

## Population modelling of humpback whales in East Australia (BSE1) and Oceania (BSE2, BSE3, BSF2)

J. A. JACKSON<sup>1</sup>, A. ZERBINI<sup>2</sup>, P. CLAPHAM<sup>2</sup>, R. CONSTANTINE<sup>3</sup>, C. GARRIGUE<sup>4</sup>, N. HAUSER<sup>5</sup>, M. M. POOLE<sup>6</sup>, C. S. BAKER<sup>3,7</sup>

<sup>1</sup>*British Antarctic Survey, High Cross, Madingley Road, Cambridge CB30ET, UK*

<sup>2</sup>*National Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA Fisheries, 7600 Sand Point Way NE, Seattle, WA 98115-6349, USA*

<sup>3</sup>*School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand*

<sup>4</sup>*Opération Cétacés, BP 12827, 98802 Nouméa, Nouvelle-Calédonie*

<sup>5</sup>*Cook Islands Whale Research, P.O. Box 3069, Avarua, Rarotonga, Cook Islands*

<sup>6</sup>*Centre de Recherches Insulaires et Observatoire de l'Environnement, BP 1013, Moorea, Polynésie Française*

<sup>7</sup>*Marine Mammal Institute, Oregon State University, 2030 SE Marine Science Drive, Newport, OR 97365 USA*

Contact email: [jennifer.jackson@bas.ac.uk](mailto:jennifer.jackson@bas.ac.uk)

### ABSTRACT

Humpback sub-stocks BSE1 (East Australia), BSE2 (New Caledonia), BSE3 (Tonga) and BSF2 (French Polynesia) show significant genetic differentiation, yet share common high latitude feeding grounds between 130°E-100°W and were subject to 41,987 whaling catches across this feeding ground between 1900-1978. In order to explore the population history and develop a population assessment for this region, we have constructed a two-stock Bayesian logistic 'FITTER' model for neighbouring pairs of breeding grounds in the South Pacific. This model allocates catches from each shared feeding ground by to breeding stocks in a ratio according to annual model predicted abundance on each breeding ground. A number of 2-stock scenarios are explored: East Australia / New Caledonia (shared Southern Ocean feeding ground 130°E-180°), Tonga / French Polynesia (shared Southern Ocean feeding ground 180-110°W), East Australia / Oceania (New Caledonia, Tonga and French Polynesia combined), and preliminary runs for a combined West Australia (BSD) / East Australia / Oceania 3-stock model. Sensitivity of models to catch allocation scenarios and other abundance indices are preliminarily explored. All model results suggest that the breeding grounds in Oceania are not yet recovered (median  $N_{2013}/K$  less than 50% for all breeding grounds).

### INTRODUCTION

The Southern Ocean region of the South Pacific spans 130° (130°E-100°W) and was subject to an enormous number of humpback whale catches during the whaling period, with 41,987 killed south of 60°S and 14,479 killed on migration and in coastal breeding grounds. This region of the Southern Ocean seasonally feeds humpbacks from a number of breeding grounds, namely East Australia, New Caledonia, Tonga and French Polynesia. The South Pacific is an enormous, remote region. Small breeding grounds are also known from American Samoa, Samoa, Fiji, Niue and Vanuatu, and there are probably a number more, as yet undiscovered. As a consequence of this remoteness, surveys of humpback abundance in the region have focused on a few populated regions in the South Pacific: New Caledonia, Tonga, French Polynesia and the Cook Islands. Between 1999 and 2005 the South Pacific Whale Research Consortium conducted a coordinated survey of these regions, collecting photo-identifications and DNA samples via biopsy sampling. Some identifications were also obtained from Samoa, American Samoa, Fiji, Niue and Vanuatu. Constantine et al. (2012) reports abundance estimates arising from this study. In this study, mark recapture evidence from individual synoptic regions is pooled to measure 'Oceania' as a single entity, and suggests that there were 4,329 humpbacks using the region in 2005 (coefficient of variance,  $CV=0.12$ ).



Considering Oceania as a single entity has been convenient for population assessment (Jackson *et al.* 2006; Jackson *et al.* 2008, 2009), since so little has been known until recently of the feeding-breeding ground connections of the individual breeding grounds, so allocation of catch to each breeding population was problematic. Photo-identification matching across the region shows some inter-annual movements between these breeding grounds in Oceania, which provides support to the grouping of Oceania as one entity (Garrigue *et al.* 2011a). However genetic measurements from breeding grounds show significant population differentiation between New Caledonia, Tonga and French Polynesia (Olavarria *et al.* 2007), suggesting that despite some level of interchange, the populations are probably demographically independent. A further question is how distinct the 'Oceania' breeding grounds are from the large western breeding ground off the coast of East Australia. This breeding ground is both large ( $N=9,683$  in 2007, Noad *et al.* 2008) and rapidly increasing (10.9%, 95% CI 10.5-11.3%, Noad *et al.* 2008). Photo-identification matching of Oceania with East Australia has suggested that interchange between Oceania and East Australia may be lower than interchange within Oceania (Garrigue *et al.* 2011b). However quantitative analysis of genotypes from East Australia and Oceania in a mark recapture framework did not support this hypothesis (Jackson *et al.* 2012), suggesting that East Australia and the breeding grounds of Oceania exchange migrants in a stepping stone manner across the region. Consistent with this, Garrigue *et al.* (2012) reported an anomalous increase in abundance in New Caledonia in recent years, with an apparent growth rate so high that it could only be possible due to presence of immigrants from other breeding grounds. Given the size of East Australia close by to the west, immigration from this breeding ground seems to be the likely culprit.

A great deal of information has been published on breeding ground- feeding ground connections in the South Pacific, which means we can now develop new catch allocation hypotheses for the breeding grounds of Oceania. This information, and the abundance estimates recently available from each breeding ground (Constantine *et al.* 2010), allows us to develop a population assessment of the Oceania breeding grounds by use of multiple 2-stock models, with reference to East Australia and preliminarily also to West Australia to the west. In order to allocate feeding ground catches to multiple stocks using the same area in a biologically realistic way, density dependent logistic models have been modified so that catches on shared grounds are taken annually from each population in proportion to the number of animals from each breeding ground using the feeding ground *in that year*. Using this type of model, it is not possible to determine initial carrying capacity using the *backwards* method (Butterworth & Punt 1995). A simple Markov Chain type model was developed in order to obtain the best fitting (highest likelihood) posterior distribution from prior distributions on carrying capacity ( $K$ ), maximal population growth rate ( $R_{max}$ ), and 'naïve' and 'fringe' catch allocations for each stock. Only those forward projected trajectories consistent with current abundance ( $N_{current}$ ) for each stock with the highest likelihood were retained. Of these, the sample set giving the maximum likelihood value, given likelihood scores for absolute abundance and indices of relative abundance for each stock, was retained after searching 35,000 prior samples. This was repeated 1,000 times to generate 1,000 posterior samples for each stock assessment scenario.

## METHODS

### Catch Allocation and rationale

In this study we only consider humpbacks killed through modern whaling, although relatively low level pre-20<sup>th</sup> century humpback whaling has been documented. Whaling catches have been compiled by the IWC by 10° longitudinal regions (Allison 2006). A schematic of catches is shown in Figure 1.

### East Australia and New Caledonia



Multiple lines of evidence from photo-identification (Constantine *et al.* 2011), Discovery Tags (Chittleborough 1965), satellite data (Gales *et al.* 2009) and genetic sampling (Steel *et al.* 2008) indicate that the 'core' feeding ground for BSE1 spans the region 130°E-180°, through humpbacks from east Australia have been sighted as far east as 170°W (Rock *et al.* 2006). The feeding ground for New Caledonia is less clearly defined, but a strong migratory link with New Zealand, via Norfolk Island has been revealed by satellite telemetry (Garrigue *et al.* 2010). Only one recapture has been made in the Southern Ocean, and this tentatively links New Caledonia to the Southern Ocean region c 171°W (Steel *et al.* 2008), slightly to the east of the 'core' East Australian feeding ground. The lack of connectivity data between New Caledonia and the Southern Ocean is likely due to the small size of the population relative to its neighbors to the east and west (Constantine *et al.* 2007; Noad *et al.* 2008). A recent and anomalous increase in abundance on the New Caledonian breeding ground has been documented however (Garrigue *et al.* 2012). Inferred growth rates of up to 20.9% since 2003 indicate that an influx to this population has occurred, rather than an increase in true population growth rate, since the biological upper limit of population growth for humpbacks is thought to be 10.6% (Zerbini *et al.* 2010). Given the proximity, size and well-documented rapid trend in abundance in neighbouring East Australia (Noad *et al.* 2008), an influx of animals from this region seems likely, and would suggest a common feeding ground or migratory route for the two breeding grounds.

