

FOR CONSIDERATION OF THE SCIENTIFIC COMMITTEE OF  
THE INTERNATIONAL WHALING COMMISSION  
AGADIR, MOROCCO: MAY 30 – 11 JUNE 2010

## **Estimation of Survival, Recruitment and Realized Growth Rates of the East Australia Humpback Population (BS-1) Using Temporal Symmetry Models**

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### **ABSTRACT**

Identifying vital rates within demographic groups is crucial for assessing the status of a species and the extent to which those changes represent a real increase to the overall breeding stock size. Realized growth and survival rates of Breeding Stock E1 humpback whales identified off Hervey Bay Queensland and Eden, New South Wales, Australia (1994 - 2009) were estimated from a photographic capture-mark-recapture study of post-yearling whales. Annual realized growth rate and seniority estimates were derived using Pradel's temporal symmetry models in the program MARK. A preliminary analysis using Cormack-Jolly-Seber models provided estimates of age-specific survival and detected potential violations of temporal symmetry models. Best fit model estimates of annual adult survival is 0.925 (0.946-0.961) and 0.70 (0.587-0.793) for sub-adults. Average realized growth rates were estimated for post yearling whales 12.4% (9.3-15.6) and reproductive females 10.7% (8.4-13.0). These estimates are consistent with findings from other surveys along the east Australian coast and support a high rate of increase for the BS E1 population of humpbacks whales. The relative contribution of survival and recruitment to population rate of change were estimated using the seniority parameter ( $\gamma$ ) and its complement ( $1-\gamma$ ). Surviving whales were the largest contributor to population growth for both reproductive females and post-yearling whales: 90.8% (SE 0.0105) and 86.2% (SE 0.132), respectively. Depending on the demographics used (reproductive females or post-yearling whales), survival is either 9.9 or 6.3 (respectively) times more important to population growth than recruitment for BS E1 humpbacks. This has strong conservation management implications, and any increased anthropogenic or environmental pressures adversely affecting survivorship will likely slow the recovery of this stock.

**KEYWORDS:** SOUTHERN HEMISPHERE, AUSTRALIA, HUMPBACK WHALE, PHOTO-ID, MARK-RECAPTURE, GROWTH RATES, SURVIVAL, RECRUITMENT, SENIORITY

## INTRODUCTION

Humpback whales that migrate along the east coast of Australia are part of the Southern Hemisphere breeding stock E, which spends 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, 1997; Kaufman *et al.* 1990, 1993; Chaloupka and Osmond 1999; Forestell *et al.* 2003). East Australia humpbacks belong to Breeding Stock E (BS E), with sub-structured breeding aggregations off northeastern Australia (BS E1), New Caledonia (BS E2), and Tonga (BS E3) (IWC 2005). Recently, BS E1 was reclassified as “Least Concern”, while BS E2, E3 and F subpopulations were IUCN Red Listed as “Endangered” (IUCN 2008).

BS E collapsed in 1962 to less than 5% of the original estimated pre-exploitation abundance due to over-exploitation and illegal whaling operations (Clapham *et al.* 2009). Land-based and aerial surveys, and fluke ID studies of BS E1 humpbacks have shown a high but steady increase in the population (Paterson *et al.* 2001; Noad *et al.* 2008; Paton *et al.* 2009; Forestell, *et al.* 2006, in press). Analyses of changes in estimated abundance and growth rates are crucial 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 BS D and E; Chittleborough 1965) or within the sub-groups of a given breeding stock (e.g. between east coast Australia and areas of Oceania; Garrigue *et al.* 2000, 2007).

Toward the end of the austral winter or early spring, large numbers of humpback whales may be reliably observed in the protected waters of Hervey Bay, Queensland, (approx. 25°S, 153° E), and feeding and migrating past Eden, NSW (approx 37°S, 150° E) (Kaufman *et al.* 1993; Forestell *et al.* 2003, Kaufman *et al.* 2006; Stamation *et al.* 2007; Gibson *et al.* 2009). The data reported here are derived from a long-term photographic identification-based capture-mark-recapture program that commenced in Hervey Bay in 1987 and Eden in 1994.

