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

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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. These stocks also share a history of intensive exploitation resulting in the removal of 41,987 whales across these feeding grounds and 14,479 whales on their breeding grounds and migratory corridors between 1900-1978. In order to explore the population history and develop a population assessment for these populations, 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 to breeding stocks in a ratio according to annual model predicted abundance on each breeding ground. A number of two-stock scenarios are explored: East Australia / New Caledonia (shared Southern Ocean feeding ground 130°E-180°), Tonga / French Polynesia (shared Southern Ocean feeding ground 180-120°W), East Australia / Oceania (New Caledonia, Tonga and French Polynesia combined), and preliminary runs for a combined West Australia (BSD) / East Australia / Oceania three-stock model. Sensitivity of models to catch allocation scenarios and other abundance indices are explored. All model results suggest that the breeding grounds in Oceania have not yet recovered (median N_{2013}/K less than 50% for all breeding grounds).

INTRODUCTION

The Southern Ocean bordering the South Pacific spans 130° of longitude (130°E-100°W) and was once feeding habitat for large numbers of humpback whales. Prior to international protection and the end of illegal Soviet whaling, catch records show 41,987 humpback whales killed south of 60°S and 14,479 killed on migration and in coastal breeding grounds (Allison, IWC catch database). During the austral winter, whales from these feeding grounds migrate north to a number of South Pacific breeding grounds, namely East Australia, New Caledonia, Tonga and French Polynesia. 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 its geographical 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 profiles via biopsy sampling. Less regular surveys were also conducted near 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). 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 (Olavarría *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=14,522 in 2010, Noad *et al.* 2011a; Noad *et al.* 2011b) and rapidly increasing (10.9%, 95% CI 10.5-11.3%, Noad *et al.* 2011b).

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. Humpback song data collected from breeding grounds also supports a similar pattern of interchange, showing regular, easterly movement of new song motifs from East Australia to French Polynesia across the South Pacific over a number of years (Garland *et al.* 2011). Garrigue *et al*. (2012) have 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. In combination, this evidence suggests that there is ongoing interchange among all breeding grounds, East Australia included. Therefore, grouping Oceania as one entity for population assessment may fail to accurately capture the population histories of these semi-autonomous and far-flung breeding grounds.

A great deal of information has been published or reported recently on breeding ground-feeding ground connections in the South Pacific, which means we can now develop new Antarctic 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), allow us to develop a more in-depth population assessment of the Oceania breeding grounds by use of two-stock population models of neighbouring breeding grounds, and also a preliminary three-stock model to include West Australia to the west. Previously, we used a two stock model to measure the population trajectories of Oceania and East Australia, treating each as a single entity (Jackson *et al.* 2006; Jackson *et al.* 2008). However the recent evidence for restricted interchange within the breeding grounds of Oceania, coupled with evidence that there may be an increasing trend in abundance in New Caledonia, led us to explore stock models for individual Oceania breeding grounds and utilize the new information on feeding-breeding ground connectivity to develop breeding ground specific catch allocation hypotheses.

Here we develop a two-stock model for East Australia and New Caledonia, exploring the impact of these breeding grounds sharing a common Southern Ocean feeding ground over 130°E-180. We also develop a two-stock model for Tonga and French Polynesia, assuming a shared common feeding ground from 180-120°W. We compare these models with a two-stock model for East Australia and Oceania, with shared catch allocation across the region 130°E-120°W. In turn we examine the impact of including West Australia in this population model.

In order to allocate feeding ground catches to multiple stocks using the same area in a way that realistically reflects their abundance, 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. A simple Markov Chain type FITTER model was therefore developed 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 estimated recent abundance values (N_{est}) for each stock with the highest likelihood were retained. For example in East Australia, the N_{2010} survey based abundance estimate from Noad *et al.* (2011a) is used to put boundaries on the minimum and maximum allowable model-predicted abundances in 2010, so N_{2010} is the N_{est} constraint for East Australia in this case. The sample sets giving the maximum likelihood values, (the sum of all likelihoods for absolute abundance and indices of relative abundance for each stock), were retained after searching 35,000 prior samples. This was repeated 1,000 times to generate 1,000 posterior samples for each stock assessment scenario. This approach is computationally tractable for two stock models but runs very slowly for models containing more than two stocks, hence the results presented here are currently limited to two-stock model analyses, with some preliminary three-stock results given.

METHODS AND RATIONALE

Catch Allocation scenarios

In this study we only consider humpbacks killed during the period of modern whaling, i.e. since 1904. Although humpback whales were also the target of 19th century whaling in parts of the South Pacific, e.g., Tonga (Ruhen 1966), these catches were not considered sufficiently large to have depleted any of the populations prior to 1904. Whaling catches have been compiled by the IWC by 10° longitudinal regions (Allison 2006). In 2009 a new catch allocation hypothesis was proposed for the South Pacific feeding grounds (IWC 2010), with 'nucleus' feeding ground regions designated as 130-160°E for East Australia and 180-120°W for Oceania. These have been used as a guide for base case catch allocation scenarios, with one variation. Firstly, since the only linkage between New Caledonia and the Southern Ocean occurs to the east of 180° and there is plenty of evidence now linking East Australia as far east as 180°, we chose the 'core' catch allocation region for East Australia/New Caledonia to be 130°E-180 rather than 130-160°E for the two stocks. This thus includes the 'fringe' region 160°E-180° proposed in IWC (2010). In the 'fringe' allocation for our East Australia / New Caledonia two-stock model, the easterly range is extended by 10° to 170°W. Figure 1 shows how catches have been allocated with respect to 'core' and 'fringe' areas.

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 East Australia spans the region 130°E-180°, though 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 circa 171°W (Steel *et al.* 2008), to the east of the 'core' East Australian feeding ground (IWC 2010). 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 neighbours 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 11.8% (Zerbini *et al.* 2010). Given the proximity, size and well-documented rapid trend in abundance in neighbouring East Australia (Noad *et al.* 2011b), 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 to a 'fringe' catch scenario, where the westerly range extends to 110°E and easterly range to 170°W, also explored (Figure 1C). Catches unique to each region were also imposed, with coastal catches from Australia assigned to East Australia, catches from Norfolk Island assigned to New Caledonia and catches from New Zealand jointly assigned to both East Australia and New Caledonia in the density dependent fashion described for the pelagic feeding catches (Constantine *et al.* 2007; Franklin *et al.* 2012; 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 have 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 genetic re-sight has been made with Colombia (South Pacific Whale Research Consortium 2008), and one photo-identification match has been made with the Antarctic Peninsula suggesting possibly that Area I is used as a feeding ground. This population shows significant differentiation from Colombia, so is likely to primarily use feeding grounds in Area VI. However very few humpback whale observations are available from Area VI with which to match to breeding grounds at that latitude.

Consequently, with limited information available, we therefore allocate catches from 180-120°W to both Tonga and French Polynesia (the IWC 2010` 'core' region for Oceania), and also explore the impact of including additional catch allocation from the Oceania 'fringe' regions 170°E-180 to the west and 120-100°W (Figure 1D).

Two Stock scenarios

The following two-stock scenarios were therefore implemented:

Neighbouring breeding stocks	'Naïve' shared catches	'Fringe' shared catches
East Australia / New Caledonia	130°E-180° (S60S) New Zealand (N40S)	110°E-180° (S60S) New Zealand (N40S)
Tonga / French Polynesia	180°-120°W	170°W-100°W
East Australia / Oceania	130°E-120°W(S60S) New Zealand (N40S)	110°E-100°W(S60S) New Zealand (N40S)

Three-stock scenarios

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 β whales on the West Australian breeding ground to a shared BSD/BSE1 feeding ground at 110-130°E, and α whales on the East Australian breeding ground to this feeding ground (Figure 2). Both Chittleborough (1965) through Discovery Tags and Gales *et al.* (2009) through satellite telemetry revealed movement of humpbacks to this Southern Ocean region from their respective coasts, suggesting some mixing of breeding stocks across this feeding area. In this model, (1- α) E1 whales share a common feeding ground with (i) Oceania between 130°E-120°W or (ii) New Caledonia between 130°E-180°, while (1- β) West Australian whales feed in the core BSD feeding area 80-110°E. The α and β priors were chosen from a uniform distribution between 0-0.5, representing between 0-50% of the total initial carrying capacity of BSD and BSE1 respectively.

Population Dynamic 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 bounds. 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[0.073,0.04]). This is the average population growth rate based on a Monte Carlo simulation using observed life history data for humpback whales worldwide (Zerbini *et al.* 2010).

Posterior distributions from the density-dependent two-stock logistic model were obtained using a simple Markov Chain. First 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 five 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.

Abundance Estimates

Multiple measurements of absolute abundance are available from East Australia (Noad *et al.* 2011a; Noad *et al.* 2008; Paton *et al.* 2012). For the base case model, we used the Noad *et al.* (2011a) absolute abundance in the likelihood weighting of trajectories (Table 1). The prior on 2010 abundance (N_{est}) 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), and thus possibly represents 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 (Table 1).

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 three-stock model, abundance for West Australia was taken from Hedley *et al.* (2011), who calculated N=28,830 in 2008 (CV=0.13) from aerial and land based surveys of Shark Bay, Western Australia.

Nmin

The N_{min} constraint has not been implemented in these population models but will be explored in future analyses. Due to the high haplotypic diversity on the Oceania breeding grounds, and low numbers of private haplotypes within breeding grounds, it is hard to identify the number of lineages unique to each breeding ground as regular interchange has been documented. For Oceania a minimum constraint could be imposed based on total N=115 haplotypes (Olavarría *et al.* 2007) and for East Australia N=42 haplotypes have been identified (Olavarría *et al.* 2006).