Hence the 'common' feeding ground for these two populations is set to the 'core' E1 range of 130°E-180, with sensitivity also explored to extending this range westwards to 110°E. Given the range of feeding ground connectivity documented for E1 to data, the region 170°E-180 was assumed to be 'core' E1. Catches unique to each region were also imposed, with coastal catches from Australia assigned to E1, catches from Norfolk Island assigned to E2 and catches from New Zealand jointly assigned to E1 and E2 (Constantine *et al.* 2007; Franklin *et al.* In press; Gales *et al.* 2009; Garrigue *et al.* 2010).

#### *Tonga/American Samoa and French Polynesia*

Photo-identification and genetic re-sightings suggest that humpbacks from the Tongan breeding ground feed over a very broad longitudinal area in the Southern Ocean. The broadest longitudes were reported from Discovery Mark deployments, which recovered Tongan whales between 172°E-c110°W (Paton & Clapham 2006). Subsequent work has revealed most recaptures between 110-125°W (Steel *et al.* 2008). This probably reflects the fact that very little data has been collected between 125-170°W, although it is also notable that all humpbacks satellite tagged passing through the Cook Islands (to the east of Tonga) travelled towards Tonga and Samoa, via the Tonga Trench (Hauser *et al.* 2010). Nearby American Samoa has also demonstrated a capacity for long easterly movements on migration, with one individual from there re-sighted on the Antarctic Peninsula (Robbins *et al.* 2011). This suggests a substantial number may come from this easterly feeding ground (the eastern edge of Area VI and probably also a few from Area I). French Polynesia is even less well understood in terms of feeding ground connectivity. One re-sight has been made with Colombia (South Pacific Whale Research Consortium 2008), suggesting possibly that Area I is used as a feeding ground, but this population also shows significant differentiation from Colombia, so is likely primarily to use feeding grounds in Area VI. Very few humpback whale observations are available from Area VI with which to match to breeding grounds at that latitude. Without much information to go on, we therefore allocate catches from 180-110°W to both Tonga and French Polynesia, and also explore a % additional allocation from Area I to the east.

#### **Statistical Model**

Priors on  $K$  and  $R_{max}$  [0-0.106] were uniformly distributed, with  $K$  bounded on the lower edge by a conservative current abundance estimate of the stock in question, and of values ranging 40,000-60,000 for the upper edge. Where no trend information was available from either population (e.g. Tonga and French Polynesia), a normally distributed prior on  $R_{max}$  was



imposed for each stock ( $N[0.067, 0.04]$ ). This is the average population growth rate based on a hierarchical meta-analysis of growth rates of large baleen whales (Branch *et al.* 2004).

Posterior distributions from the density dependent two-stock logistic model were obtained using a simple Markov Chain. Firstly the chain was used to pick combinations from prior distributions of  $K$  and  $R_{max}$  and retain those that fell within the prior range for current abundance for both stocks (upper and lower bounds equivalent to 4 x the CV of the abundance estimate). Each 'generation' of the model was run in parallel as  $n$  chains (chosen as 7 in this analysis after an initial survey of  $n=4, 7, 12$  and 50). Likelihood scores were summed for fit to absolute abundance (3) and relative abundance indices (4) for each parameter set. A single 'cold' chain was used to retain the parameters yielding the highest likelihood score in each generation. Each 'maximum likelihood' parameter set found over the course of 5,000 generations (i.e. 35,000 prior samples over 7 chains) was kept. This approach was repeated 1,000 times from a different initial point in parameter space each time, giving a total of 5 million generations of analysis (35 million  $K$  and  $R_{max}$  parameter sets visited) and 1,000 maximum likelihood posterior samples. For some initial starting points, the priors did not find a parameter set compatible with the  $N_{obs}$  uniform priors over 5,000 generations, and these were discarded from the posterior set.

### *Three-stock population model*

We also explored a three-stock model: (West Australia BSD, East Australia BSE1 and Oceania). Here an additional prior parameter is required in the model to allocate catch from  $\beta$  whales on the west Australian breeding ground to a shared BSD/BSE1 feeding ground at 110-130°E, and  $\alpha$  whales on the East Australian breeding ground to this feeding ground. Both Chittleborough (1965) and Gales *et al.* (2009) through Discovery Tags and satellite telemetry revealed movement of humpbacks to this Southern Ocean region from their respective coasts, suggesting there may be breeding ground mixing across this feeding area. In this model,  $(1 - \alpha)$  E1 whales share a common feeding ground with (i) Oceania or (ii) New Caledonia between 130°E-180°, while  $(1 - \beta)$  West Australian whales feed in the core BSD feeding area 80-110°E. The  $\alpha$  and  $\beta$  priors were chosen from a uniform distribution between 0-0.3, representing between 0-30% of the total initial carrying capacity of BSD and BSE1 respectively.

## **Abundance**

Multiple measurements of absolute abundance are available from East Australia (Noad *et al.* 2011; Noad *et al.* 2008; Paton *et al.* In Press). For the base case model, we used the Noad *et al.* (2008) absolute abundance in the likelihood weighting of trajectories. The prior on abundance was always uniform and bounded at 4 x CV of the abundance estimate in question.

Multiple mark recapture based estimates of abundance are also available from New Caledonia (Garrigue *et al.* 2012; Garrigue *et al.* 2004). These suggest either  $N=758$  (CV=0.3) in 2001 (Garrigue *et al.* 2004) or  $N=562$  (CV=0.19) in 2008 (Garrigue *et al.* 2012). The latter estimate is based on photo-ID, which may be male biased (Constantine *et al.* 2012), so may be an underestimate of the number of whales of both sexes visiting the region. However this also provides a measure of abundance trend for the breeding ground, so this measure has been applied as a base case abundance for New Caledonia.

Overall abundance in Oceania has also been calculated using mark recapture approaches (Constantine *et al.* 2012) and is estimated at  $N=4,329$  (CV=0.12) across the region in 2005. Individual abundance estimates are also available from Tonga (E3,  $N=1,840$ ) and French Polynesia (F2,  $N=934$ ), by doubling male specific estimates obtained from genotypes (Constantine *et al.* 2010). There is considerable uncertainty in these estimates however (CV=0.23 and 0.64 respectively) so the uniform prior on each is quite large. An additional estimate of abundance is available from French Polynesia (Albertson-Gibb *et al.* 2009) based



on photo ID. Since the genotypic data allows for measurement of abundance of both sexes, the genotypic estimates were used in the Tonga/French Polynesia two-stock model.

For the 3-stock model, abundance for West Australia was taken from Hedley et al. (2011), who calculated  $N=28,830$  in 2008 from aerial surveys of the region.

## Trends

Indices of abundance are available from East Australia from the Bryden Brown surveys (1981-2004) and from a longer survey by Paterson, Paterson and Cato (1984-2007). Because CV data are only available from the Bryden-Brown surveys, these were used in the base-case model (Brown *et al.* 1997). An abundance trend has also been calculated using photo-ID mark recapture data from New Caledonia (Garrigue *et al.* 2012). This trend was included in the East Australia/New Caledonia 2-stock model. For the 3-stock model, abundance for West Australia was taken from Hedley et al. (2011), who reported regional relative abundances from 1999, 2005 and 2008.

## Two-stock model construction

$$+1 = + \cdot \cdot 1- - \cdot + - (1)$$

$$+1 = + \cdot \cdot 1- - \cdot + -$$

Subscripts  $A$  and  $B$  represent the two stocks.

$N_t^i$  is the stock abundance in year  $t$  for stock  $i$

$K^i$  is the stock carrying capacity in 1900 for stock  $i$

Exponent  $z$  is fixed at 2.39.

$r^i$  is the maximum population growth rate for stock  $i$

$C_t^A$ : catches allocated to stock A only

$C_t^B$ : catches allocated to stock B only

$C_t^{AB}$ : catches allocated to both stocks jointly.

## Likelihood components

### Scaling parameter

Abundance indices were scaled to model predicted population sizes in each year  $i$  using the  $q$  scaling parameter, assuming that residuals are log-normally distributed (following Zerbini 2011, eqn 3). This scaling was calculated for the Bryden Brown abundance trend (Brown *et al.* 1997) and for the West Australia abundance trend (Hedley *et al.* 2011).

$$= =1 \quad 2 =1 \quad 1 \quad 2 (2)$$

### Absolute abundance

Assuming that the error distribution of the total stock size is log-normally distributed, the negative log likelihood of absolute stock size for each stock is as follows, from Zerbini et al. (2011, eqn 4). Absolute abundance for each stock are summarized in Table 1:

$$-\ln = =1 \ln \quad +\ln \quad +0.5 \cdot (\ln \quad -\ln( \quad ))^2 \quad 2 (3)$$

where:

$\hat{N}_t^i$  is the model predicted abundance in year  $i$

is observed abundance in year  $i$

$$= \ln(1 + \frac{1}{2})$$

#### Relative abundance

Since the Bryden-Brown surveys in E1 have coefficients of variance available, these are assumed to be log normally distributed. The contribution of the Bryden-Brown survey to the negative of the log-likelihood function is therefore as follows, following Zerbini et al. (2011 eqn 5). The same weighting was also used for the Hedley et al. (2011) abundance trend from West Australia.

$$-\ln L = \frac{1}{2} \ln \left( \frac{1}{2\pi} \right) + \frac{1}{2} \ln \left( \frac{1}{\sigma^2} \right) + \frac{1}{2} \left( \frac{\ln \left( \frac{y_i}{\hat{y}_i} \right)}{\sigma} \right)^2$$

is the model predicted abundance in year  $i$

is observed abundance in year  $i$

$q_j$  is the scale parameter for the abundance index  $j$

$$= \ln(1 + \frac{1}{2})$$

The total negative logarithm of the likelihood is the sum of equations (3: E1) (3: Oceania) and (4: E1) for East Australia/Oceania; (3: E1), (3: E2), (4: E1) and (4: E2) for East Australia/New Caledonia [2]; and (3) for Tonga and French Polynesia. Posterior probability distributions were calculated for  $R_{max}$ ,  $K$ ,  $N_{min}$ ,  $N_{current}$ , and population recovery status in 2013 ( $N_{2013}/K$ ).

