstrap samplings of the abundance estimates (N_i in Table 1) was 855 (95% empirical percentile CI: 750 to 936), which suggests a significant increase since the end of commercial whaling in 1962. Clearly the Group V humpback stock is recovering at a slow but steady rate. The seasonal abundance of EAGVS humpbacks in Hervey Bay was estimated to be increasing at 6% pa. However, the growth or recovery rate was not constant over the 9 yr study (1988 to 1996) but was interval-specific. For instance, the estimated rate over the 4 yr period (1988 to 1991) was 15% pa but over the next 4 yr period (1991 to 1994) it was -6%. On the other hand, the long-term 9 yr mean bootstrap estimate was 6.3% (95% CI: 2 to 11%), which emphasises why long-term studies are needed to reliably estimate trends in humpback abundance and temporal variability.

Paterson et al (1994) suggested that the EAGVS has increased rapidly since the 1980s with a sustained annual growth rate of 12% pa (95% CI: 10 to 14%). This estimate was derived from a program of shore-based observations of humpbacks passing northward along the east Australian coast prior to entering southern GBR waters. Chaloupka & Osmond (in press) suggested from a long-term aerial surveillance study of the frequency of humpback sightings in GBR waters that the EAGVS increased between 1982 to 1996 at 4% pa (95% CI: 2 to 6%), which is much lower than 12% pa suggested by Paterson et al (1994) but consistent with the recovery rate estimated over the same sampling period for the seasonal population in Hervey Bay (see Fig 2b).

Chittleborough (1965) estimated that the intrinsic rate of increase for both the Group IV and V stocks was 4.6% (range: 1 to 8%) assuming no density-dependent affects. A sustained mean annual population growth rate >7% pa seems demographically implausible given the range of birth and mortality rates estimated for northern and southern hemisphere humpback stocks (Chittleborough 1965, Volgenau et al 1995, Barlow & Clapham 1997, Chaloupka & Osmond in press).

Survival rate estimate

The resight of a humpback during a sampling period t+1 that was sighted during sampling period t depends on 3 probabilities: (1) the probability of surviving from period t to period t+1, (2) the probability of being present in the study site during period t+1 given that it is still alive and (3) the probability of being resighted in the study site during period t+1 given that it is both still alive and also present in the study site. Few studies distinguish between sources (2) and (3) and therefore confound temporary emigration (if it occurs) with resight likelihood giving biased estimates of survival. All 3 probabilities were estimated separately in the current study using a seasonally sequential 2-site robust sampling design with estimators to account for the presence of temporary emigration (Kendall et al 1997).

The robust CJS survival rate estimate for post-yearling EAGVS humpbacks was estimated in the current study at 0.966 (95% CI: 0.87 to 1.0). Survival was high and constant over the study period while resight likelihood was time-varying. There was no evidence over the 4 yr sampling period (1993 to 1996) of any significant random or Markovian temporary emigration that assumes resight likelihood in period t is dependent on resight likelihood in period t-1 (Table 2). However, this methodology cannot account for the presence (if it exists) of more complex forms of temporary emigration such as resight likelihood in period t being dependent on say resight likelihood in period t-5 (ie 5 yr quasi-periodicity), which is quite possible for the EAGVS (Brown et al 1995). Much longer-term mark-resight studies of the EAGVS are needed to address this important issue further.

There have been very few studies that have presented estimates of humpback survivorship. Chittleborough (1965) used age-specific catch-per-unit-effort and linear regression (OLS) to estimate mean annual sex-specific survival rates for the Group V stock and the Group IV stock that migrates along the west Australian coast. This enumeration method estimates the probability of remaining available in the sampling area for capture (or return rate) rather than survival because capture is confounded with survival unless capture probability p=1. If capture probability is <1 then return rates are biased and underestimate true survival. The Group V data were inadequate for any statistical analysis (Chittleborough 1965) but the Group IV data were suitable assuming p=1. Chittleborough (1965) estimated mean return rates between 1949 and 1961 at 0.92 (95% CI: 0.74 to 1.15) for male and 0.92 (95% CI: 0.76 to 1.10) for female Group IV humpbacks.