Estimates of Trends

Indices of abundance are available from East Australia from the Bryden and Brown surveys (1981-2004) and from a longer survey by Paterson, Paterson and Cato (1984-2007). Because a CV is only available from the Bryden and 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 two-stock model. For the three-stock model, abundance for West Australia was taken from Hedley et al. (2011), who reported regional relative abundances from 1999, 2005 and 2008 (Table 1).

Two-stock model construction

$$N_{t+1}^{A} = N_t^A + N_t^A \cdot R_{max}^A \cdot \left[1 - \left(\frac{N_t^A}{K^A}\right)^z\right] - \frac{C_t^{AB} \cdot N_t^A}{N_t^A + N_t^B} - C_t^A \quad (1)$$

$$N_{t+1}^{B} = N_t^B + N_t^B \cdot R_{max}^B \cdot \left[1 - \left(\frac{N_t^B}{K^B}\right)^z\right] - \frac{C_t^{AB} \cdot N_t^B}{N_t^A + N_t^B} - C_t^B \quad (2)$$

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_{max}^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 *et al.* 2011, eqn 3). This scaling was calculated for the Bryden and Brown abundance trend (Brown *et al.* 1997) and for the West Australia abundance trend (Hedley *et al.* 2011).

$$q = e^{\left[\frac{\sum_{i=1}^{n} \frac{ln\left[\frac{IA_i^{obs}}{N_i^{pred}}\right]}{\sigma_i^2}}{\sum_{i=1}^{n} \frac{1}{\sigma_i^2}}\right]} \quad (3)$$

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:

$$-\ln L = \sum_{i=1}^{n} \left[\ln\left(\sigma_{N_i^{obs}}\right) + \ln\left(N_i^{obs}\right) + 0.5 \cdot \frac{(\ln\left(N_i^{pred}\right) - \ln\,(N_i^{obs}))^2}{\sigma_{N_i^{obs}}^2} \right] \quad (4)$$

where:

N_i^{pred} is the model predicted abundance in year *i*

N_i^{obs} is observed abundance in year *i*

$$\sigma_{N_i^{obs}} = \sqrt{\ln\,(1 + CV_{N_i^{obs}}^2)}$$

Relative abundance

Since the Bryden and Brown surveys in East Australia have coefficients of variance available, these are assumed to be log normally distributed. The contribution of the Bryden and 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.

$$-\ln L = \sum_{i=1}^{n} \sum_{j=1}^{m} \left[\ln\left(\sigma_{IA_{ij}^{obs}}\right) + \ln\left(IA_{ij}^{obs}\right) + 0.5 \cdot \frac{(\ln\left(q_j \cdot N_i^{pred}\right) - \ln\,(IA_{ij}^{obs}))^2}{\sigma_{IA_{ij}^{obs}}^2} \right] \quad (5)$$

N_{ij}^{pred} is the model predicted abundance in year *i*

IA_{ij}^{obs} is observed abundance in year *i*

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

$$\sigma_{IA_{ij}^{obs}} = \sqrt{\ln (1 + CV^2_{IA_{ij}^{obs}}}$$

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 α (feeding in 110-130°E) and (1- α) (feeding in 130°E-120W° with whales from Oceania), each of which follow separate population trajectories with carrying capacities of α and (1- α) respectively. BSD has Southern Ocean feeding components β (feeding in 110-130°E) and (1-β) (feeding in 80-110°E). As above, these feeding components also follow separate population trajectories, with initial carrying capacities set as β and (1- β). The prior distributions of α and β = U[0,0.5]. Preliminary results of this model were reported for 1 million generations only (200 posterior samples).

East Australia stock components:

$K^{E1} = K^{E1}\alpha + K^{E1}(1\text{-}\alpha)$ is carrying capacity of total E1 and stock components in 1900
N_t^{E1a} is the annual abundance of the stock component feeding in 110-130°E in year t
N_t^{E1b} is the annual abundance of the stock component feeding in 130°E-180° in year t
R_{max}^{E1} is the maximal rate of growth of E1
C_t^{E1} is E1 coastal catches
$C_t^{110-130E}$ is catches south of 40S between 110-130°E
$C_t^{130E-180,NZ}$ is catches south of 40S between 130°E-180° and catches from NZ

$$N_{t+1}^{E1a} = N_t^{E1a} + N_t^{E1a} \cdot R_{max}^{E1} \cdot \left[1 - \left(\frac{N_t^{E1a}}{K^{\alpha}}\right)^z\right] - \frac{C_t^{110-130E} \cdot N_t^{E1a}}{N_t^{E1a} + N_t^{Da}} - \frac{C_t^{E1} \cdot N_t^{E1a}}{N_t^{E1a} + N_t^{E1b}} \quad (6)$$

$$N_{t+1}^{E1b} = N_t^{E1b} + N_t^{E1b} \cdot R_{max}^{E1} \cdot \left[1 - \left(\frac{N_t^{E1b}}{K^{(1-\alpha)}}\right)^z\right] - \frac{C_t^{130E-180,NZ} \cdot N_t^{E1b}}{N_t^{E1b} + N_t^{Oc}} - \frac{C_t^{E1} \cdot N_t^{E1b}}{N_t^{E1a} + N_t^{E1b}} \quad (7)$$

West Australia stock components:

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

$$N_{t+1}^{Da} = N_t^{Da} + N_t^{Da} \cdot R_{max}^{D} \cdot \left[1 - \left(\frac{N_t^{Da}}{K^{\beta}}\right)^z\right] - \frac{C_t^{110-130E} \cdot N_t^{Da}}{N_t^{E1a} + N_t^{Da}} - \frac{C_t^{D} \cdot N_t^{Da}}{N_t^{Da} + N_t^{Db}} \quad (8)$$

$$N_{t+1}^{Db} = N_t^{Db} + N_t^{Db} \cdot R_{max}^{D} \cdot \left[1 - \left(\frac{N_t^{Db}}{K^{(1-\beta)}}\right)^{z}\right] - C_t^{80-110E} - \frac{C_t^{D} \cdot N_t^{Db}}{N_t^{Da} + N_t^{Db}} \quad (9)$$

Oceania stock component:

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

$$N_{t+1}^{Oc} = N_t^{Oc} + N_t^{Oc} \cdot R_{max}^{Oc} \cdot \left[1 - \left(\frac{N_t^{Oc}}{K^{Oc}}\right)^{z}\right] - \frac{C_t^{130E-180,NZ} \cdot N_t^{Oc}}{N_t^{Oc} + N_t^{E1b}} - C_t^{Oc} \quad (10)$$

RESULTS

Model results are shown in Tables 2-4 and posterior distributions are shown in Figures 3-10. The high posterior R_{max} values for East Australia in Table 2 reflected the Bryden and Brown abundance index in the likelihood. A normally distributed R_{max} prior (7.3%, Zerbini *et al.* 2010) was used for Oceania. However the posterior estimate had a median value of 4.3%, reflecting a skew towards lower values in the distribution. There was not much difference between the naïve and fringe catch allocations in terms of posterior estimates, aside from an increase in *K* and parallel, small decrease in population recovery. These models were consistent with Jackson *et al.* (2009) in suggesting a median 50% recovery of East Australia and 40% recovery of Oceania in 2013, but confidence intervals on the latter are wide as the peak of the distribution (at 25%, see Figure 4) is not pronounced. The East Australia/ Oceania results had a high *K* for East Australia (median 39-42,000 whales), because the largest amount of catch is allocated to East Australia in this model (i.e. 130°E-120°W). The results are broadly similar to those of Müller and Butterworth (2012) in terms of recovery, though estimated *K* for East Australia is higher, due to a slightly lower R_{max} and probably also to the different way that catch is allocated in this model. All results gave N_{min} values much higher than the total numbers of haplotypes currently estimated for each region, suggesting that applying this constraint will not have a strong impact on modeling trajectories.

The East Australia / New Caledonia region is assumed to span up to 110°E-170°W, so contains less catches than in the East Australia / Oceania model. Consequently, estimated *K* was lower for East Australia (median 26-31,000, Figure 5) and recovery higher- ranging 63-73% depending on the catch allocation model and New Caledonia abundance metric used. The New Caledonian abundance trend (Garrigue *et al.* 2012) was used as a likelihood weighting in all models, yielding a posterior R_{max} of 6.4-7.5%. This is probably because N_{min} is extremely low, ranging from 52 to 64 individuals. Interestingly the New Caledonian recovery levels do not seem to depend on whether N_{2001} or N_{2008} are used in the likelihood fitting- ranging from 13-14% across both models (Figures 5 and 7). The fringe model of catch allocation increases estimated recovery due to a combination of increased R_{max} and slightly increased abundance (Figure 6). Estimated N_{min} for New Caledonia was very low (median values all less than 100 individuals). This may not be biologically unrealistic since the population is very small, but a high number of haplotypes (N=61) has been found in New Caledonia (Olavarría *et al.* 2007), suggesting that more haplotype lineages may have survived the bottleneck than the N_{min} estimates would predict.

There was no trend information available to inform the population trajectories for Tonga and French Polynesia, hence the normally distributed prior on R_{max} was used (Zerbini *et al.* 2010).

Posterior estimates of R_{max} were 4.3-4.5% for Tonga and 3.6-3.9% for French Polynesia, but with wide confidence intervals suggesting the prior was fairly uninformative for both populations (Figure 8). There were wide confidence intervals on all estimates, reflecting the fact that current abundance estimates have large CVs and there is no additional information to inform the likelihood. Estimated median carrying capacity was 5,000-9,000 for Tonga and 4,000-5,700 for French Polynesia depending on the catch allocation model. Since a large number of catches were taken from this region over the whaling period relative to abundance, estimated median recovery on both breeding grounds is low (<50%), although posterior distributions (Figures 8 and 9) show that these posterior distributions are bimodal, which may reflect a lack of information for updating R_{max}.