### Three stock model

A schematic of this base case model is shown in Figure 3. East and West Australia breeding grounds both contain two feeding ground components (effectively like sub-stocks) which feed in different parts of the Southern Ocean. BSE1 has Southern Ocean feeding components  $\alpha$  (feeding in 110-130°E) and  $(1 - \alpha)$  (feeding in 130°E-180°). BSD has Southern Ocean feeding components  $\beta$  (feeding in 110-130°E) and  $(1 - \beta)$  (feeding in 80-110°E). The prior distributions of  $\alpha$  and  $\beta$  = U[0,0.3].

#### East Australia stock components:

$K^{E1} = K^{\alpha} + K^{(1-\alpha)}$  is carrying capacity of total E1 and stock components in 1900

$1$  is the annual abundance of the stock component feeding in 110-130°E in year  $t$

$1$  is the annual abundance of the stock component feeding in 130°E-180° in year  $t$

$1$  is the maximal rate of growth of E1

$1$  is E1 coastal catches

110-130 is catches south of 40S between 110-130°E

130 -180, is catches south of 40S between 130°E-180° and catches from NZ

$$-\ln L = \frac{1}{2} \ln \left( \frac{1}{2\pi} \right) + \frac{1}{2} \ln \left( \frac{1}{\sigma^2} \right) + \frac{1}{2} \left( \frac{\ln \left( \frac{y_i}{\hat{y}_i} \right)}{\sigma} \right)^2$$

$$-\ln L = \frac{1}{2} \ln \left( \frac{1}{2\pi} \right) + \frac{1}{2} \ln \left( \frac{1}{\sigma^2} \right) + \frac{1}{2} \left( \frac{\ln \left( \frac{y_i}{\hat{y}_i} \right)}{\sigma} \right)^2$$



*West Australia stock components:*

$K^D = K^D\beta + K^D(1-\beta)$  is carrying capacity of total BSD and stock components in 1900  
 is the annual abundance of the stock component feeding in 110-130°E in year  $t$   
 is the annual abundance of the stock component feeding in 80-110°E in year  $t$   
 is the maximal rate of growth of BSD  
 is BSD coastal catches  
 110-130 is catches south of 40S between 110-130°E  
 80-110 is catches south of 40S between 80-110°E

$$+1 = + \cdot \cdot 1- - 110-130 \cdot 1 + - \cdot$$

+ (7)

$$+1 = + \cdot \cdot 1- 1- - 80-110 - \cdot +$$

(8)

*Oceania stock component:*

$K^{Oe}$  is carrying capacity of Oceania in 1900  
 is the annual abundance of Oceania in year  $t$   
 is the maximal rate of growth of Oceania (BSE2, E3, F2)  
 is coastal catches from Tonga and Norfolk Island  
 130 -180 , is catches south of 40°S between 130°E-180° and catches from NZ

$$+1 = + \cdot \cdot 1- - 130 -180, \cdot + 1$$

- (9)

## RESULTS

Model results are shown in Table 1 and posterior distributions are shown in Figures 4-8. There are marked differences in the posterior estimates for East Australia, depending on whether the Southern Ocean feeding region 130°E-180 is shared with New Caledonia or with the whole Oceania population. When the latter is modelled (i.e. East Australia/Oceania), posterior current abundance is low relative to current estimates, and recovery ( $N_{2013}/K$ ) is estimated to be virtually 100%, which is inconsistent with recent observations of a continued, rapid upward trend in abundance for this breeding ground (Noad *et al.* 2011). Considering the East Australia/Oceania model, increasing the Southern Ocean catch allocation to East Australia (i.e. extending catches 20° westwards) makes no difference to posterior  $R_{max}$  and  $N_{min}$ , while slightly increasing  $K$  and  $N_{current}$  and reducing posterior recovery ( $N_{2013}/K$ ) by 5%. The impact on  $K$ ,  $R_{max}$  and  $N_{current}$  for Oceania is also minimal, but in this case median  $N_{min}$  reduces (though is still high at 1,847) and median recovery also decreases. Since the 3-stock model (Table 2) shares catches at 110-130°E between the breeding stocks in East Australia and West Australia, the posterior outcomes for East Australia in this model would be expected to be somewhere between the naïve and fringe two stock models for East Australia / Oceania (since the fringe model includes all catches between 110-130°E). This appears to be the case,

as preliminary runs from the 3-stock model (Table 2, 100 resamples) provide an intermediate median  $K$  for East Australia (median 11,738) and similar recovery levels to the 2-stock model.

The results of the two-stock model for East Australia and New Caledonia allocate many more catches from 130-180°E to East Australia (as it is the much larger of the two breeding grounds) - hence the posterior carrying capacity for East Australia is now much higher. Both breeding populations have high  $R_{max}$  (driven by relative abundance indices available for both regions).  $R_{max}$  and  $N_{min}$  are not influenced by the different catch allocations explored, while  $N_{current}$  and recovery  $N_{2013}/K$  both decrease slightly. Carrying capacity is increased for East Australia under the fringe hypothesis, as might be expected.

The results of the two-stock model for Tonga and French Polynesia give relatively low posterior  $R_{max}$  values (c 4%), with a combined estimated carrying capacity of c. 10,000 whales. Current recovery is estimated at 40% for both populations. Confidence intervals on all of these outputs are wide, reflecting the fact that no trends in abundance can be applied to these breeding grounds, and current abundance is uncertain, with large coefficients of variance.

## DISCUSSION

Results for the Oceania region suggest that, either as a single stock or as multiple stocks using different regions of the Southern Ocean feeding ground, levels of recovery of individual breeding stocks remain low at present. Some model inconsistencies were revealed by this analysis, suggesting areas where further work would be useful. For example, it may be worth extending the easterly Southern Ocean catch allocation range of East Australia to 170°W, since East Australian whales have been recaptured this far east (Rock *et al.* 2006), and the apparent high rate of growth in East Australia (Noad *et al.* 2011) is incompatible with the BSE1/Oceania model results, which suggest East Australia is very nearly recovered. The results from the 3-stock model are very preliminary and suggest very high levels of recovery (c. 99%) for another breeding ground (West Australia), although this breeding ground is still showing high apparent rates of population increase (Hedley *et al.* 2011). This suggests that other catch allocations need to be explored for this model, though it is heartening that this preliminary work suggests that including West Australia in the population assessment model seems to have little influence on posterior estimates for Oceania. A further exploration of this model could involve co-assessing West Australia, East Australia and New Caledonia.

Future work to improve this assessment could focus on improving regional abundance measurement for Oceania, and implementing mark recapture trends directly into the likelihood fitting of these models. Recent work by Carroll *et al.* (2013) demonstrates the type of mark recapture models that could be very usefully applied within this framework. A number of sensitivities of the model still remain to be investigated, including the influence of other relative and absolute abundance indices, such as regional catch per unit effort data.