Neither of the OLS models actually fitted the data because of data anomalies such as measurement error and inter-annual variability (see Chittleborough 1965) giving biased estimates of return rate. A reanalysis here of these data using robust linear regression models (L1 estimator, Judge et al 1985) that fit the data well estimated Group IV return rates at 0.91 (95% CI: 0.88 to 0.95) for males and 0.86 (95% CI: 0.79 to 0.94) for females. It is doubtful whether there is any significant sex-specific difference in these high return rates that probably underestimate survival rates for this stock. This is especially so for female humpbacks that are likely to skip migration in some years (Brown et al 1995, Craig & Herman 1997) ensuring that capture probability <1 and in fact confounding capture with temporary emigration.

Buckland (1990) used a cohort-based CJS approach to estimate mean annual post-yearling survival rate between 1976 and 1984 for WNAS humpbacks in the Gulf of Maine feeding ground at 0.951 (95% CI: 0.93 to 0.97). Barlow & Clapham (1997) used the same statistical procedure and Gulf of Maine feeding ground data as Buckland (1990) to estimate the mean annual female survival rate between 1979 and 1991 at 0.96 (95% CI: 0.94 to 0.98). Again there is little evidence for any sex-specific difference in survival rates. The rather precise survival rate estimates for the Gulf of Maine WNA substock are due to the small population size and high resight likelihood coupled with the deletion of anomalous estimates (Buckland 1990).

Clearly, post-yearling humpback survival rates are high and show no evidence of any significant inter-annual variability or stock- or sex-specific differences (NWAS: Buckland 1990, Barlow & Clapham 1997; EAGVS & Group IV, current study). High (> 0.90) and constant adult survival is a common characteristic of large mammal species (Gaillard et al 1998) suggesting that it is environmentally-induced variability in female migration and juvenile recruitment that are the demographic factors significantly influencing humpback population dynamics.

Management implications

Associated with the EAGVS population recovery over the last 10 yr has been an increasing demand for commercial whale-watching opportunities (Chaloupka 1990, 1996). Clearly the EAGVS is recovering but at a slow and variable rate. Based on the CJS abundance estimates in the current study it is unlikely that the Group V stock has increased to more than 25% of the pre-whaling stock assessment of > 10,000 post-yearlings. There is no basis for relaxing exisiting regulatory mechanisms at this stage for non-consumptive use of EAGVS humpbacks in Queensland waters until a better understanding of population dynamics has been gained and the risks of whale-watching activities on population viability have been adequately assessed.

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Table 1. Mark-resight summary statistics and Cormack-Jolly-Seber population estimates for adult/subadult EAGVS humpbacks resident in Hervey Bay Marine Park during the annual southward migration (1987 to 1996). Summary notation as follows: n_i = total number of adult/subadult 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, N_i = estimated population size of adult/subadult EAGVS at *i*th period, $se(N_i)$ = standard error of population estimate at *i*th period including sampling error and temporal variability terms (Pollock et al 1990), $se_{adj}(N_i)$ = standard error of population estimate at *i*th period excluding sampling error (Link & Nichols 1994). Annual adult/subadult population abundance estimates derived from a constant survival/ time-varying resight likelihood model (Model B - see Pollock et al 1990). tse_i = total sampling effort in boat-days in *i*th period.

Period	Year	n_i	m_i	R_i	r_i	z_i	N_i	$se(N_i)$	$se_{adj}(N_i)$	tse_i
1	1987	37		37	23					32
2	1988	227	13	227	97	10	554	115	91	59
3	1989	190	54	190	75	53	712	65	52	31
4	1990	104	35	104	34	93	847	95	75	30
5	1991	125	35	125	46	92	1040	131	104	34
6	1992	115	39	115	36	99	935	108	86	36
7	1993	209	67	209	58	68	1004	103	82	48
8	1994	169	79	169	33	47	816	75	60	57
9	1995	83	40	83	7	40	830	93	74	16
10	1996	119	47	119			921	118	94	22