Here we present an analysis and assessment of realized growth and annual survival rates for east Australia humpback whales (BS E1) using individual fluke identification photographs, and discuss potential biases affecting these estimates.

## MATERIALS AND METHODS

### *Study area and data set*

This study was conducted in the Hervey Bay region of the Great Sandy Straits Marine Park, Queensland and offshore of Eden, NSW (Figure 1). Hervey Bay (HB) is a large, shallow embayment on the east coast of Australia (25° 00'S, 152° 52'E) and is the major southbound stop-over site for humpback whales returning to Antarctic waters from over-wintering in Great Barrier Reef waters (Forestell *et al.* 2003).

Eden (ED) is located on the southeastern Australian coast (37° 16'S, 150° 17'E), and is an area subject to high pelagic plankton productivity and phytoplankton blooms during the austral Spring (September – November) when nutrient-rich sub-Antarctic water is overlain with warmer waters from the East Australia Current (Hallegraeff and Jeffery 1993; Bax *et al.* 2001; Prince 2001). Humpback whales, particularly sub-adults and mother calf pairs, opportunistically feed on small pelagic fish and coastal krill (*Nyctiphanes australis*) attracted to temporary phytoplankton blooms in waters off Eden (Kaufman *et al.* 2006; Stamation *et al.* 2007)

Boat-based surveys were conducted daily (depending upon weather conditions), during each field season (HB: Aug – Oct; ED: Sept – Nov), using small (5 – 6 m) rigid hull inflatable vessels equipped with outboard motors (75-150 hp), and opportunistically from a 15 m Eden whalewatch vessel *Cat Balou*.

Fluke and lateral body photographs (when possible) were collected for each identified whale using established procedures using 35mm film or digital cameras equipped with motor drives and telephoto or fixed lenses up to 400 mm (Kaufman *et al.* 1987, 1993; Forestell *et al.* 2003). Photographs were used to create an identification-based recapture history for each humpback whale encountered in the sampling areas. In order to quality control individual identifications suitable for re-sight analysis, all images were scored according to the Cascadia Research Collective's fluke image screening criteria (Calambokidis *et al.* 2008).

Age class for individual whales was determined by applying standard field assessments; i.e. sub-adults were perceived by experienced observers to be unambiguously small relative to adults, but too large to be calves-of-the-year. Calves were classified in the field based on their physical size and close, consistent association with a single animal at least twice their size.(Craig *et al.* 2003). For the purpose of this analysis, we designated animals as either adult, sub-adult, unknown (not clearly distinguishable between adult or sub-adult) or reproductive female. Only one age class designation was assigned for each animal, if an animal was sighted previously as a sub-adult and then again as an adult, the animal was designated as an adult (Zablan *et al.* 2003).

#### *CURRENT CATALOG HOLDINGS*

Since 1984, data has been collected by Pacific Whale Foundation and/or submitted from collaborators working in the following areas in eastern Australia, Oceania and Antarctica: Port Douglas/Cairns, Whitsunday Islands, Capricorn Bunker Group, Hervey Bay and Point Lookout, Queensland; Byron Bay, Coffs Harbour, Sydney, Eden, New South Wales; American Samoa, Tonga and Antarctica. To date, Pacific Whale Foundations' 'Breeding Stock E/Area V Humpback Whale Catalogue' contains fluke photo-identification records of 5,460 individuals (across all areas).

*Data sets — Capture-Mark-Recapture profiles:* A data set comprised of annual capture-mark-recapture (CMR) history profiles for 4717 individual post yearling humpback whales collected in HB waters 1987 - 2009, and ED waters 1994 - 2009 was created. Only photo-identifications obtained during documented field effort were used for this data set, in order to improve effort consistency across locations and seasons.