## REFERENCES

- Albertson-Gibb R, Poole MM, Constantine R, Baker CS (2009) Capture-recapture estimation of abundance for humpback whales of French Polynesia (Breeding Stock F) using photo-identification. In: *Paper SC/61/SH14 presented to the IWC Scientific Committee, May 2009 (unpublished)*. 8pp. [Available from the office of this Journal].
- Allison C (2006) The Southern Hemisphere Catch Series Feb 2006. International Whaling Commission [Available from the office of this Journal].
- Branch TA, Matsuoka K, Miyashita T (2004) Evidence for increases in Antarctic blue whales based on Bayesian modelling. *Marine Mammal Science* **20**, 726-754.
- Brown MR, Field MS, Clarke ED, Butterworth DS, Bryden MM (1997) Estimates of abundance and rate of increase for East Australian humpback whales from the 1996 Land-based survey at Point Lookout, North Stradbroke Island, Queensland. In: *Paper SC/49/SH35 presented to the IWC Scientific Committee, May 1997 (unpublished)*. 15pp. [Available from the office of this Journal].
- Butterworth D, Punt AE (1995) On the Bayesian approach suggested for the assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales. *Report of the International Whaling Commission* **45**, 303-311.
- Chittleborough RG (1965) Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Australian Journal of Marine and freshwater research* **16**, 33-128.
- Constantine R, Allen J, Beeman P, *et al.* (2011) Comprehensive photo-identification matching of Antarctic Area V humpback whales. In: *Paper SC/63/SH16 presented to the IWC Scientific Committee, June 2011 (unpublished)*. 11pp. [Available from the office of this Journal].
- Constantine R, Garrigue C, Steel D, *et al.* (2010) Abundance of humpback whales in Oceania based on fluke photo-identification and DNA profiling. In: *Paper SC/62/SH18 presented to the IWC Scientific Committee, May 2010 (unpublished)*. 30pp. [Available from the office of this Journal].
- Constantine R, Jackson JA, Steel D, *et al.* (2012) Abundance of humpback whales in Oceania using photo-identification and microsatellite genotyping. *Marine Ecology Progress Series* **453**, 249-261.
- Constantine R, Russell K, Gibbs N, Childerhouse S, Baker CS (2007) Photo-identification of humpback whales (*Megaptera novaeangliae*) in New Zealand waters and their migratory connections to breeding grounds of Oceania. *Marine Mammal Science* **23**, 715-720.
- Franklin W, Franklin T, Gibbs N, *et al.* (In press) Photo-identification confirms that humpback whales (*Megaptera novaeangliae*) from eastern Australia migrate past New Zealand but indicates low levels of interchange with breeding grounds of Oceania. *Journal of Cetacean Research and Management*.
- Gales N, Double MC, Robinson S, *et al.* (2009) Satellite tracking of southbound East Australian humpback whales (*Megaptera novaeangliae*): challenging the feast or famine model for migrating whales. In: *Paper SC/61/SH17 presented to the IWC Scientific Committee, May 2009 (unpublished)*. 12pp. [Available from the office of this Journal].
- Garrigue C, Albertson R, Jackson JA (2012) An anomalous increase in the New Caledonia humpback whales breeding sub-stock E2. In: *Paper SC/64/SH6*



- presented to the IWC Scientific Committee, June 2012 (unpublished). 25pp. [Available from the office of this Journal].*
- Garrigue C, Baker CS, Constantine R, *et al.* (2011a) Movement of individual humpback whales between the breeding grounds of Oceania, South Pacific 1999-2004. *Journal of Cetacean Research and Management (Special Issue)* **3**.
- Garrigue C, Dodemont R, Steel D, Baker CS (2004) Organismal and 'gametic' capture-recapture using microsatellite genotyping confirm low abundance and reproductive autonomy of humpback whales on the wintering grounds of New Caledonia. *Marine Ecology Progress Series* **274**, 251-262.
- Garrigue C, Franklin T, Russell K, *et al.* (2011b) First assessment of interchange of humpback whales between Oceania and the east coast of Australia. *Journal of Cetacean Research and Management (Special Issue)* **3**, 269-274.
- Garrigue C, Zerbini AN, Geyer Y, *et al.* (2010) Movements of satellite-monitored humpback whales from New Caledonia. *Journal of Mammalogy* **91**, 109-115.
- Hauser N, Zerbini AN, Geyer Y, Heide-Jørgensen M-P, Clapham P (2010) Movements of satellite-monitored humpback whales, *Megaptera novaeangliae*, from the Cook Islands. *Marine Mammal Science* **26**, 679-685.
- Hedley SL, Dunlop RA, Bannister JL (2011) Evaluation of WA Humpback surveys 1999, 2005, 2008: Where to from here? In: *Report to the Australian Marine Mammal Centre on work done to 6th May, 2011*, p. 28.
- Jackson JA, Anderson M, Steel DS, *et al.* (2012) Multistate measurements of genotype interchange between East Australia and Oceania (IWC breeding sub-stocks E1, E2, E3 and F) between 1999 and 2004. In: *Paper SC/64/SH22 presented to the IWC Scientific Committee, June 2012 (unpublished). 16pp. [Available from the office of this Journal].*
- Jackson JA, Zerbini A, Clapham P, *et al.* (2006) A Bayesian assessment of humpback whales on breeding grounds of eastern Australia and Oceania (IWC Stocks E1, E2, E3 and F). In: *Paper SC/A06/HW52 submitted to the IWC southern hemisphere humpback workshop, Hobart, April 2006*.
- Jackson JA, Zerbini A, Clapham PJ, *et al.* (2008) Progress on a two-stock catch allocation model for reconstructing population histories of east Australia and Oceania. In: *Paper SC/60/SH14 presented to the IWC Scientific Committee, May 2008 (unpublished). 12pp. [Available from the office of this Journal].*
- Jackson JA, Zerbini A, Clapham PJ, *et al.* (2009) Update to SC/60/SH14: Progress on a two-stock catch allocation model for reconstructing population histories of east Australia and Oceania. In: *Paper SC/F09/SH8 submitted to the IWC Intersessional Workshop on Southern Hemisphere Humpback Whale Modelling Assessment Methodology. 12pp. [Available from the office of this Journal].*
- Noad M, Dunlop RA, Paton D, Kniest H (2011) Abundance estimates of the east Australian humpback whale population: 2010 survey and update. In: *Paper SC/63/SH22 presented to the IWC Scientific Committee, May 2011 (unpublished). 12pp. [Available from the office of this Journal].*
- Noad MJ, Dunlop RA, Paton D, Cato DH (2008) An update of the east Australian humpback whale population (E1) rate of increase. In: *Paper SC/60/SH31 presented to the IWC Scientific Committee, May 2008 (unpublished). 13pp. [Available from the office of this Journal].*
- Olavarria C, Baker CS, Garrigue C, *et al.* (2007) Population Structure of South Pacific humpback whales and the origin of the eastern Polynesian breeding grounds. *Marine Ecology Progress Series* **330**, 257-268.



- Paton DA, Brooks L, Burns D, *et al.* (In Press) Abundance estimate of east coast Australian humpback whales (*Megaptera novaeangliae*) in 2005 estimated using multi-point sampling and capture-recapture analysis *Journal of Cetacean Research and Management*.
- Paton DA, Clapham PJ (2006) An assessment of Southern Hemisphere humpback whale population structure and migratory interchange based on Discovery mark data. In: *Paper SC/A06/HW33 submitted to the IWC southern hemisphere humpback workshop, Hobart, April 2006*.
- Robbins J, Dalla Rosa L, Allen JM, *et al.* (2011) Return movement of a humpback whale between the Antarctic Peninsula and American Samoa: a seasonal migration record. *Endangered Species Research* **13**, 117-121.
- Rock J, Pastene LA, Kaufman G, *et al.* (2006) A note on East Australia Group V Stock humpback whale movement between feeding and breeding areas based on photo-identification. *Journal of Cetacean Research and Management* **8**, 301-305.
- South Pacific Whale Research Consortium (2008) Report of the Annual Meeting of the South Pacific Whale Research Consortium. In: *Paper SC/60/SH21 presented to the IWC Scientific Committee, May 2008 (unpublished)*. 14pp. [Available from the office of this Journal].
- Steel D, Garrigue C, Poole M, *et al.* (2008) Migratory connections between humpback whales from South Pacific breeding grounds and Antarctic feeding areas based on genotype matching. In: *Paper SC/60/SH13 presented to the IWC Scientific Committee, May 2008 (unpublished)*. 9pp. [Available from the office of this Journal].
- Zerbini AN (2011) A Bayesian Assessment of the Conservation Status of Humpback Whales (*Megaptera novaeangliae*) in the Western South Atlantic *Journal of Cetacean Research and Management (Special Issue)* **3**, 131-144.
- Zerbini AN, Clapham PJ, Wade PR (2010) Assessing plausible rates of population growth in humpback whales from life-history data. *Marine Biology*.