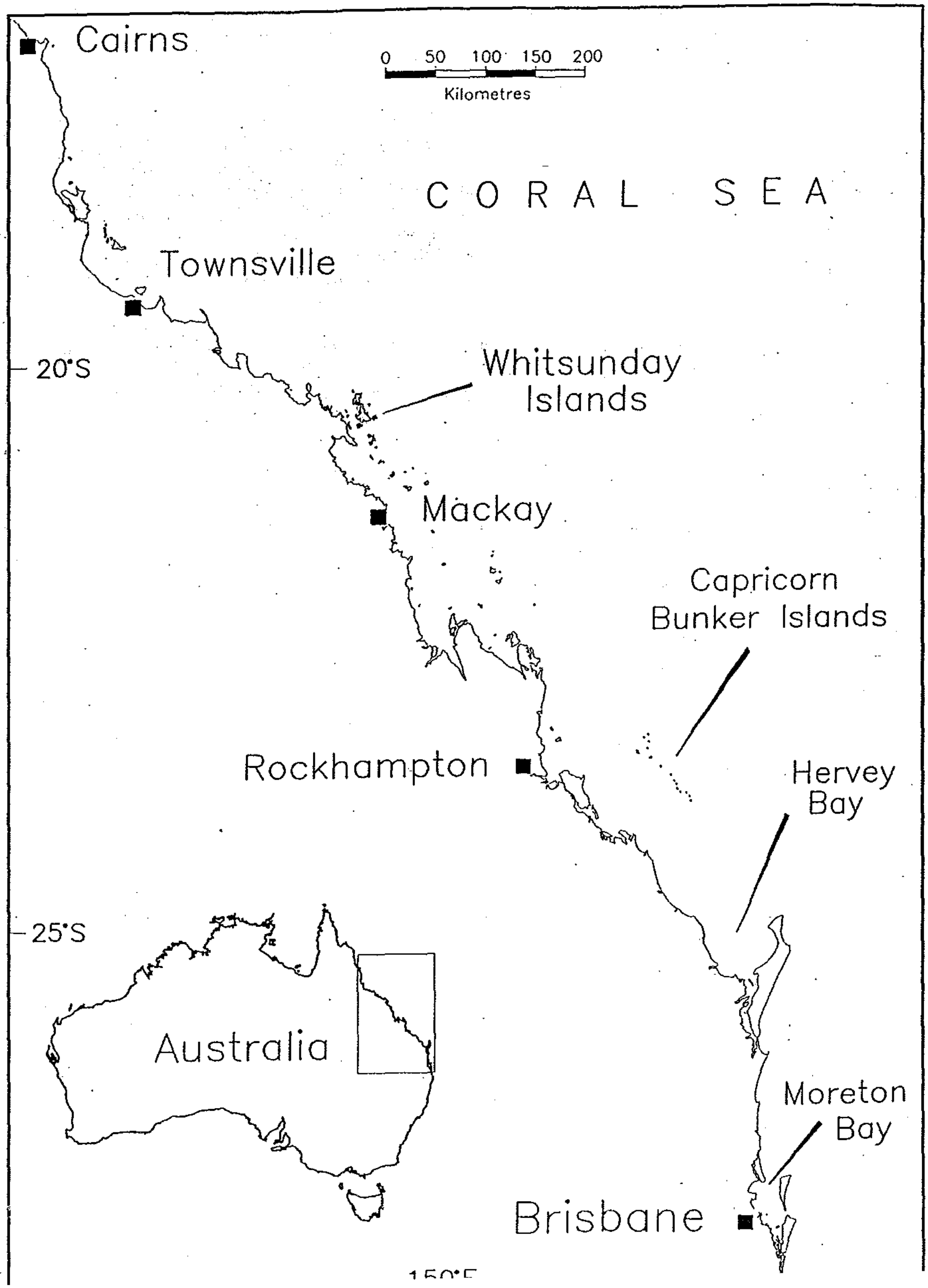
Table 2. Survivorship modelling summary for the adult/subadult EAGVS humpbacks at 2 overwintering sites (Whitsundays, Hervey Bay) based on Pollock's robust design for capture-recapture type data (Pollock et al 1990) and accounting for potential temporary emigration (see Kendall et al 1997). Robust design comprises 2 secondary samples (Whitsundays, Hervey Bay) each year within 4 primary (1993 to 1996) annual sampling periods. Model descriptions given below in Lebreton et al (1992) notation with Kendall et al (1997) extensions for temporary emigration. GoF = goodness-of-fit tests, df = degrees of freedom, dev = relative deviance, AIC = Akaike Information Criterion (see Lebreton et al 1992). Model 3 is the standard Cormack-Jolly-Seber model. Best fit model shown by lowest AIC value (Model 2), which is equivalent to the Pollock et al (1990) Model B used in the current study to estimate annual adult/subadult EAGVS population size from 1988 to 1996 (see Table 1).