### *Statistical Modeling Approach*

Realized growth rates ( $\lambda$ ) were estimated with the  $\lambda$ -parameterized temporal symmetry models of Pradel (1996) implemented in the program MARK version 6.0 (White and Burnham 1999). Pradel models have several assumptions that must be met, with most evaluated for sensitivity to non-compliance by Nichols and Hines (2002a). To minimize bias, study sites and demographics were preliminarily investigated using Cormack-Jolly-Seber (CJS) models. The seniority parameter ( $\gamma$ ), which measures the probability that a member of the population at time  $t+1$  was a survivor from time  $t$  and its complement ( $1-\gamma$ ), was used to estimate the relative contributions of survival and recruitment to growth rate (Nichols *et al.* 2000; Nichols and Hines 2002b).

Structural integrity of models and compliance with model assumptions were assessed through goodness-of-fit (GOF) test components of the program RELEASE and when applicable, the median c-hat procedure both implemented in the program MARK. If lack of fit was detected, starting models were restructured to account for the failing test component and the goodness of fit was reassessed as the sum of the other test components. Variance inflation factors, presented as a measure of fit, were calculated by median c-hat or as the sum of program RELEASE test components divided by the sum of their degrees of freedom.

To account for transients, time-since-marking (TSM) models were used as the global model (denoted as 2ac). Information-theoretic approaches were used to test biological hypotheses by comparing the fit of several candidate models. The Akaike Information Criterion (AIC) was used for model selection and was corrected for sample size (AICc) as well as over-dispersion (QAICc). Models were ranked based on the model weights ( $\Delta QAICc$ ) procedure described by Burnham and Anderson (2002).

Overall means were estimated using variance components to account for both sampling variability and the true process variance (Gould and Nichols 1998; Cooch and White 1998). The number of on-water survey hours was incorporated into the likelihoods as a covariate via the logit link function by constraining parameters to be a function of effort (denoted in models with “e”).

## **Results**

### *Preliminary Cormack-Jolly-Seber Analysis*

A preliminary analysis using CJS models compared best fitting models from the study sites. Sites HB and ED, and combined (HBED) all failed goodness-of-fit test3.sr and had best fitting TSM model suggesting similar biological processes in both sites (Table 1). The datasets were therefore combined for demographic analyses. Failure of test3.sr may be a result of transients or of considerable differences in vital rates of demographic groups. To evaluate the cause of test3.sr failure, the vital rates and best model fit of three demographics were compared using CJS models.

The global model from reproductive females ( $n=714$ ) for all years (1987-2009) had good fit (c-hat 1.13) and best fitting candidate model of  $\phi(.)p(t)$ . There is temporal variation in recapture probabilities with an average rate of  $p=0.129$  (SE 0.0137). Annual survival is estimated at 1.0 and assumed to be constant for the duration of this study.

Adult (n=1860) and sub-adult (n=1233) groups were modeled together for comparison. Adults failed test3.sr suggesting the presence of transients in this group, however, the sub-adult group had insufficient data for a reliable evaluation of test3.sr. Candidate models were constructed to test for transients in both groups by using TSM, as well as differences in survival and recapture probabilities.  $\Delta\text{QAICc}$  values indicate two competing models from the candidate set (Table 2). Consistencies between best models indicate the presence of transients in adults and no differences in recaptures between groups. However, the presence of transients in the sub-adult group cannot be confirmed ( $\phi_{2ac}$  in model 1 and  $\phi(.)$  of model 2). Annual adult survival is estimated as 0.925 (0.946-0.961) and 0.70 (0.587-0.793) for sub-adults. Mean annual recapture probability for both groups is 0.102 (SE 0.017).