Catch hypothesis	A	B	C	D	C
Type	Naïve	Fringe	Naïve	Fringe	Naïve
Stock 1:	<b>East Australia</b>	<b>East Australia</b>	<b>East Australia</b>	<b>East Australia</b>	<b>Tonga</b>
N <sub>abs</sub>	N2007=9,683 CV=0.13	N2007=9,683 CV=0.13	N2007=9,683 CV=0.13	N2007=9,683 CV=0.13	N2005=1,840 CV=0.23
I. Abundance	Bryden Brown	Bryden Brown	Bryden Brown	Bryden Brown	N/A
<b>Posteriors</b>					
R <sub>max</sub>	10.5% 10.2-10.6%	10.5% 10.2-10.6%	9.3% 8.9-9.9%	9.12% 8.54-9.71%	4.0% 0.1-9.8%
K	9,227 8,305-10,674	13,613 12,574-15,324	28,250 25,195-28,671	34,506 32,967-35,181	6,296 1,761-10,807
N <sub>min</sub>	247 180-385	281 249-337	344 252-448	363 239-508	491 109-1,830
N <sub>current</sub>	7,101 6,342-8,202	10,169 9,304-11,574	10,001 7,423-13,832	9710 6767-13646	1,807 1,487-2,181
N <sub>2013</sub> /K	0.99 0.98-0.99	0.94 0.91-0.96	0.60 0.47-0.77	0.49 0.36-0.65	0.40 0.17-1.00
Stock 2:	<b>Oceania</b>	<b>Oceania</b>	<b>New Caledonia</b>	<b>New Caledonia</b>	<b>French Polynesia</b>
N <sub>abs</sub>	N2005=4,329 CV=0.12	N2005=4,329 CV=0.12	N2008=562 CV=0.19	N2008=562 CV=0.19	N2005=934 CV=0.64
I. Abundance	N/A	N/A	Garrigue et al. (2012)	Garrigue et al. (2012)	N/A
R <sub>max</sub>	2.8% 0.1-8.9%	2.4% 0.1-8.6%	10.3% 6.5-10.6%	9.83% 5.85-10.56%	3.9% 0.2-9.7%
K	37,194 29,318-48,014	36,891 28,165-46,518	3,503 3,319-7,221	4,077 3,840-6,089	3,269 932-9,244
N <sub>min</sub>	2893 1841-5498	1847 236-4365	14 10-89	14 7-76	280 62-1,065
N <sub>current</sub>	4,201 3,442-4,983	4,265 3,532-4,987	634 475-953	530 340-838	962 651-1,500
N <sub>2013</sub> /K	0.26 0.11-0.98	0.14 0.09-0.32	0.30 0.17-0.39	0.21 0.12-0.34	0.41 0.10-1.00

**Table 1. Base case 2-stock results for Oceania population assessment. For catch hypotheses see Figure 2. N<sub>current</sub> represents abundance in the year for which a measure of absolute abundance is available.**



Type	Naive	Naive	Naive
Stock 1:	West Australia	East Australia	Oceania
N <sub>abs</sub>	N2008=28,830 CV=0.13	N2007=9,683 CV=0.13	N2005=4,329 CV=0.12
Stock component	$\beta$ : 0.17 (0.00-0.29)	$\alpha$ : 0.16 (0.01-0.29)	
R <sub>max</sub>	6.58% (0.86-10.28%)	7.04% (4.77-10.42%)	3.26% (0.10-7.32%)
K	38,927 (25,512-58,585)	11,738 (9,162-16,395)	35,869 (28,275-46,862)
N <sub>current</sub>	33,168 (16,398-42,673)	8,340 (4,867-12,563)	4,532 (2,311-6,132)
N <sub>2013</sub> /K	1.00 (0.44-1.00)	0.79 (0.35-0.98)	0.10 (0.03-0.28)

**Table 2. Base case 2-stock results for Oceania population assessment. For catch hypothesis see Figure 3.**



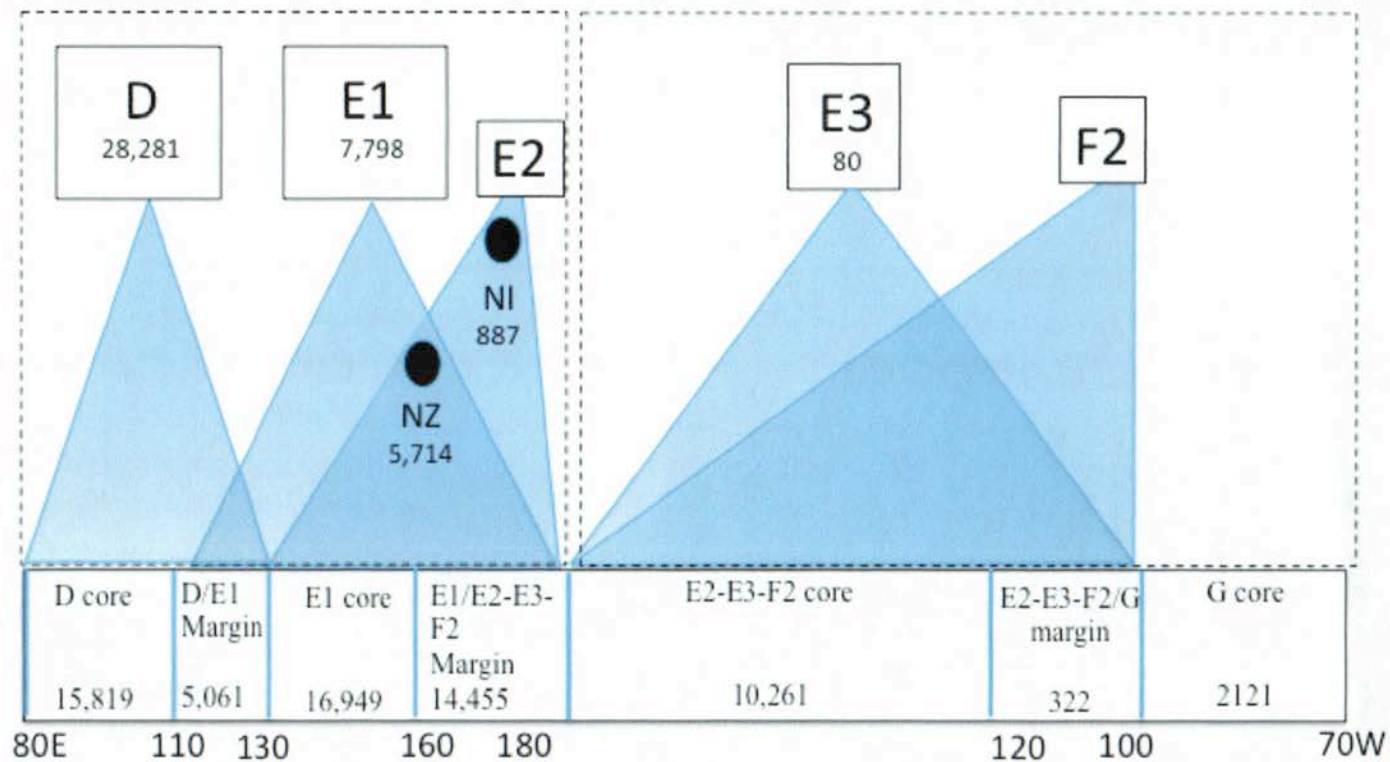


Figure 1. 20<sup>th</sup> century catches of humpback whales between 80°E-70°W (Allison per comm), with each breeding ground shown in a black box. Boxes at the base of the diagram show catches taken from the Southern Ocean (>60°S) across the longitude of the region.