Model description					GoF			
#	survival rate (σ)	recapture rate (ρ)	emigration (γ)	notation	χ^2	df	dev	AIC
1	constant	constant	permanent	σ, ρ	238.4	21	323.5	333.5
2	constant	time-dependent	permanent	σ, ρ_t	21.8	17	106.9	124.9
3	time-dependent	time-dependent	permanent	σ_t, ρ_t	20.9	15	105.9	127.9
4	constant	time-dependent	temporary	$\sigma, \rho_t, \gamma_{random}$	20.9	14	105.9	129.9
5	constant	time-dependent	temporary	$\sigma, \rho_t, \gamma_{markovian}$	20.9	13	105.9	131.9

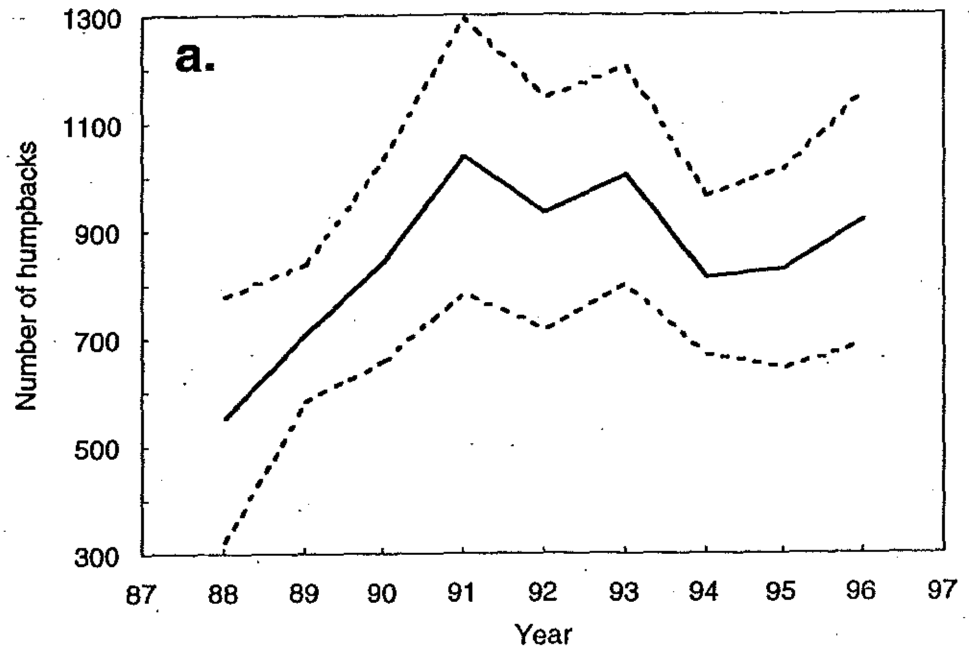
Fig. 1. *Megaptera novaeangliae*. Map showing the location of the Hervey Bay study area in southeastern Queensland (Australia) and the secondary sampling site in the Whitsunday Islands (southern Great Barrier Reef).