Since the three-stock model (Table 3, Figure 10) 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). However the carrying capacity for East Australia here is much lower than expected at circa 20,000. In addition, estimates for West Australia suggest a population that is nearly fully recovered, in possible contrast to recent abundance surveys, which still show a strong upward trend in this region (Hedley *et al.* 2012). This is because estimated K is between 20-30,000 whales for West Australia, so very similar to current abundance estimates. This result is closely consistent with previous population models of West and East Australia developed by Johnston and Butterworth (2005) and Müller and Butterworth (2012) and suggests that alternate catch allocations for the three-stock model need to be explored to evaluate the robustness of this result.

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, 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 over the feeding ground area 80°E-170°W.

A number of sensitivities of the population model still remain to be investigated using these models, including the influence of other relative and absolute abundance indices, such as regional catch per unit effort data (Chittleborough 1965), measurements of feeding ground abundance (Branch 2012; Matsuoka *et al.* 2012) and alternative measurements of breeding ground abundance (Paton *et al.* 2012). In addition to further refinements of the model and allocation of catches presented above, future work to improve this modelling should also focus on improving regional abundance measurement for Oceania, and implementing mark recapture trends directly into the likelihood fitting of these models, as has been developed by Johnston and Butterworth (2008). Recent work by Carroll et al. (In press) demonstrates the type of mark recapture model that could also be usefully applied within this framework. This model explicitly accounts for heterogeneity in capture probability driven by female reproductive cycles *i.e.* the differential availability for capture of males and females on their breeding grounds.

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	Base case	Sensitivity	Sensitivity
Breeding ground abundance			
West Australia	2008 N=28,830 CV=0.13* Hedley *et al*. (2011)		
East Australia	2010 N=14,522 CV=0.07* Noad *et al.* (2011a)	2005 N=7,041 Paton *et al.* (2012)	
Oceania	2005 N=4,329 CV=0.12 Constantine *et al*. (2012)		
New Caledonia	2008 N=562 CV=0.19 Garrigue *et al*. (2012)	2001 N=758 CV=0.3 Garrigue *et al*. (2004)	
Tonga	2005 N=1840 CV=0.23 Constantine *et al*. (2010)		
French Polynesia	2005 N=934 CV=0.64 Constantine *et al*. (2010)		
Feeding ground abundance			
West Australia		Branch (2012)	Matsuoka *et al*. (2012)
East Australia		Branch (2012)	Matsuoka *et al*. (2012)
Oceania		Branch (2012)	
Relative abundance indices			
West Australia	Hedley *et al*. (2011)	Chittleborough (1965)	
East Australia	Noad *et al.* (2011a)	Chittleborough (1965)	
New Caledonia	Garrigue *et al*. (2012)		

Table 1. Abundance and trend metrics used in this study (base case) and still to be explored (sensitivities). * Coefficients of variance were derived by assuming that confidence intervals around estimates from Noad *et al.* (2011a) and Hedley *et al*. (2011) are log-normally distributed.

Catch allocation type	Naive	Fringe	Naïve	Naïve	Fringe
Shared catches	130E-120W	110E-100W	130E-180	130E-180	110E-170W
	New Zealand	New Zealand	New Zealand	New Zealand	New Zealand
Stock 1:	**East Australia**	**East Australia**	**East Australia**	**East Australia**	**East Australia**
N_{abs}	N2010=14,522	N2010=14,522	N2010=14,522	N2010=14,522	N2010=14,522
	CV=0.07	CV=0.07	CV=0.07	CV=0.07	CV=0.07
I. Abundance	Bryden & Brown	Bryden & Brown	Bryden & Brown	Bryden & Brown	Bryden & Brown
Posteriors					
R_{max}	9.17%	9.11%	9.30%	9.40%	9.12%
	[8.35-10.13%]	[8.28-9.84%]	[7.48-10.54%]	[7.83-10.55%]	[7.58-10.50%]
K	39,565	41,535	26,922	26,741	30,904
	[31,493-47,639]	[32,670-50,662]	[20,331-29,944]	[22,494-29,347]	[24,110-34,199]
N_{min}	452	434	430	394	407
	[256-684]	[257-656]	[178-867]	[175-726]	[162-825]
N_{est}	16,827	16,382	15,395	16,135	15,652
	[9,952-22,375]	[10,145-22,295]	[7,105-22,335]	[7,299-22,232]	[7007-22,433]
N_{2013}/K	0.52	0.50	0.69	0.73	0.63
	[0.32-0.76]	[0.29-0.74]	[0.34-0.93]	[0.34-0.93]	[0.29-0.87]
Stock 2:	**Oceania**	**Oceania**	**New Caledonia**	**New Caledonia**	**New Caledonia**
N_{abs}	N2005=4,329	N2005=4,329	N2008=562	N2001=758	N2008=562
	CV=0.12	CV=0.12	CV=0.19	CV=0.30	CV=0.19
I. Abundance	N/A	N/A	Garrigue *et al*. (2012)	Garrigue *et al*. (2004)	Garrigue *et al.* (2012)
R_{max}	4.22%	4.26%	6.35%	7.54%	6.46%
	[0.02-10.1%]	[0.20-9.81%]	[2.45-10.17%]	[4.54-10.36%]	[2.89-10.15%]
K	15,366	17,404	5,304	5,293	6,125
	[5,256-32,093]	[6,119-36,305]	[3,170-13,230]	[3,451-10,344]	[3,382-14,583]
N_{min}	982	1001	56	64	52
	[182-4406]	[190-4,698]	[8-287]	[10-250]	[9-245]
N_{est}	4,543	4,447	651	796	674
	[2,917-6,239]	[2,944-6,094]	[218-1066]	[167-1568]	[241-1,067]
N_{2013}/K	0.39	0.36	0.14	0.33	0.13
	[0.13-0.97]	[0.12-0.95]	[0.05-0.40]	[0.08-0.71]	[0.05-0.36]

Table 2. Oceania population model results for (i) East Australia and Oceania and (ii) East Australia and New Caledonia. For catch hypotheses see Figure 1. N_{est} represents model predicted abundance in the year for which a measure of absolute abundance is available. I. Abundance represents indices of annual abundance used in the model.

Catch allocation type	Naïve	Fringe
Shared catches	180-120W	170E-100W
Stock 1:	**Tonga**	**Tonga**
N_{abs}	N2005=1,840 CV=0.23	N2005=1,840 CV=0.23
I. Abundance	N/A	N/A
Posteriors		
R_{max}	4.51% [0.26-9.97%]	4.27% [0.35-9.96%]
K	5,651 [1,759-10,672]	8,701 [1900-16,167]
N_{min}	437 [111-1,759]	418 [88-1,659]
N_{est}	1,787 [1,475-2,217]	1,859 [1,520-2,239]
N_{2013}/K	0.44 [0.17-1.00]	0.31 [0.12-1.00]
Stock 2:	**French Polynesia**	**French Polynesia**
N_{abs}	N2005=934 CV=0.64	N2005=934 CV=0.64
I. Abundance	N/A	N/A
R_{max}	3.62% [0.21-9.80%]	3.86% [0.16-9.75%]
K	4,065 [961-9,277]	5,691 [1,018-14,290]
N_{min}	313 [63-1,159]	265 [48-1020]
N_{est}	1,014 [572-1,735]	1,010 [588-1,667]
N_{2013}/K	0.32 [0.10-1.00]	0.24 [0.06-1.00]

Table 3. Oceania population model results for Tonga and French Polynesia. For catch hypotheses see Figure 1. N_{est} represents model predicted abundance in the year for which a measure of absolute abundance is available. I. Abundance represents indices of annual abundance used in the model.

Type	Naive	Naive	Naive
Stock 1:	West Australia	East Australia	Oceania
N_{abs}	N2008=28,830 CV=0.13	N2010=14,522 CV=0.14	N2005=4,329 CV=0.12
Stock component	β: 0.25 (0.01-0.48)	α: 0.25 (0.02-0.49)	
R_{max}	6.65% (0.57-10.3%)	9.00% (6.42-10.55%)	3.75% (0.57-9.34%)
K	36,362 (23,083-54,863)	19,511 (11,524-31,708)	25,655 (9,224-41,730)
N_{min}	16,584 (2,792-28,441)	840 (198-2,296)	938 (197-3,800)
N_{est}	32,743 (17,751-42,621)	13,342 (7,215-21,917)	4,216 (2,362-6,318)
N_{2013}/K	0.99 (0.36-0.99)	0.80 (0.43-0.99)	0.22 (0.08-0.84)
I. Abundance	Hedley et al. (2011)	Bryden & Brown	N/A

Table 4. Preliminary base case three-stock results for East Australia /Oceania/ West Australia. For catch hypotheses see Figure 2. I. Abundance represents indices of annual abundance used in the model.