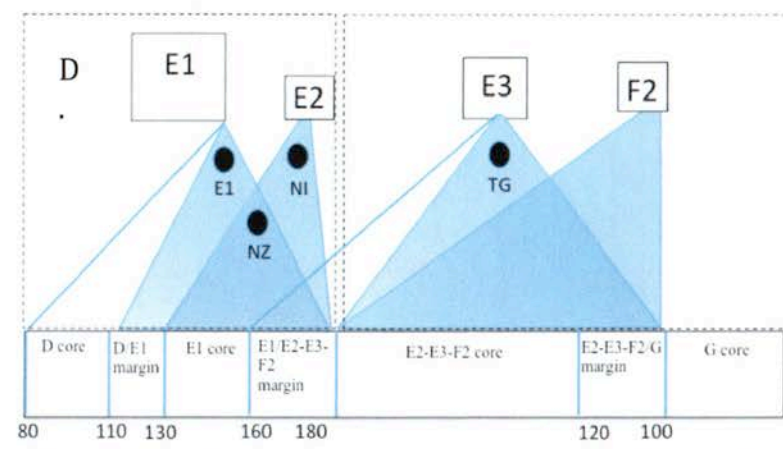
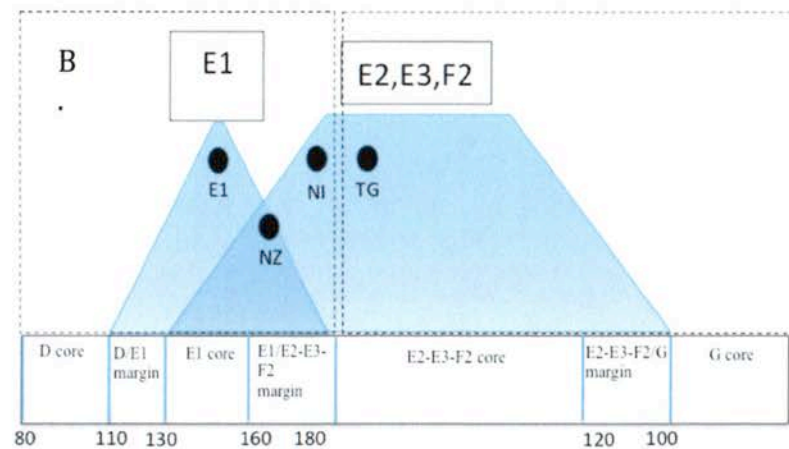
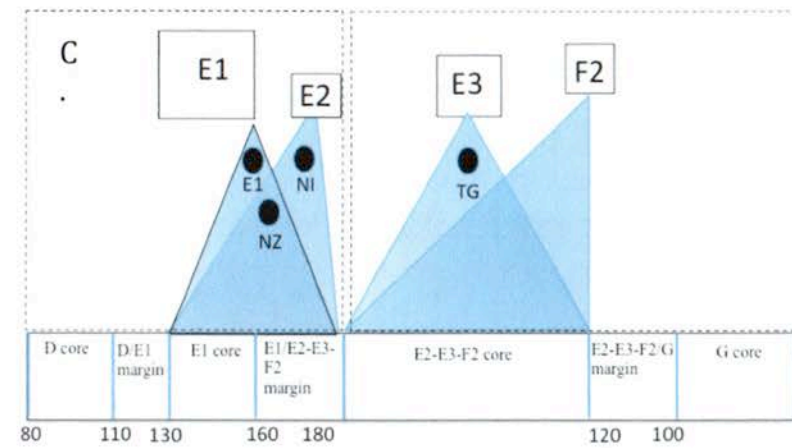
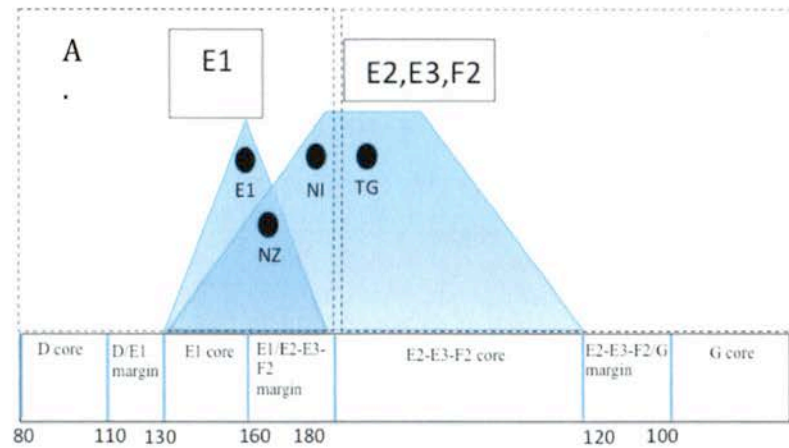


Figure 2A-D: Catch allocations for 2-stock models developed for the East Australia-Oceania assessment. Black circles represent catches north of 40°S (New Zealand, Norfolk Island, Tonga and coastal East Australia (BSE1))



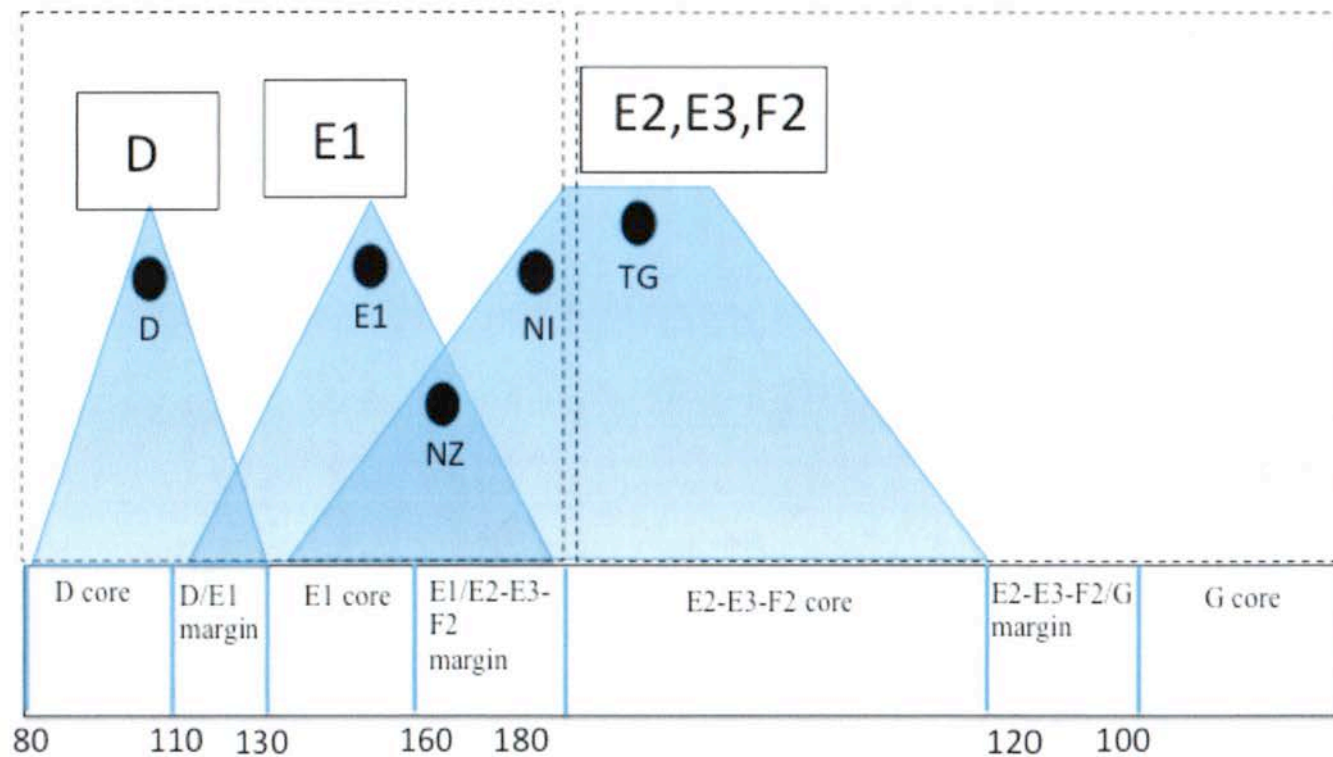


Figure 3. Catch allocation scheme for 3-stock model for West Australia, East Australia and Oceania



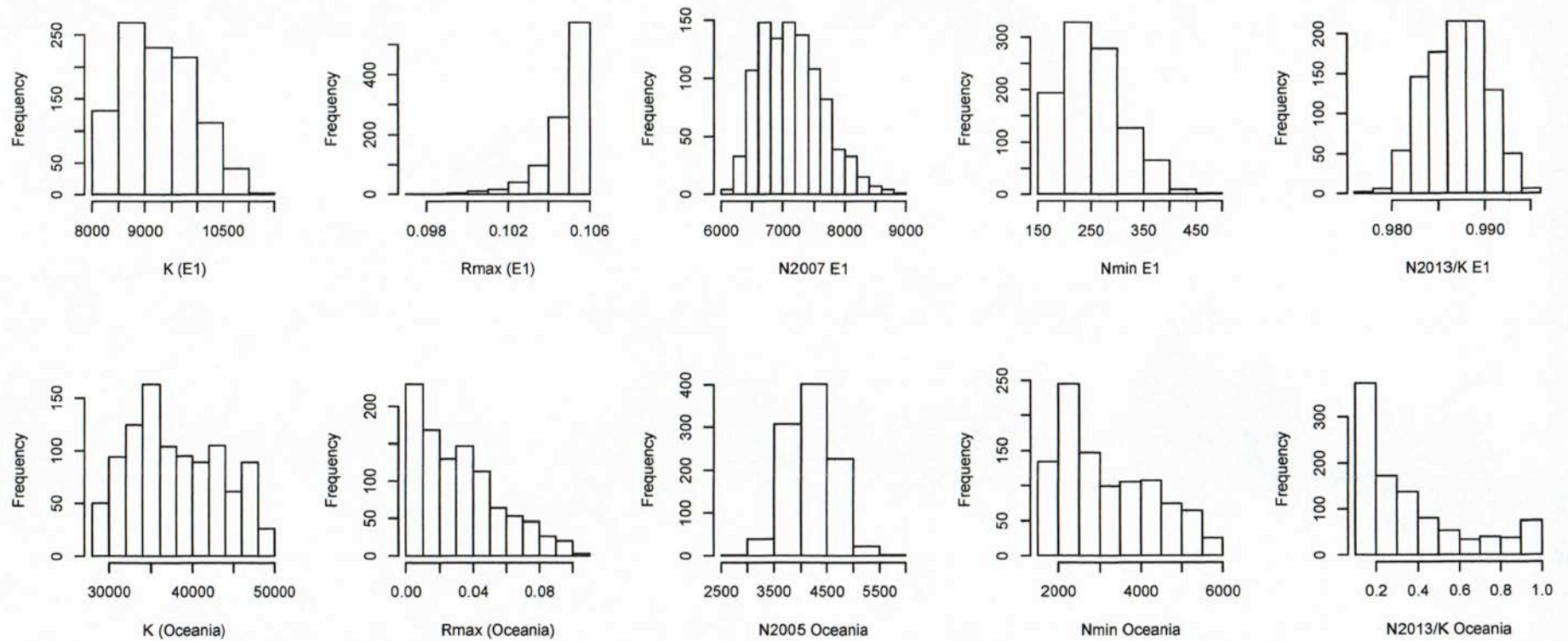


Figure 4. Posterior distributions of parameters from 2-stock 'naïve' model of catch allocation for East Australia and Oceania