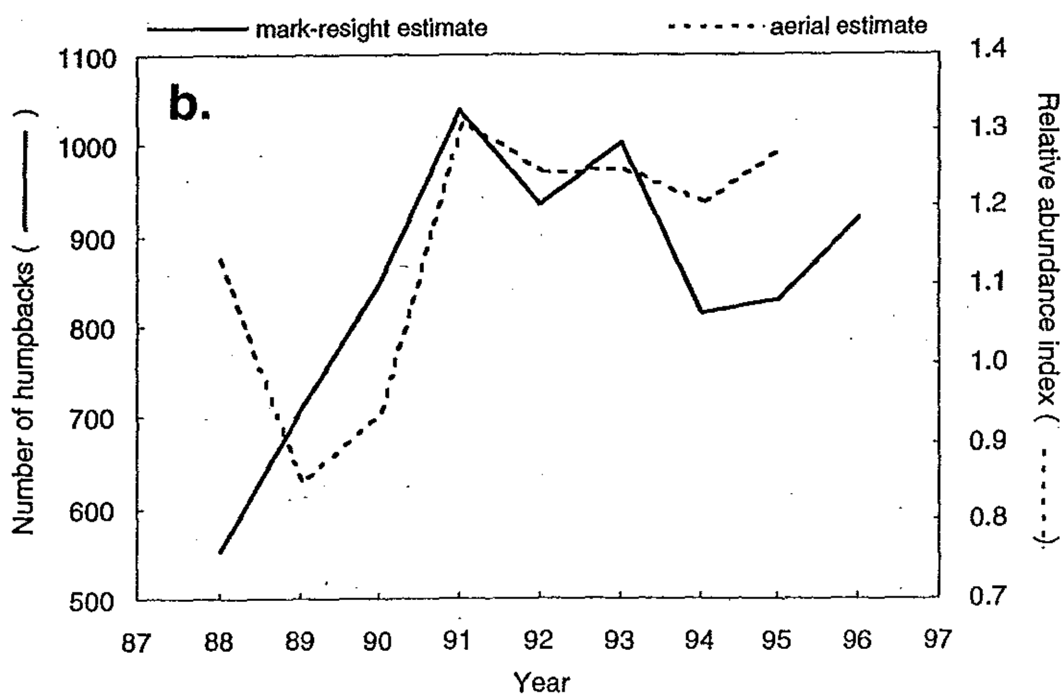
Fig. 2. *Megaptera novaeangliae*. Population abundance estimates for the east Australian Group V humpback stock that overwinters each year in Queensland waters. Estimated annual abundance of humpback whales resident seasonally in Hervey Bay from 1988 to 1996 shown in (a). Solid curve is the mean annual population estimate. Dotted curves are the pointwise 95% confidence curves around the annual estimate. Comparison shown in (b) of the estimated annual abundance of humpback whales resident seasonally in Hervey Bay from 1988 to 1996 (solid curve) and the estimated relative abundance of humpbacks in the nearby Great Barrier Reef region for the same period (dotted curve).