### Temporal Symmetry Modeling

#### *Datasets for Pradel Models*

Utilizing results from the CJS analysis, two datasets that comply with Pradel model assumptions were defined. Data was too sparse to model adult and sub-adult groups separately, and were combined to incorporate unknown whales (of undetermined age); here forward referred to as the 'post yearling' group. Pradel models require that animals have some probability of recapture throughout the study (Franklin 2001); moreover, TSM models cannot be incorporated into temporal symmetry models. Therefore transients were removed from the post yearling dataset by using Pradel *et al.*'s (1997) *ad hoc* method of suppressing first encounters. CJS modeling detected no difference in recapture probabilities between adult and sub-adult groups which complies with the assumption of homogeneous capture probabilities. A second dataset for temporal symmetry modeling was comprised of reproductively active females (known mothers), with all individuals included since no transients were detected in this demographic.

For both datasets, a subset of the data (HBED 1994 – 2009) was used in order to eliminate potential bias associated with changes in study area boundaries. Trap response can bias estimates when using Pradel models (Nichols and Hines 2002a). Trap response was assumed negligible for the benign methods used in this study. However, Nichols and Hines (2002a) extend the concept of trap response to include changes in capture probability as a result of the investigator(s) actions. Parameters were therefore constrained to be a function of survey effort.

The resulting truncated datasets for temporal symmetry modeling included post yearlings (n=765) and reproductively active females (n=692) encountered in Hervey Bay and Eden from 1994-2009 and are summarized in m-array format (Tables 3 and 4).

#### *Realized Growth Rate*

Realized growth rates for both groups were estimated using the  $\lambda$ -parameterized temporal symmetry models. Variance inflation factor estimates of the fully parameterized model for both post yearlings (c-hat 1.25) and reproductive females (c-hat 1.35) suggested good model fit. For both groups, the reduced model structure of  $\phi(.)\rho(t)\lambda(.)$ , had the lowest QAICc and full weight from the candidate set. Annual realized growth rates are estimated at a constant rate of 1.124 (1.93-1.156) or 12.4% for post yearlings and 1.107 (1.084-1.130) or 10.7% per annum for reproductively active females.

### *Relative Contributions of Survival and Recruitment*

Pradel's temporal symmetry models were also used to estimate the relative contributions to  $\lambda$  by using the seniority parameter ( $\gamma$ ). Where  $\gamma$  is the relative contribution of survival to population growth, and its complement ( $1-\gamma$ ) is a measure of the contribution of recruitment (Nichols *et al.* 2000; Nichols and Hines 2002b).

Two competing models from the candidate model set were detected for post yearlings (Table 5. Model  $\gamma(t+e)p(t)$ , suggesting temporal variation in  $\gamma$  and includes survey effort as a covariate for  $\gamma$ . This model has 1.7 times more support than model  $\gamma(.)p(t)$ . Annual estimates of  $\gamma$  were derived from model averaging procedures and are plotted in Figure 2. Post yearlings have an average  $\gamma$  of 0.862 (SE 0.0132) and a corresponding recruitment rate of 0.138 (SE 0.0132). Survival is therefore 6.3 times  $\{\gamma/(1-\gamma)\}$  more important to the population growth of post yearlings than recruitment.

Competing models from the analysis of reproductively active females are also apparent. (Table 6). Model  $\gamma(.)p(t)$  has 1.9 times more support than  $\gamma(t+e)p(t)$ . Plotted results of model averaged  $\gamma$  estimates reveal much less temporal variation in  $\gamma$  than post yearlings (Figure 2), and suggests the constant  $\gamma$  estimate from model  $\gamma(.)p(t)$  is relevant. The average seniority rate is 0.908 (SE 0.0105). Therefore the relative contribution of survival to  $\lambda$  for reproductively active females is higher than the post yearling group and is 9.9 times more important to population growth than recruitment (9.2 percent).