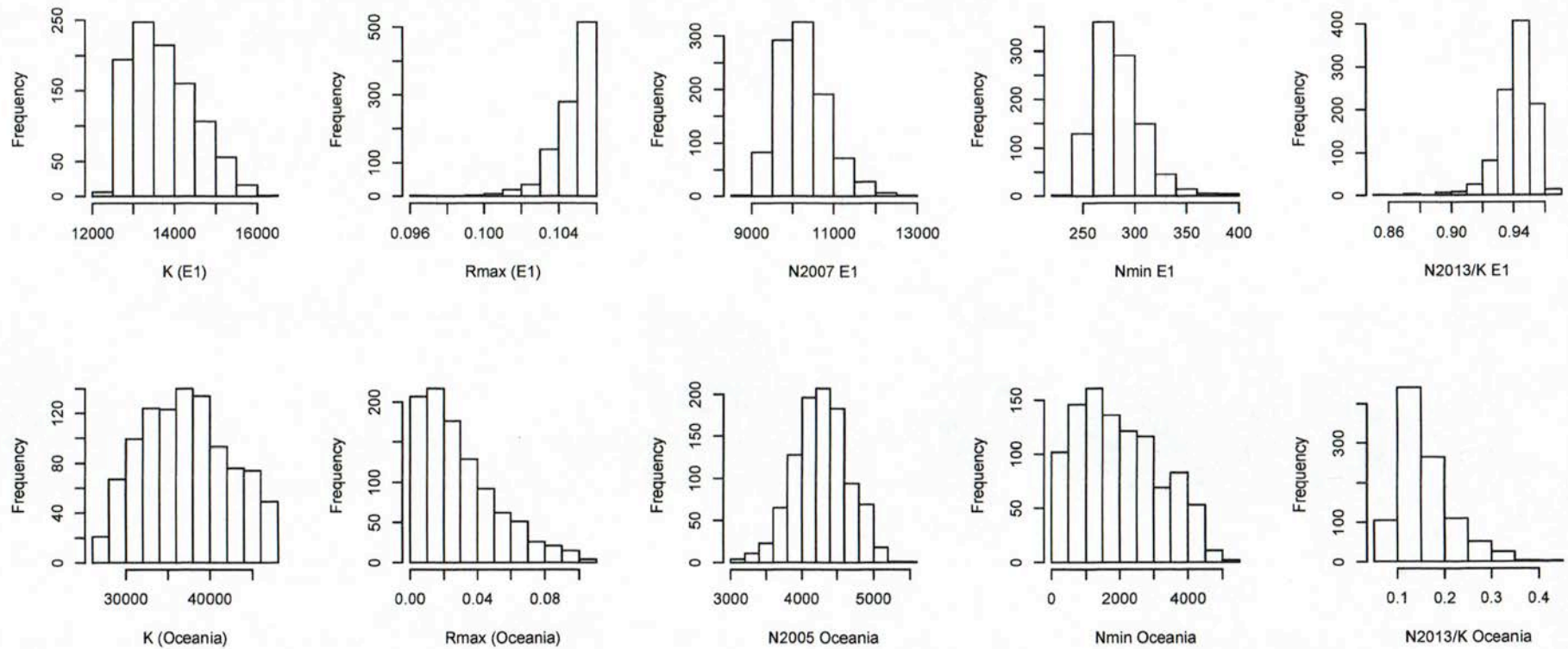


Figure 5. Posterior distributions of parameters from 2-stock 'fringe' model of catch allocation for East Australia and Oceania



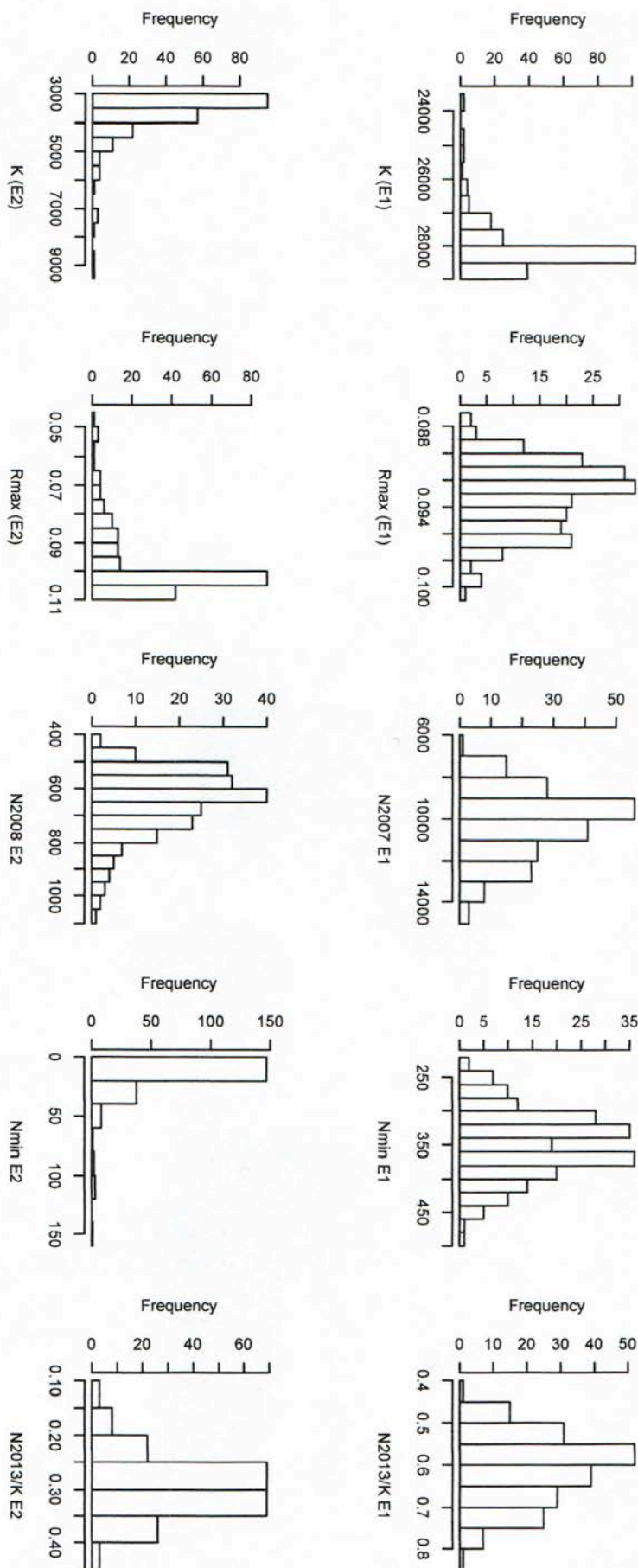


Figure 6. Posterior distributions of parameters from 2-stock 'naïve' model of catch allocation for East Australia and New Caledonia