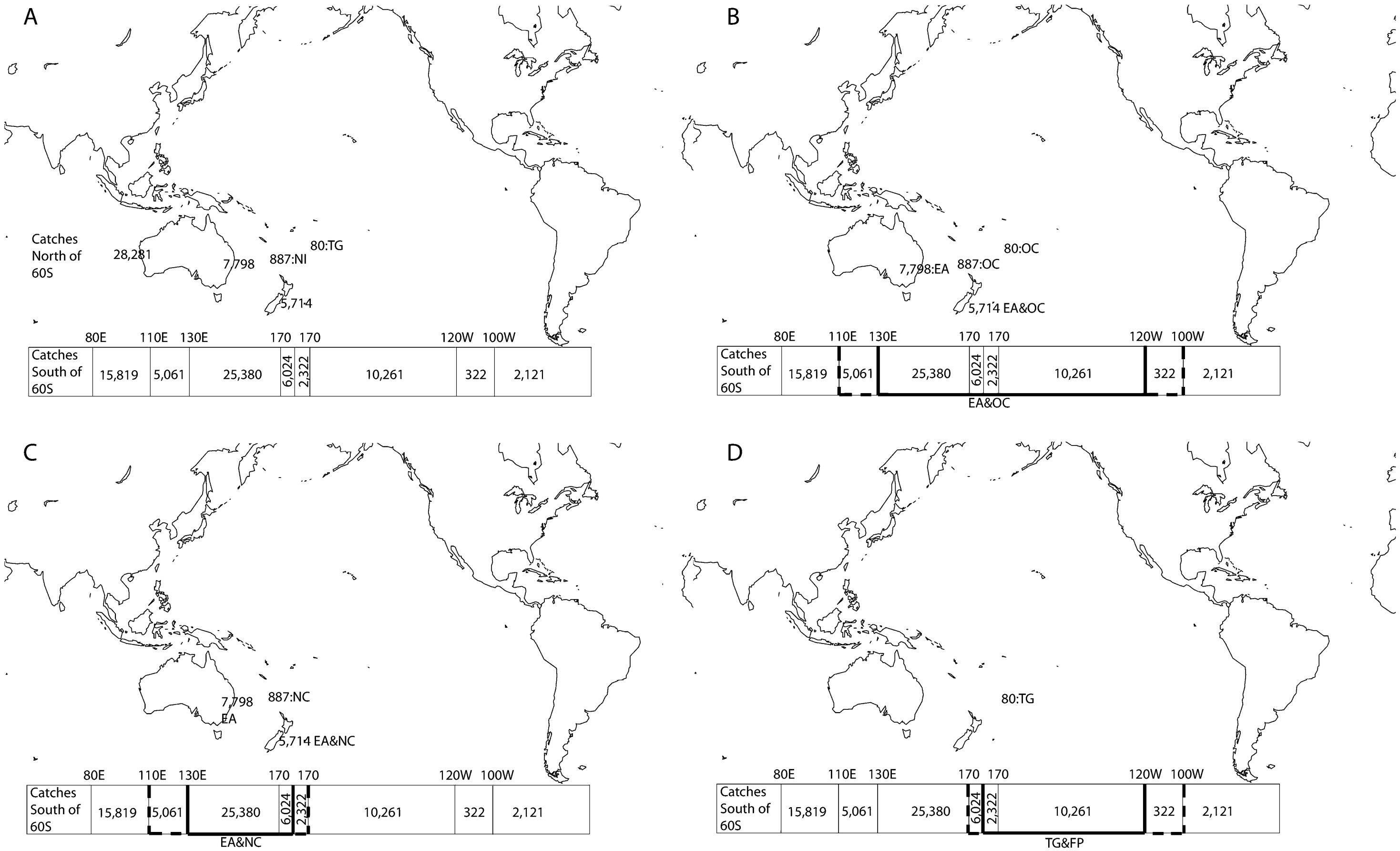


Figure 1. 20th century catches of humpback whales between 80°E-100°W (Allison IWC Catch Database). Catches north of 60S are shown for East Australia, West Australia, New Zealand, Norfolk Island (NI) and Tonga (TG). Figure 1A shows the divisions of catches by longitude for the purposes of population assessment. Figures 1B-D show the catch allocations used for- B: the East Australia / Oceania population model, C: the East Australia / New Caledonia population model D: the Tonga / French Polynesia population model. Catch allocations are indicated by each catch North of 60S (EA=East Australia, NC=New Caledonia, OC=Oceania). ’Naïve’ catches on feeding grounds are shown as black lines and ‘fringe’ catches as dotted lines.

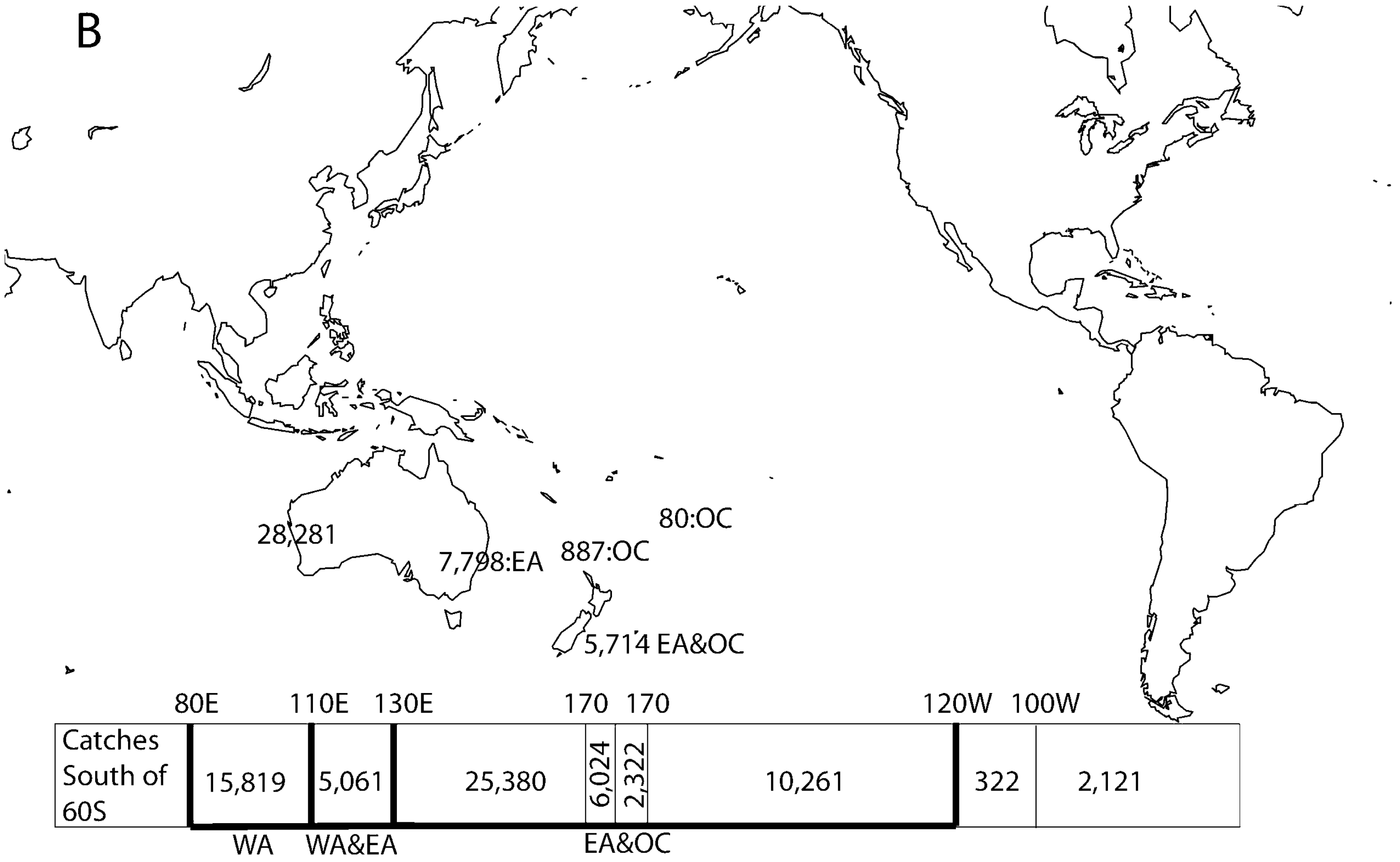


Figure 2. Catch allocation scheme for 3-stock model for West Australia, East Australia and Oceania. The Southern Ocean feeding grounds are divided into three areas: (1) 'core' West Australia feeding ground only, (2) mixed West Australia/East Australia feeding ground, (3) mixed East Australia / Oceania feeding ground.