## **DISCUSSION**

### *Population Rate of Change*

To limit bias in parameter estimates several precautions were taken to define datasets for temporal symmetry modeling that would comply with Pradel model assumptions, with some notable caveats. First, it cannot be assumed that a stable-age-distribution has been achieved in BS E1 so the results from the post yearling group will be the cumulative effect of all age groups included. Second, the dataset for the post yearling group excluded transient whales to comply with temporal symmetry model assumptions. Attempts to model post yearlings with transients yielded unreasonably high estimates of  $\lambda$ , and excluding transients (by grouping them separately) also resulted in spurious estimates. The effect of transients in estimating population rate of changes is an important area in need of further investigation and beyond the scope of this paper. For our purposes, Pradel's (1997) ad hoc method of suppressing first encounters provided the most reasonable results. However, since Pradel models condition on the entire encounter history, significant information may have been lost. Results from the truncated post yearling group were very similar to estimates from the reproductively active female group.

Our estimates of population rate of change based on CMR profiles from Hervey Bay and Eden of 12.4 (9.3-15.6) for post yearling whales and 10.7% (8.4-13.0) for reproductive females are within the range of recent estimates from land-based counts, vessel surveys and photo ID studies (Branch 2006; Noad *et al.* 2008; Forestell *et al.* 2006, in press).

### *Relative Contributions to Growth Rate*

For post yearling and reproductive females, surviving whales were the largest contributor to population growth; whereas contributions from recruitment were low. However, using Pradel's temporal symmetry models it is not possible to formally distinguish whether recruitment is a result of reproduction or immigration.

A growth rate of 12.4% for post yearling whales slightly exceeds the calculated maximum plausible biological rate of increase (11.8%) for this species (Zerbini *et al.* 2010). This is in contrast to other breeding stocks in the southwest Pacific (BS E2, E3, F) that are showing limited or no signs of recovery (Gibbs and Childerhouse 2004, 2006; Garrigue *et al.* 2000, 2002, 2007; Paton *et al.* 2009, Childerhouse *et al.* in press). Future growth and stability of the BS E population is dependent upon continued survival of post yearlings and reproductively active females.

### *Management Implications*

Careful use of Pradel's temporal symmetry models can provide an effective means to assess the relative contributions to  $\lambda$  when population vital rates required for projection matrices are difficult to obtain or have a high degree of uncertainty. Moreover, the finding of temporal variation in  $\gamma$  should be taken into consideration for projection matrix analyses that incorporate a constant estimate of vital rates (Nichols *et al.* 2000).

This paper highlights the importance of demographics used when estimating population rates of change. The effect of transients on these estimations needs to be further investigated. Regardless of demographics, relative contribution of survival to realized growth rate is very high and significantly more important than recruitment. The relative importance of survivorship is consistent with findings from other studies on long-lived species (Heppell *et al.* 1999). In our study, the relative contribution of survival is as at least 6.3 times more important to population growth than recruitment.

The population stability for long-lived species (with delayed sexual maturity) is sensitive to changes in post-yearling survival (Congdon *et al.* 1993). Our finding that survivorship is important to the population growth rate of Breeding Stock E1 humpback whales has strong implications for the conservation and management of the species..

Identifying and assessing threats to post yearling and/or reproductively active female survival is critical. The effect of transients over extended time periods on estimates of population abundance and rate of increase will require a comprehensive comparison of all available photo-id images for this stock of whales. Given our current understanding of the diminished state of humpbacks in Oceania (BS E2, E3 & F), and the uncertainty of relatedness and interchange with east Australia whales (BS E1 any increased anthropogenic or environmental pressures adversely affecting survivorship will likely slow the recovery of these populations.

## ACKNOWLEDGEMENTS

The members and supporters of the Pacific Whale Foundation contributed funding for this work. Research was conducted under permit granted by the Australia Department of Environment and Heritage, NSW Parks and Wildlife Service, the Queensland Department of Environment and Resource Management, and the Great Barrier Reef Marine Park Authority. Special thanks to Ros and Gordon Butt (Cat Balou Cruises, Eden, NSW), for providing valuable photo images and logistical support. We thank Annie Macie, Amanda Hutsel, Alicia Malo, Quincy Gibson, Trish Naessig, Paul Forestell, Erin Iberg, Amy Hellrung, Ashley Justice, and Lucia de la Paz, for their assistance in the field and lab, the Hervey Bay whalewatch operators, and the countless individuals who facilitated our research in Australia by working as volunteers and research assistants, and by contributing identification photographs.