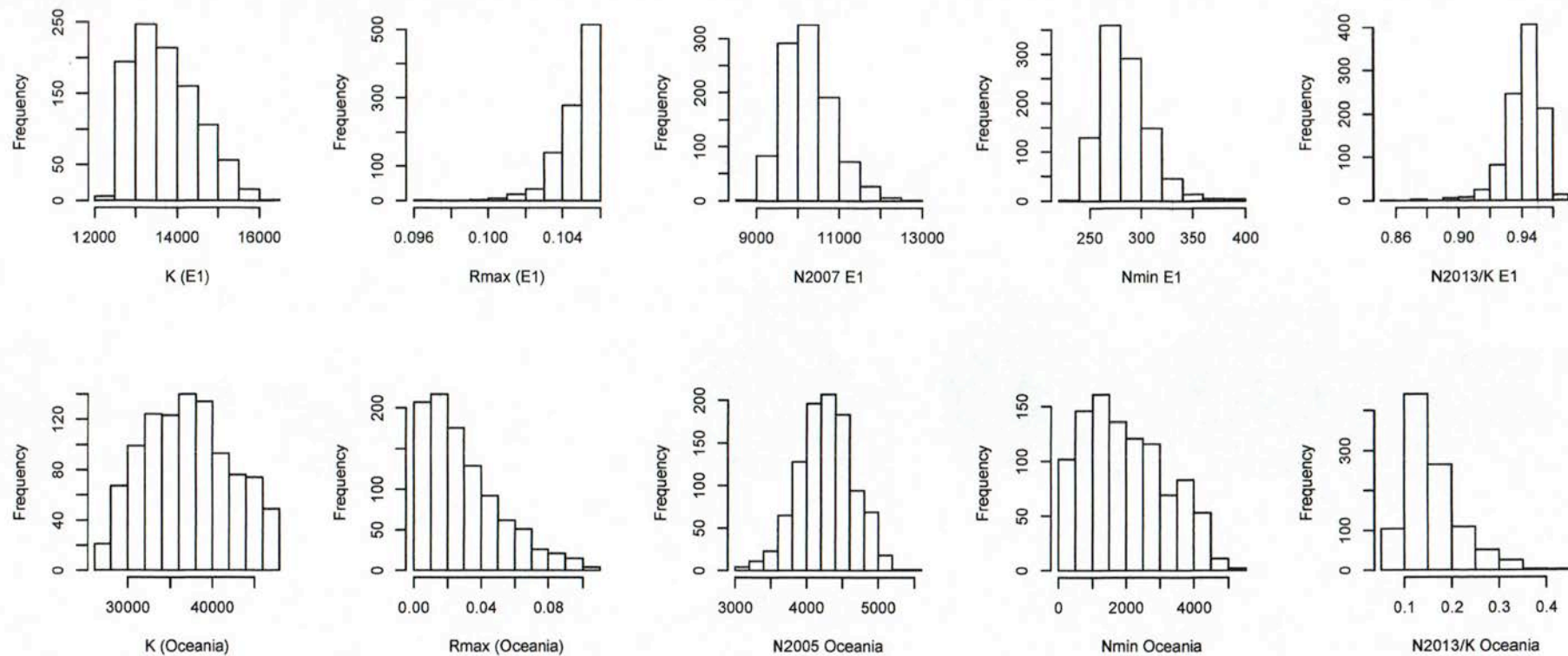


Figure 7. Posterior distributions of parameters from 2-stock 'fringe' model of catch allocation for East Australia and New Caledonia



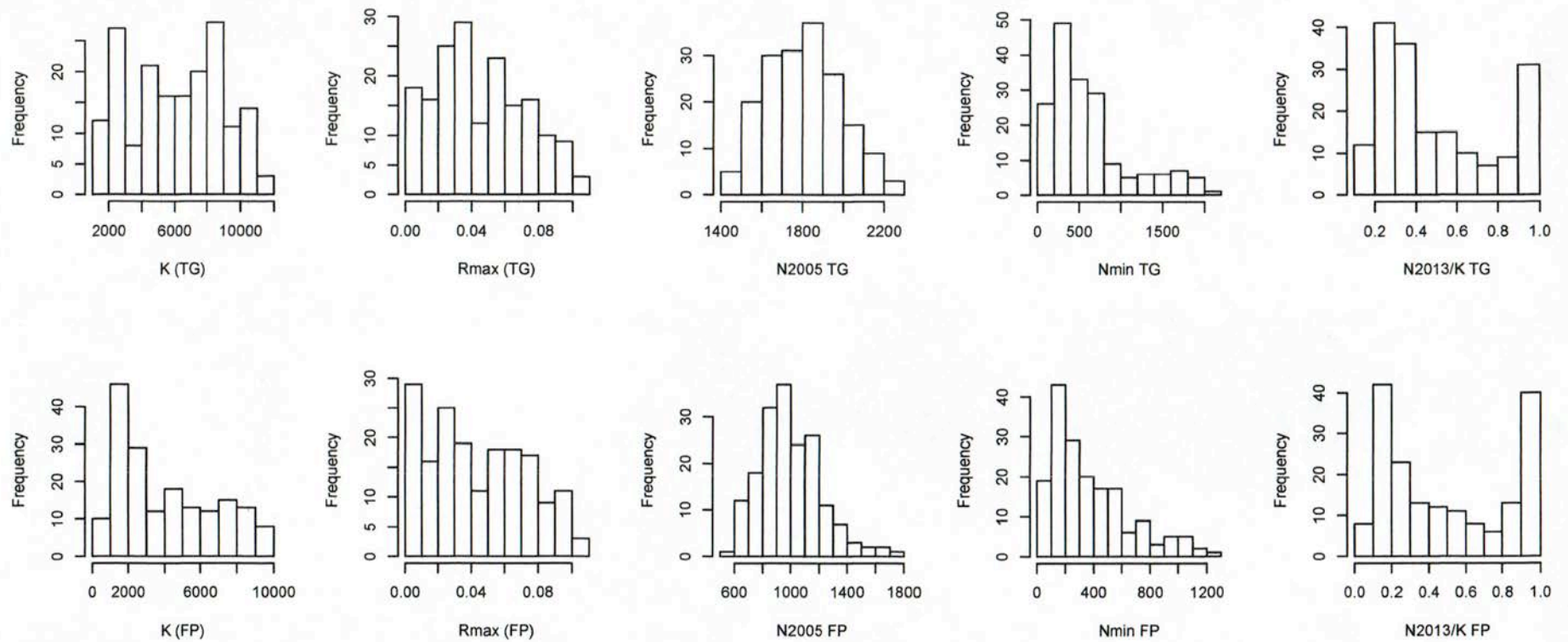
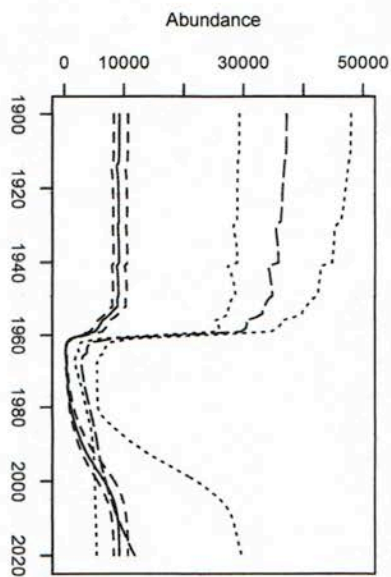
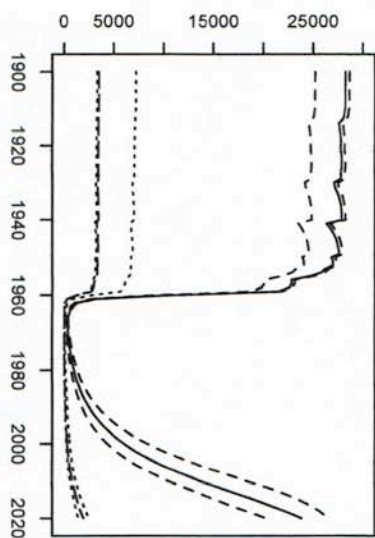


Figure 8. Posterior distributions of parameters from 2-stock 'naive' model of catch allocation for Tonga and French Polynesia

E1/Oceania



E1/E2



E3/F2

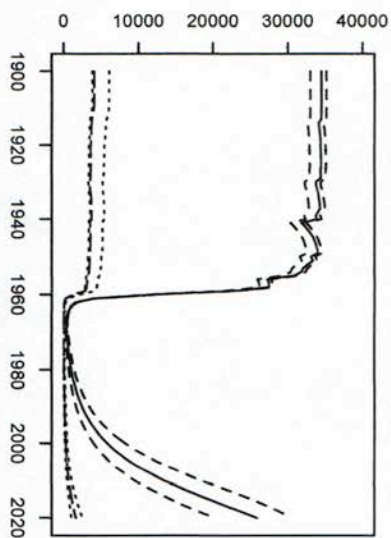
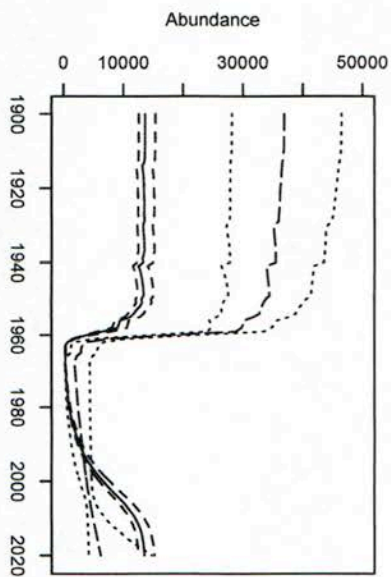
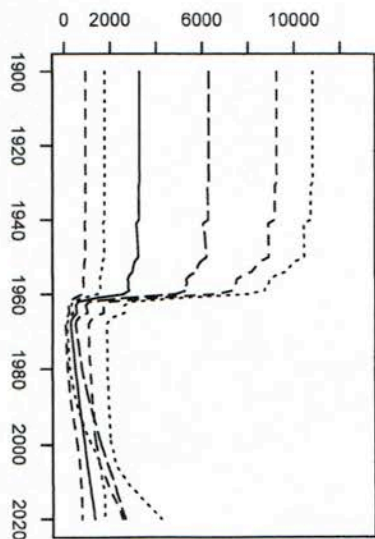




Figure 9. Abundance trajectories from 1900-2020 for 2-stock models with naïve (top row) and fringe (bottom row) catch allocations. E1/F2=black line, Oceania/E2/E3 = long dashes. Upper and lower percentiles are shown with small dashed lines.