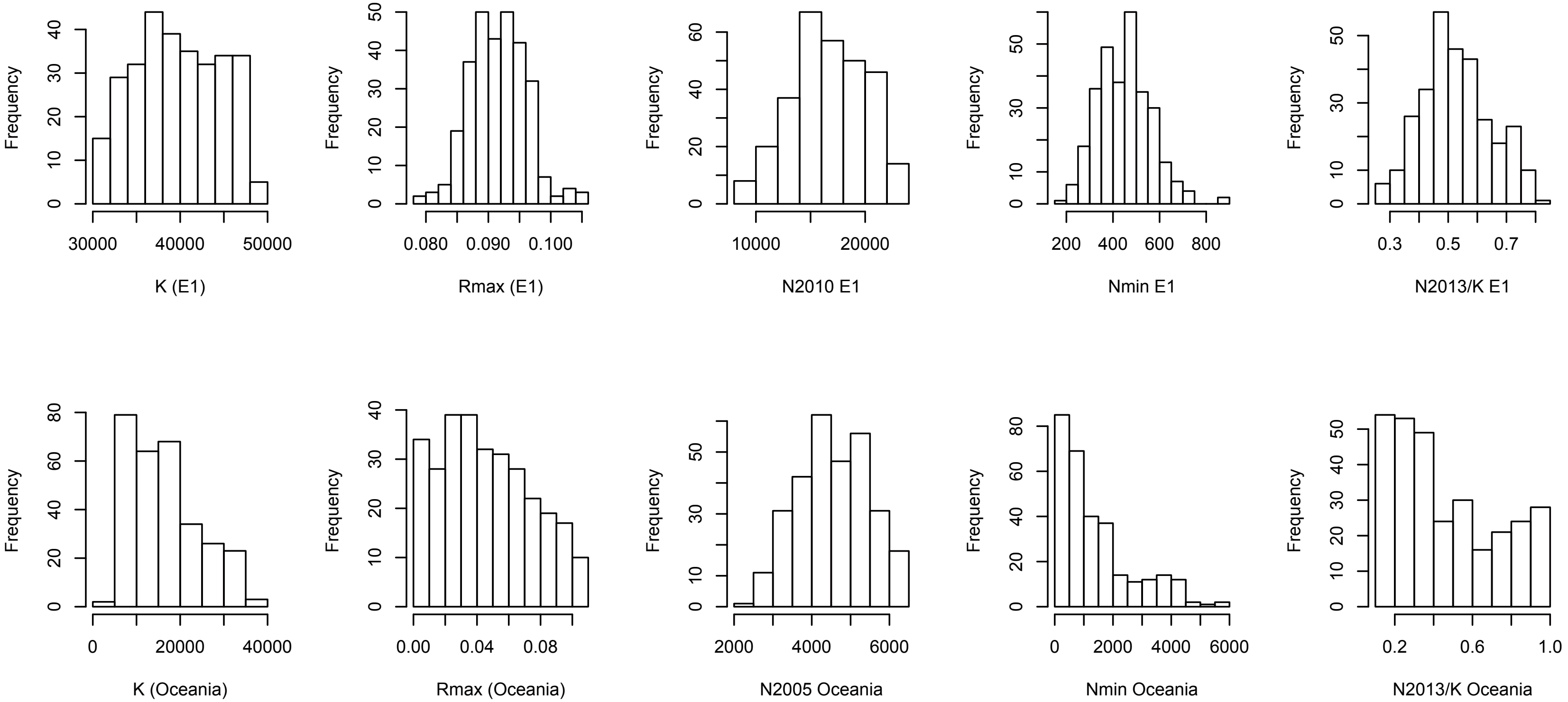


Figure 3. Posterior distributions of parameters from 2-stock ‘naïve’ model of catch allocation for East Australia and Oceania

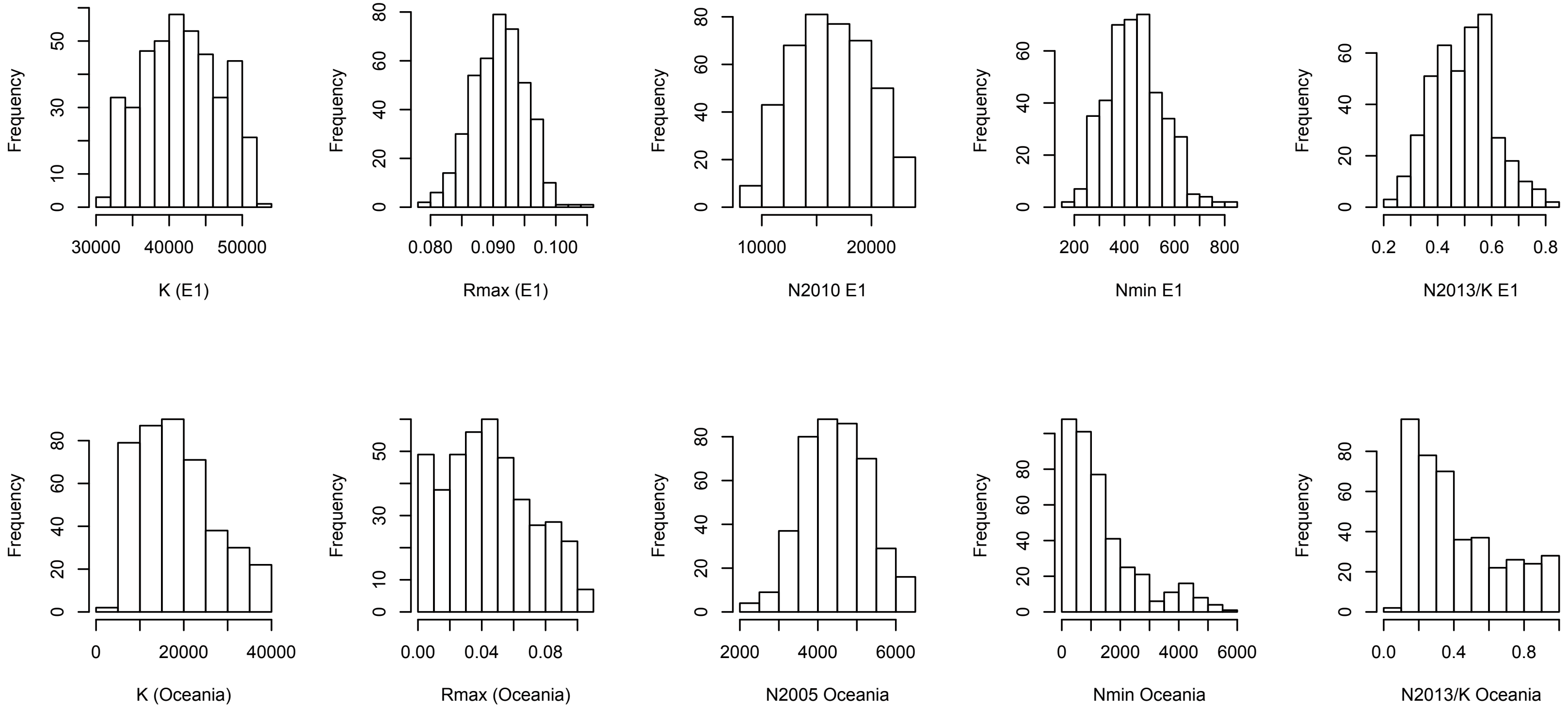


Figure 4. Posterior distributions of parameters from 2-stock ‘fringe’ model of catch allocation for East Australia and Oceania

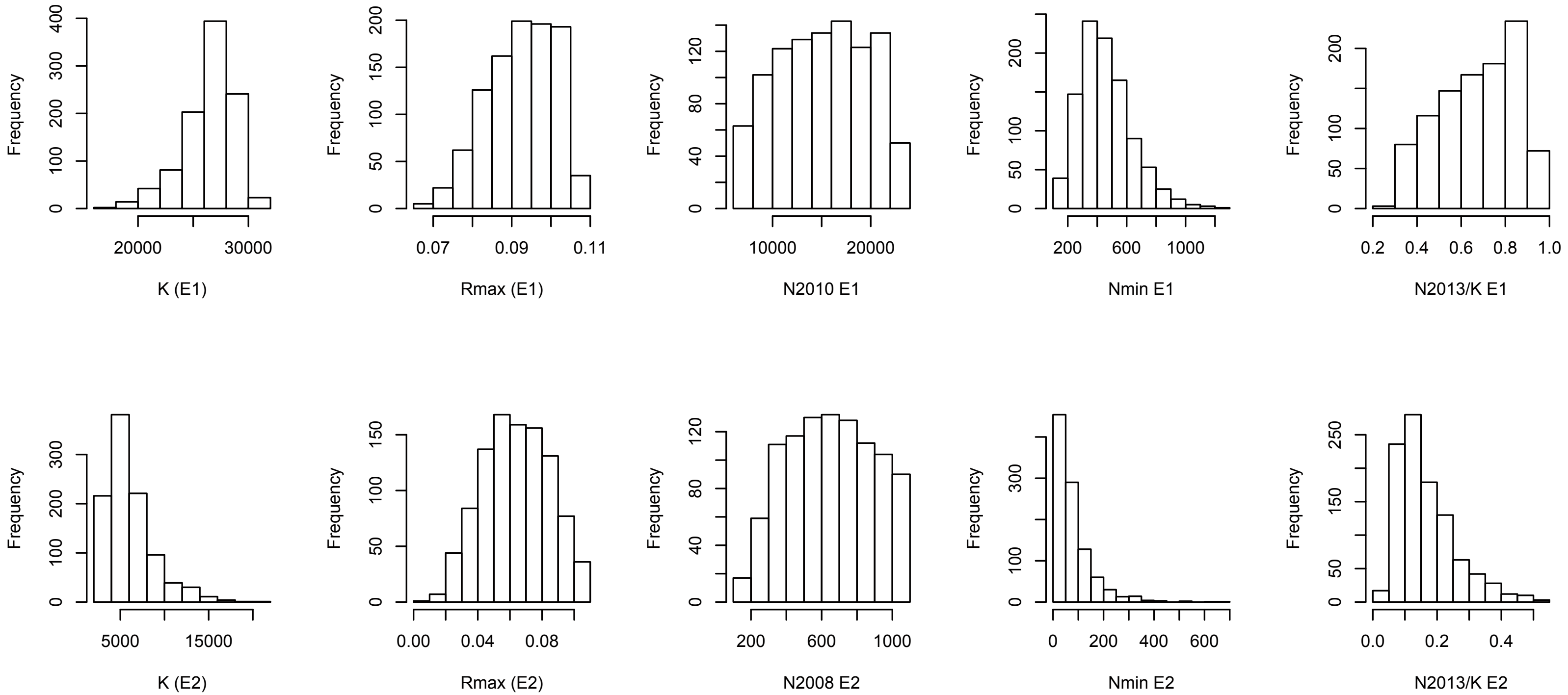


Figure 5. Posterior distributions of parameters from 2-stock ‘naïve’ model of catch allocation for East Australia and New Caledonia, using New Caledonia N2008 abundance from Garrigue *et al*. (2012).