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## TABLES

Table 1. Summary of best fit models for Hervey Bay (HB), Eden (ED) and the combined CMR datasets (HBED) indicating a TSM (2ac) model for all datasets.

Region	Model	C-hat	$\phi$	Mean $\rho$	Number	Years Sampled
HB	$\phi(2ac)\rho(t)$	1.13	$\phi^1 0.614, \phi^2 0.943$	0.124	3737	1987-2009
ED	$\phi 2(ac)\rho(t)$	1.27	$\phi^1 0.560, \phi^2 N/A$	0.0246	1370	1994-2009
HBED	$\phi(2ac)\rho(t)$	1.13	$\phi^1 0.603, \phi^2 0.963$	0.117	4717	1987-2009

Table 2 Two best fit models (c-hat 1.37) of the candidate set for adult (A) and sub-adult (S) whales using Cormack-Jolly-Seber models. Consistencies between models suggest the presence of transients in the adult population (A2ac) and homogenous recapture rates ( $\rho(g+t)$ ). The evaluation of the presence of transients in sub-adults is inconclusive because of inconsistent model structures for survival (S2ac and S.).

Model	QAICc	$\Delta$ QAICc	QAICc weights	Mod. likelihood	Num Par	-2 log(L)	AD Survival w/ (CI)	SA Survival w/ CI	Average Recapture
$\phi(A2ac*S2ac) p(g+t)$	4605.7	0	0.5747	1	26	3502.35	0.946 (0.925-0.961)	0.7 (0.587-0.793)	0.102 (SE 0.017)
$\phi(A2ac*S.) p(g+t)$	4606.7	0.71	0.403	0.701	25	3501.81	0.948 (0.927-0.963)	0.635 (0.558-0.705)	0.0987 (SE 0.016)

Table 3 . M-Array summary of reproductively active female dataset (N=692) 1994-2009 for temporal symmetry modeling. Includes the total number of whales encountered on each

<i>Occasion</i>	<i>Sighted</i>	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	<i>Resighted</i>
1994	52	7	8	5	3	6	1	1	3	1	1	6	0	0	3	0	45
1995	35		5	2	7	2	3	1	1	1	1	3	2	1	0	0	29
1996	48			10	9	6	6	0	3	1	2	3	3	0	1	0	44
1997	75				12	3	8	2	7	2	3	8	4	5	4	1	59
1998	71					5	9	1	7	3	2	8	4	1	3	0	43
1999	52						6	0	4	4	2	6	3	9	1	0	35
2000	68							0	12	2	6	9	11	3	1	1	45
2001	9								1	1	0	1	1	1	1	0	6
2002	87									1	11	12	11	7	4	1	47
2003	39										2	6	2	1	1	0	12
2004	75											11	13	7	4	0	35
2005	148												11	16	18	2	47
2006	120													14	20	3	37
2007	136														16	3	19
2008	159															3	3

occasion (sighted) and their resightings by year, followed by total number of whales resighted across all occasions (resighted).