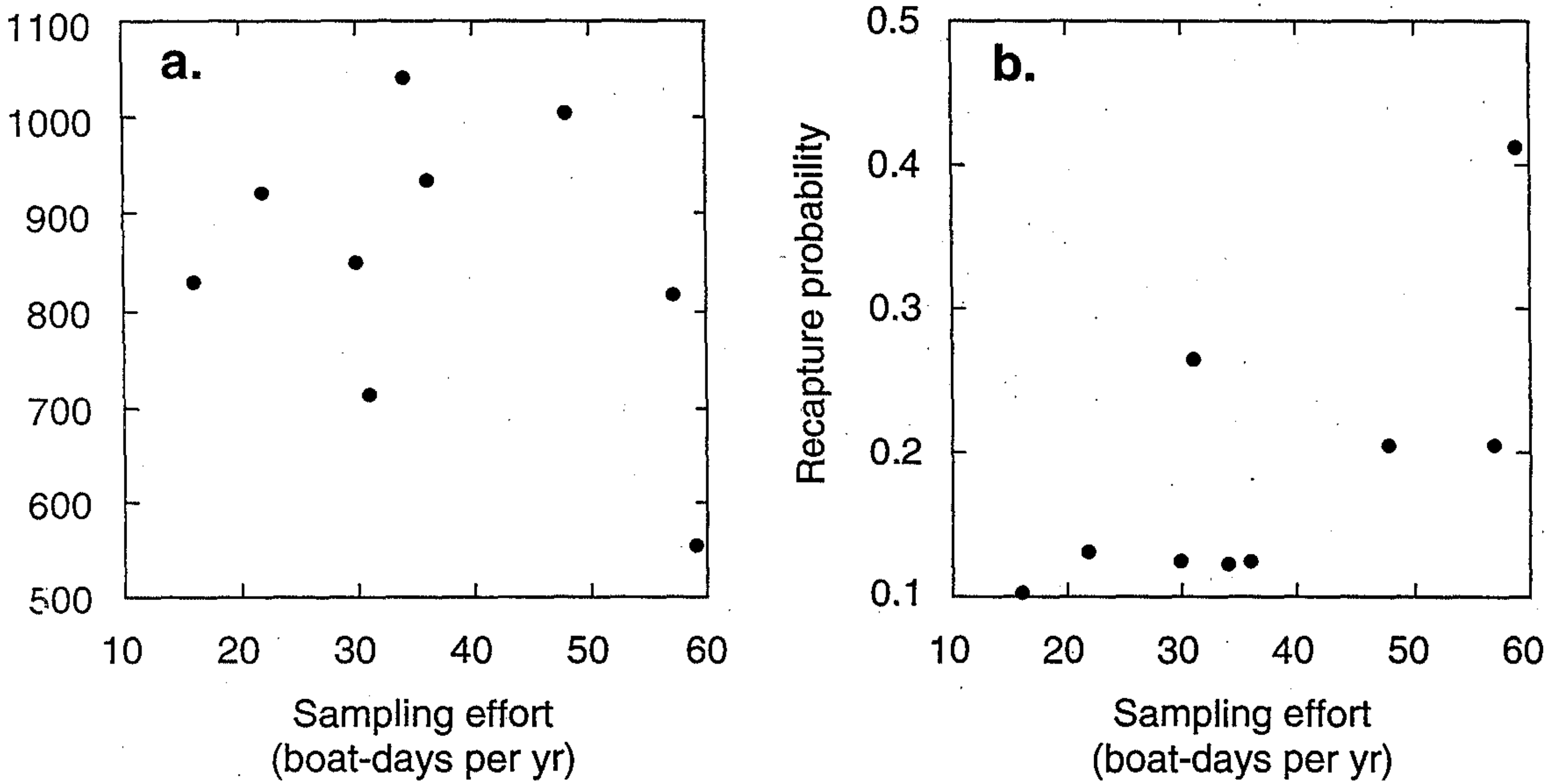
Fig. 3. *Megaptera novaeangliae*. Relationship between annual sampling effort in Hervey Bay (boat-days pa) and (a) estimated annual humpback abundance in Hervey Bay (1988 to 1996, Table 1) and (b) estimated resight or recapture probability (1988 to 1996) derived from Model B (constant survival, time-varying resight).



Cairns
0 50 100 150 200
Kilometres
CORAL SEA
Townsville
20°S
Whitsunday Islands
Mackay
Capricorn Bunker Islands
Rockhampton
Hervey Bay
25°S
Australia
Moreton Bay
Brisbane


a.
1300
1100
900
700
500
300
Number of humpbacks
87
88
89
90
91
92
93
94
95
96
97
Year


mark-resight estimate
aerial estimate
b.
1100
1000
900
800
700
600
500
Number of humpbacks (
)
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
Relative abundance index (
)
87
88
89
90
91
92
93
94
95
96
97
Year


a.
1100
1000
900
800
700
600
500
10
20
30
40
50
60
Sampling effort
(boat-days per yr)
b.
Recapture probability
0.5
0.4
0.3
0.2
0.1
10
20
30
40
50
60
Sampling effort
(boat-days per yr)