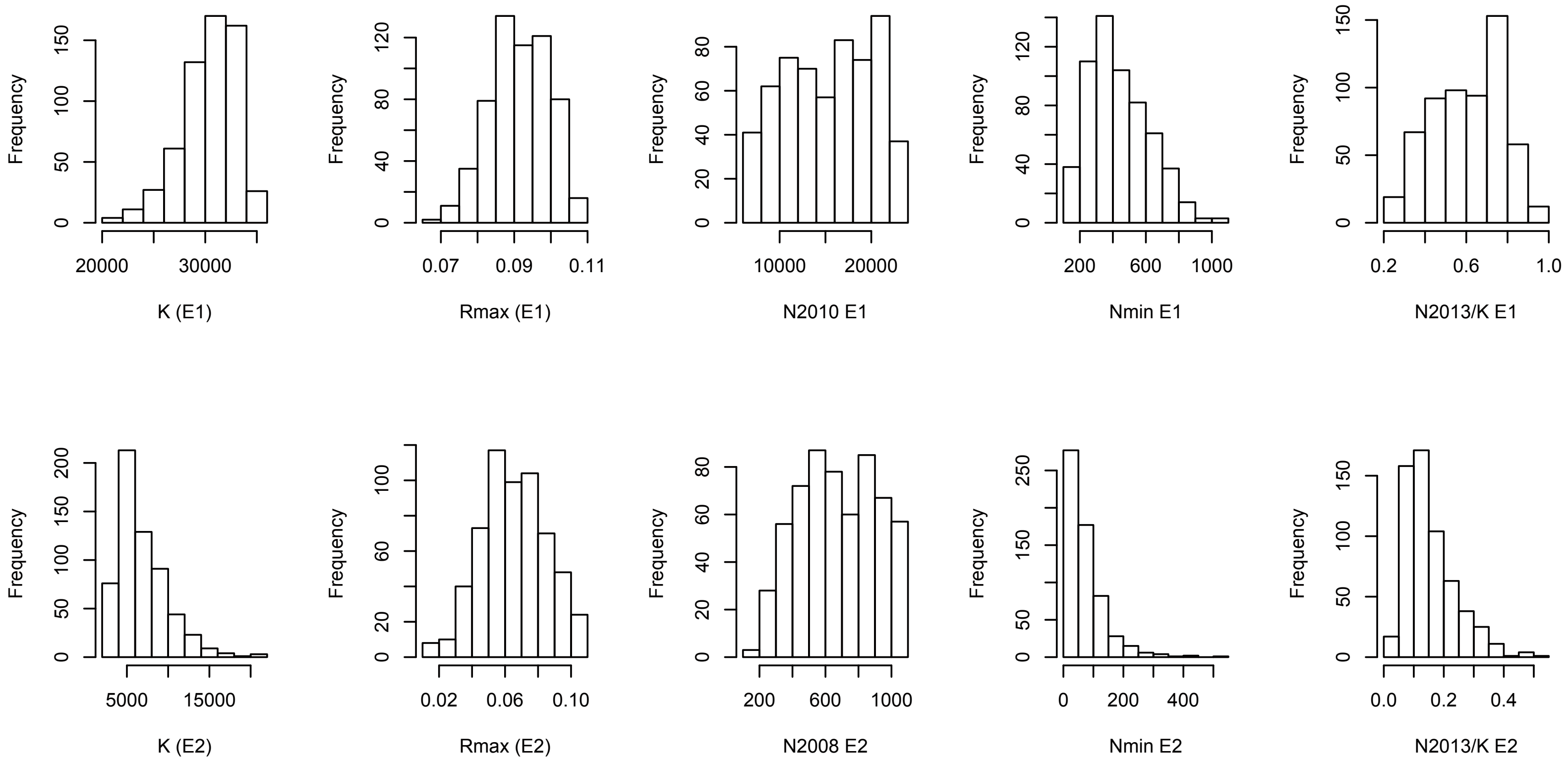


Figure 6. Posterior distributions of parameters from 2-stock ‘fringe’ model of catch allocation for East Australia and New Caledonia

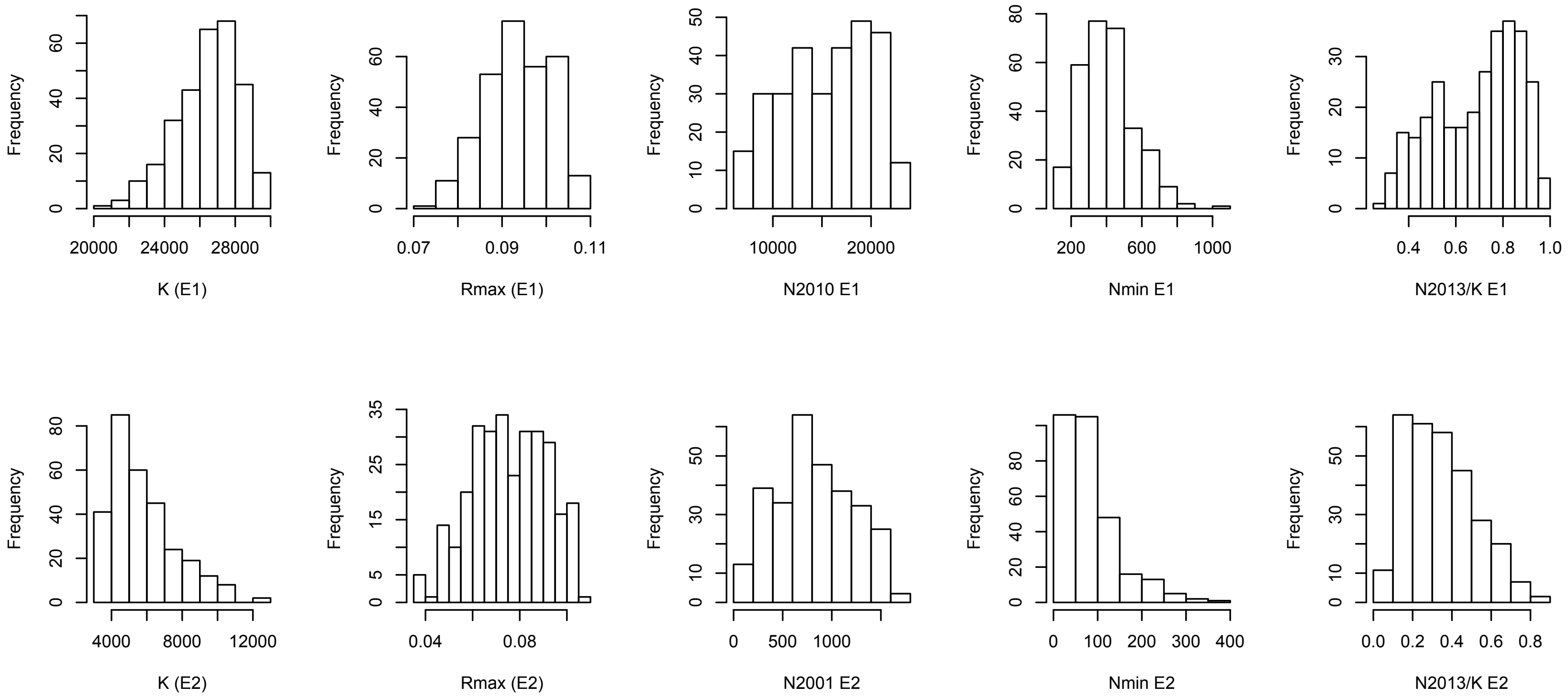


Figure 7. Posterior distributions of parameters from 2-stock 'naïve' model of catch allocation for East Australia and New Caledonia, using New Caledonia N2001 abundance from Garrigue *et al*. (2004)

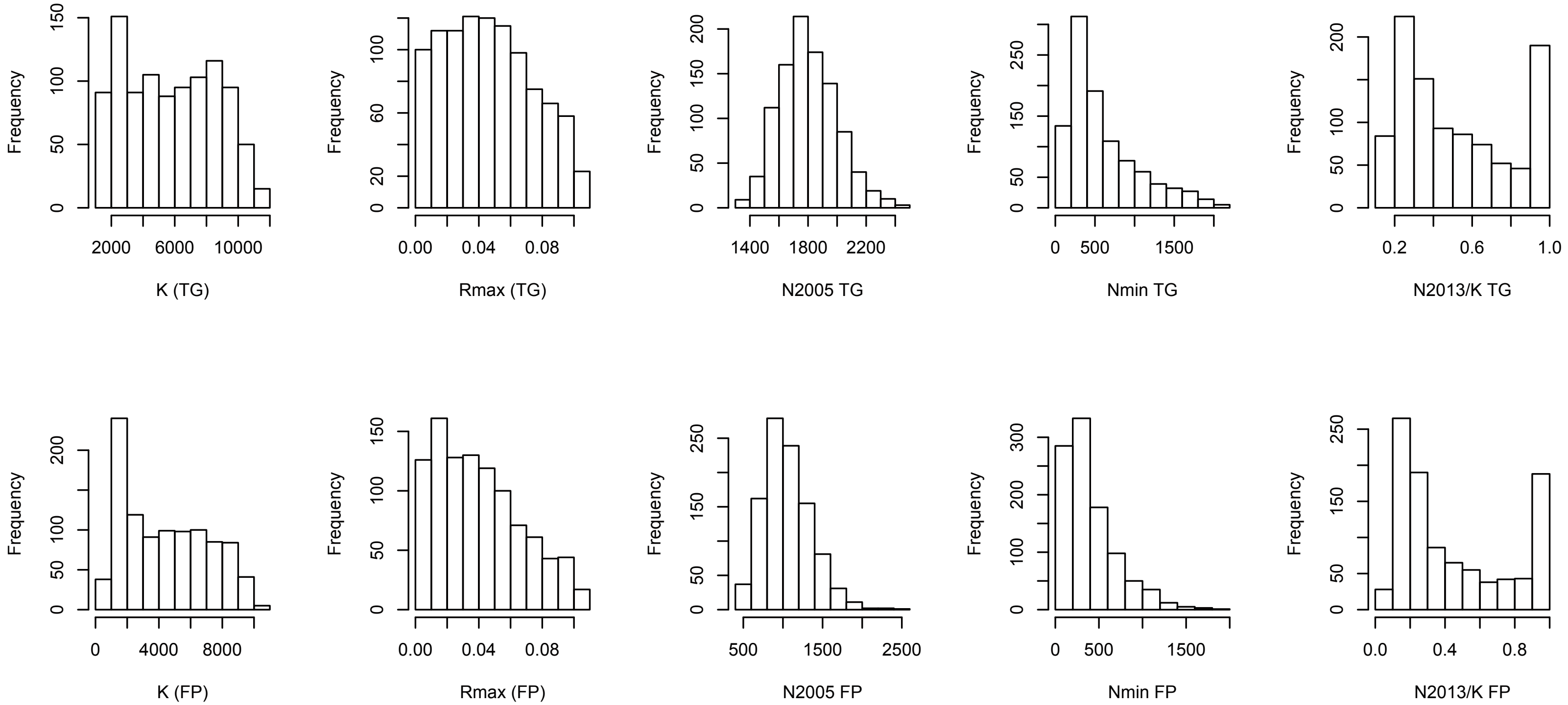


Figure 8. Posterior distributions of parameters from 2-stock ‘naive’ model of catch allocation for Tonga and French Polynesia.