Table 4. M-Array summary of post yearlings dataset (N=765), 1994-2009, for temporal symmetry modeling.. Includes the total number of whales encountered on each occasion

<i>Occasion</i>	<i>Sighted</i>	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	<i>Resighted</i>
1994	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1995	23		4	1	4	1	2	2	0	2	0	1	1	0	0	0	18
1996	35			8	6	1	2	0	0	0	0	2	1	0	0	0	20
1997	59				10	4	5	0	1	1	3	4	5	0	0	1	34
1998	83					12	7	1	4	2	1	5	2	5	3	0	42
1999	57						5	0	5	3	2	0	5	5	0	0	25
2000	63								9	3	2	6	6	4	1	1	32
2001	8								1	0	0	0	1	1	2	0	5
2002	50									1	6	14	7	4	2	1	35
2003	38										6	3	3	0	2	0	14
2004	52											8	8	4	3	0	23
2005	122												11	14	17	0	42
2006	144													16	18	4	38
2007	167														23	4	27
2008	181															7	7

(sighted) and their resightings by year, followed by total number of whales resighted across all occasions (resighted).

Table 5. Competing models from the candidate set for seniority parameter ( $\gamma$ ) modeling of post yearlings. Best model has 1.9 times more support.

<b>Model</b>	<b>QAICc</b>	<b><math>\Delta</math>QAICc</b>	<b>QAICc weights</b>	<b>Model likelihood</b>	<b>Num. Par</b>	<b>-2log(L)</b>	<b><math>\gamma</math> estimate</b>
$\gamma(\cdot)p(t)$	2153.2	0	0.6953	1	16	2650.88	0.862 (SE 0.0132)
$\gamma(e)p(t)$	2154.3	1.11	0.3645	0.5741	16	2652.27	0.840 (SE 0.0143)

Table 6. Competing models from the candidate set for seniority parameter ( $\gamma$ ) modeling of reproductively active females. Best model has 1.7 times more support.

Model	QAICc	$\Delta$ QAICc	QAICc weights	Model likelihood	Num. Par	-2log(L)	$\gamma$ estimate
$\gamma(\cdot)p(t)$	2626.8	0	0.6965	1	16	3502.35	0.908 (SE 0.0105)
$\gamma(e)p(t)$	2628.45	1.66	0.3035	0.4358	17	3501.81	0.927 (SE 0.0094)

## FIGURES



Figure 1. Study sites along the East Coast of Australia - Hervey Bay, QLD and Eden, NSW (indicated by black stars)



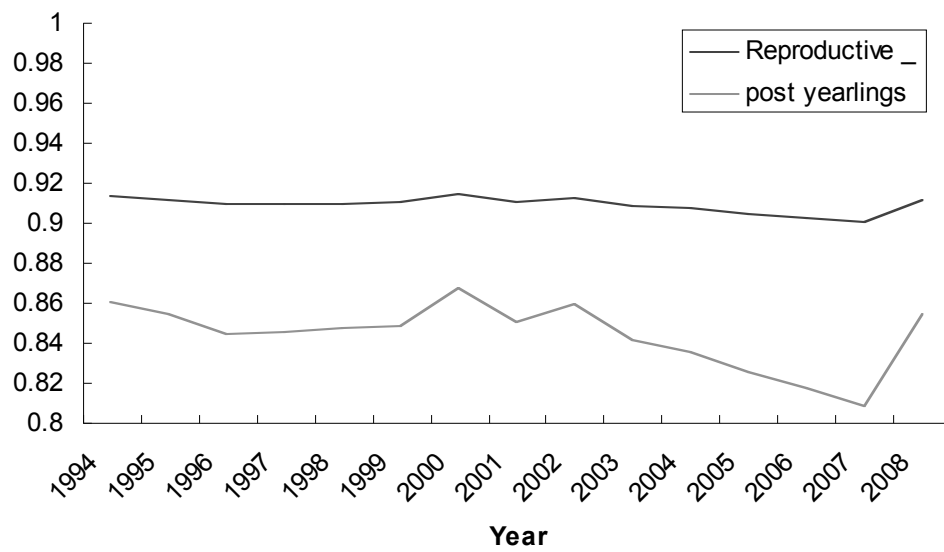


Figure 2. Model averaged annual estimates of the seniority parameter ( $\gamma$ ) for reproductive females and post yearling groups. Supportive of a time constant  $\gamma$  model for reproductive females, and time variant model for post yearlings.