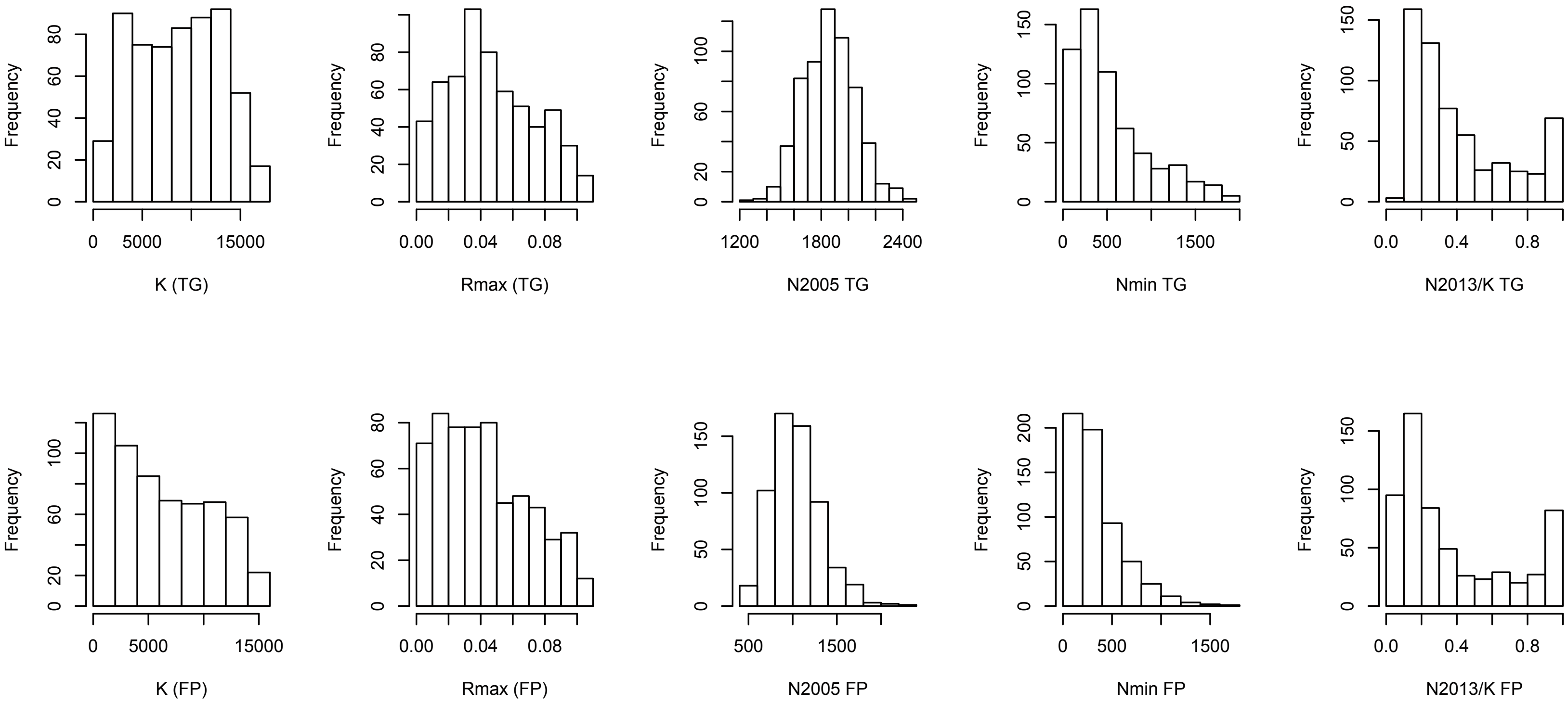


Figure 9. Posterior distributions of parameters from 2-stock ‘fringe’ model of catch allocation for Tonga and French Polynesia.

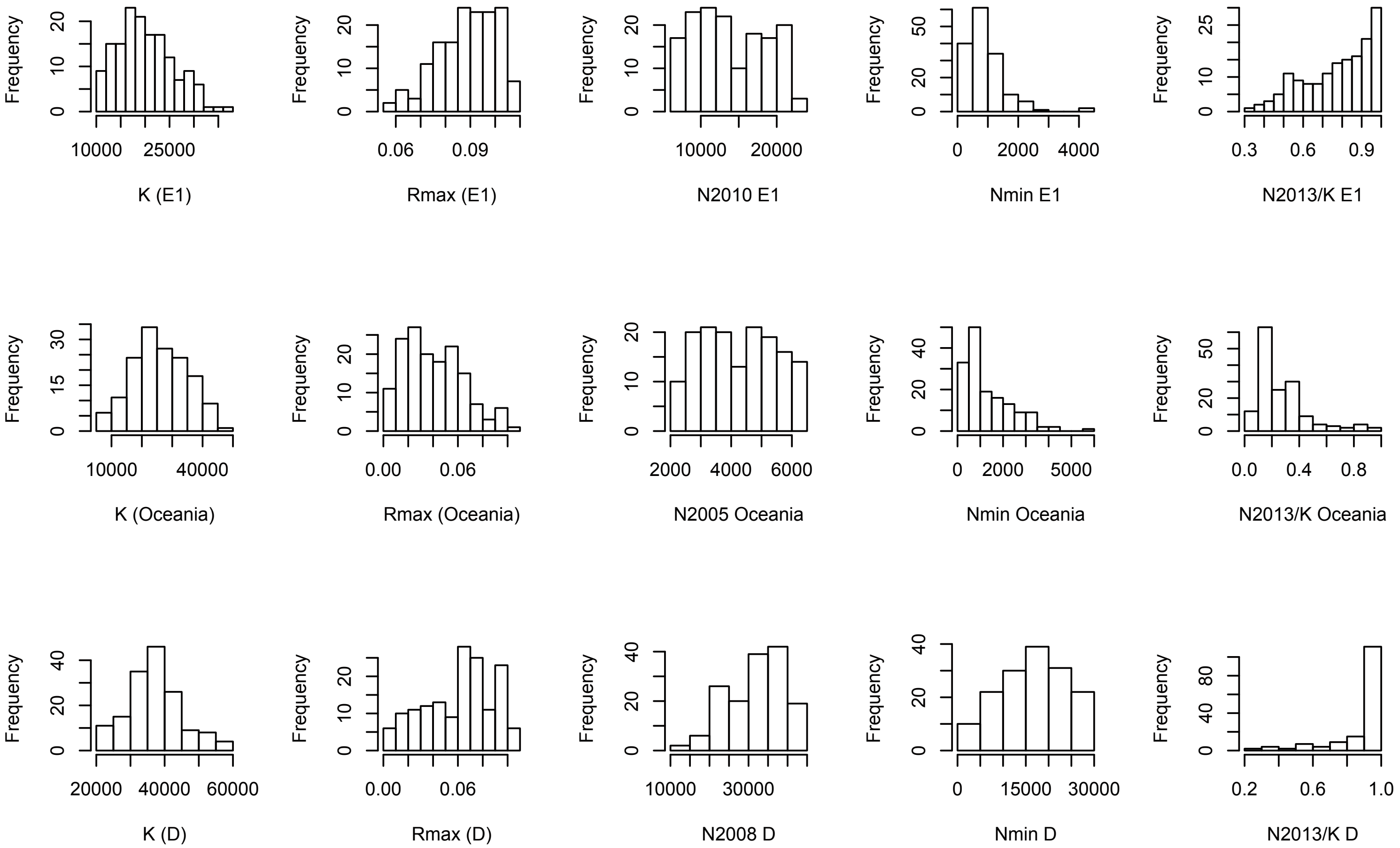
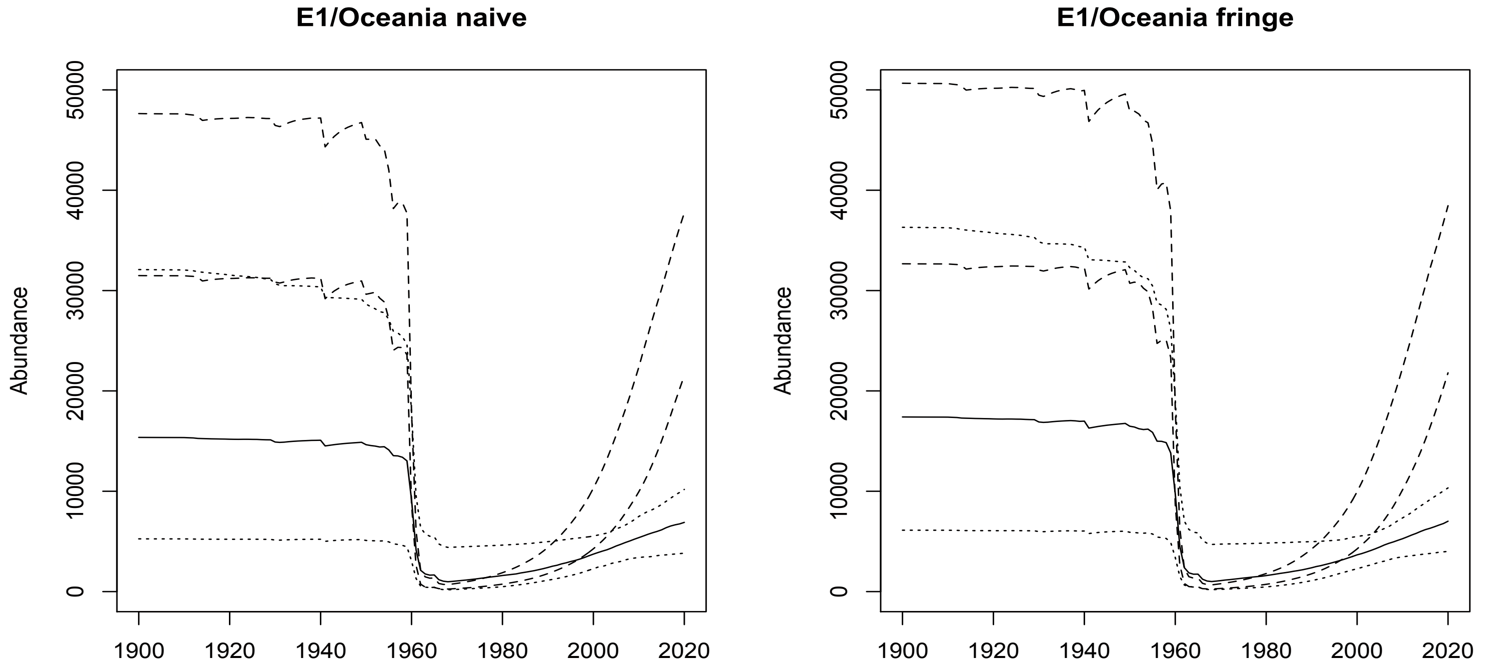


Figure 10. Posterior distributions of parameters from 3-stock naïve model of catch allocation for West Australia (D), East Australia (E1) and Oceania



E1/Oceania naive

E1/Oceania fringe

Figure 11. Abundance trajectories for East Australia (red) and Oceania (black) from 1900-2020 for 2-stock models with naïve (130E-120W) and fringe (110E-100W) catch allocations. Thick dashed lines represent 95% confidence intervals for East Australia, narrow dashed lines represent 95% confidence intervals for Oceania.

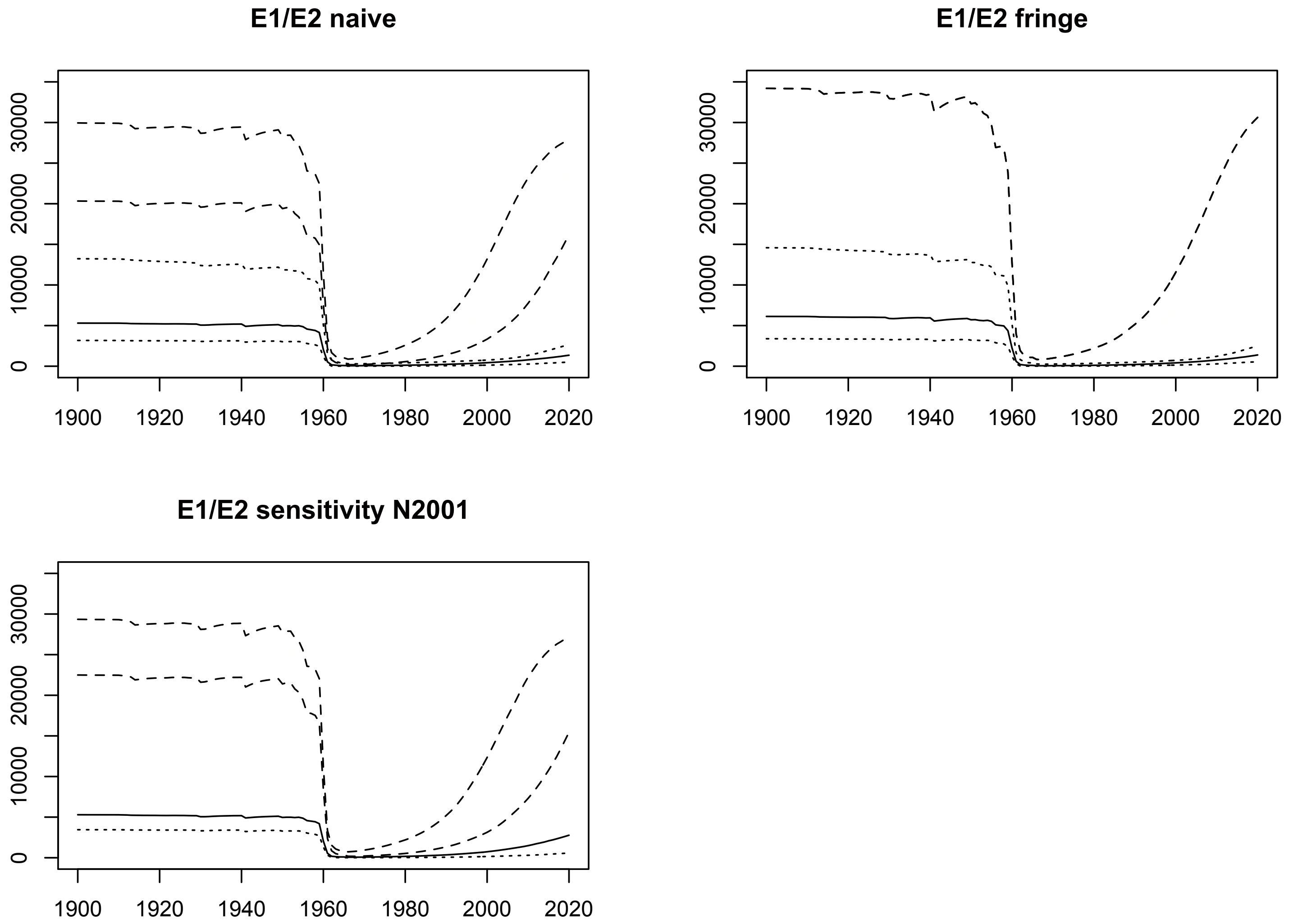


Figure 12. Abundance trajectories for East Australia (red) and New Caledonia (blue) from 1900-2020 for 2-stock models with naïve (130E-180) and fringe (110E-170W) catch allocations. Thick dashed lines represent 95% confidence intervals for East Australia, narrow dashed lines represent 95% confidence intervals for New Caledonia.

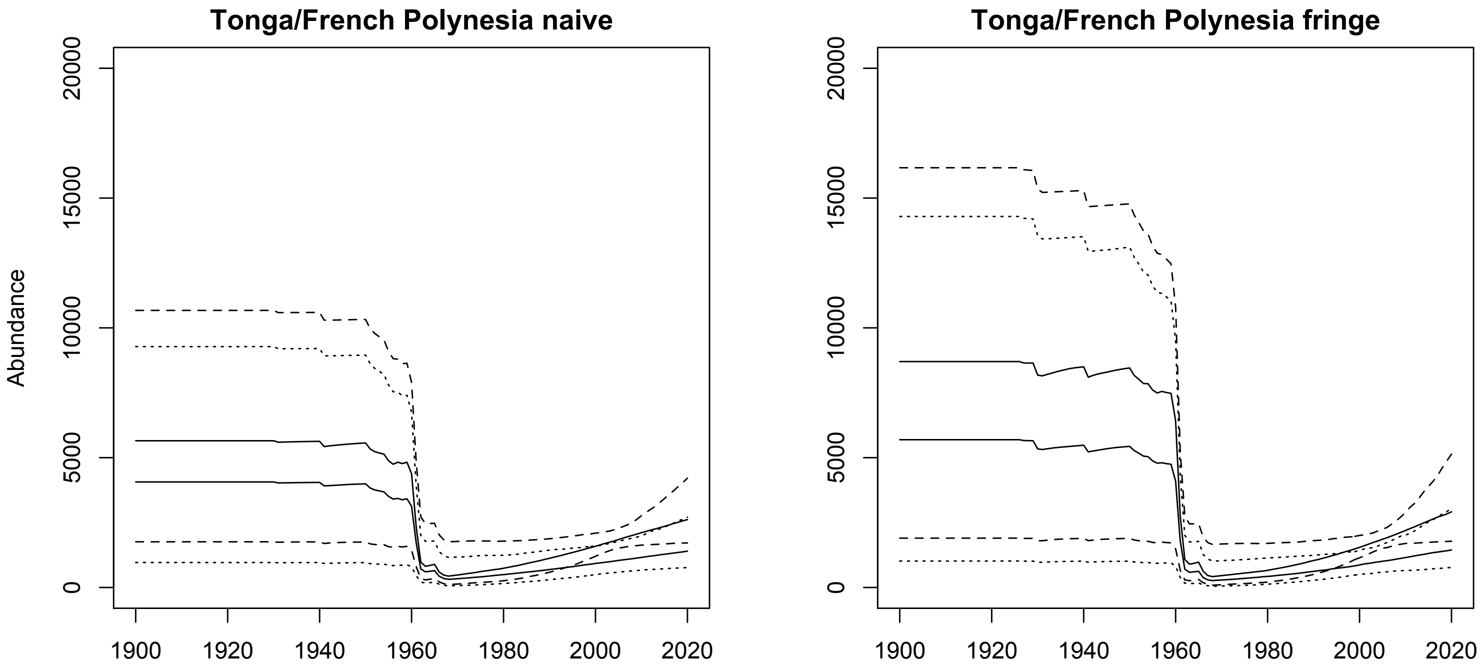


Figure 13. Abundance trajectories for Tonga (blue) and French Polynesia (black) from 1900-2020 for 2-stock models with naïve (180-120W) and fringe (170E-100W) catch allocations. Thick dashed lines represent 95% confidence intervals for Tonga, narrow dashed lines represent 95% confidence intervals for French Polynesia.