



Original Article

Seabird bycatch in a sardine purse seine fishery

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Limited understanding of seabird bycatch in purse seine fisheries has been highlighted as a key information gap in assessments of seabird bycatch in fisheries globally. This study documents the bycatch of breeding flesh-footed shearwaters (*Ardenna carneipes*) in a sardine purse seine fishery on the southern coast of Western Australia. Fishery-dependent bycatch records from 2009/2010 to 2017/2018 showed a strong peak in the mortality rate per fishing trip during March and April, closely associated with the final stage of chick rearing. Observers during those peak months in 2007, 2008, 2017, and 2018 recorded 171 mortalities during 222 trips at per trip rates ($\pm 95\%$ confidence limits) ranging from 0.59 (0.25–1.17) in 2017 to 1.10 (0.56–1.96) in 2007. Zero mortalities were recorded on at least 70% of trips in any year, suggesting infrequent formation of net folds that can trap birds. Total annual mortalities estimated for 2016/2017 and 2017/2018 were 123 (52–251) and 172 (91–302), respectively. Although within a sustainable anthropogenic limit of 495 (369–660) estimated from conservative application of the potential biological removal method, the extent of other anthropogenic mortalities is unknown. Further research on the effect of distance of breeding colonies from fishing operations is required.

Keywords: *Ardenna carneipes*, bycatch, fishery, flesh-footed shearwater, potential biological removal, purse seine, sardine, seabird

Introduction

Fisheries have profound impacts on seabirds globally (Tasker *et al.*, 2000) including substantial bycatch mortalities in longline (Anderson *et al.*, 2011), trawl (Croxall, 2008), and gillnet (Zydalis *et al.*, 2013) fisheries. For purse seine fisheries, however, there are very few reports of seabird bycatch, partly due to lack of monitoring in some regions (Moore *et al.*, 2009) or the target fish may be too large to attract seabirds. For example, independent observer records show that tuna purse seine vessels in the Indian and Pacific Oceans have very low seabird bycatch (Romanov, 2002; Molony, 2007; Hall and Roman, 2013). Only where purse seine vessels target small pelagic fish such as sardines and anchovy have limited reports of significant seabird bycatch emerged. On the Portuguese coast, independent observers recorded bycatch of 38 seabirds of several species from 353 net deployments between 2010 and 2012 (Oliveira *et al.*, 2015). Chile's industrial and artisanal purse seine fleets have recorded a range of seabird species as bycatch (Suazo *et al.*, 2014; Carle *et al.*, 2019). Even though small

pelagic fish comprise a large proportion of the world-wide catch by marine fisheries (Fréon *et al.*, 2005; FAO, 2018), a persistent lack of understanding of seabird bycatch in purse seine fisheries has recently been highlighted as a key information gap in an attempt to assess the impact of seabird bycatch in fisheries globally (Pott and Wiedenfeld, 2017).

In Western Australia (WA) the flesh-footed shearwater (*Ardenna carneipes*) is taken as bycatch by the South Coast Purse Seine Fishery (SCPSF) (Lavers, 2015; Baker and Hamilton, 2016), which targets Australian sardines (*Sardinops sagax*) (Norriss and Webster, 2019). Flesh-footed shearwaters are pursuit predators capable of diving to at least 66.7 m (Thalman *et al.*, 2009) and may drown when attempting to surface underneath a net fold that has formed underwater (Puglisi, 2007). This species is a trans-equatorial migrant that nests in burrows during the austral summer on southern hemisphere islands ranging from St Paul Island in the southern Indian Ocean to New Zealand, including islands off Australia's south coast and Lord Howe Island (Ross

et al., 1996; Lavers, 2015). In WA flesh-footed shearwaters nest in burrows on at least 40 islands along the southern coastline, from about Cape Leeuwin to the Recherche Archipelago (Figure 1; Burbidge and Fuller, 1996; Lavers, 2015). Limited published accounts show that bycatch mortalities of this species in WA occur in King George Sound (Zone 1 of the SCPSF, Figure 1) and peak in March and April (Puglisi, 2007; Powell *et al.*, 2007; Lavers, 2015; Baker and Hamilton, 2016). Understanding the temporal patterns of flesh-footed shearwater bycatch in the SCPSF, and the factors that affect these patterns, is important to inform the timing of observer monitoring programmes and bycatch mitigation initiatives, and to calculate annual mortality estimates for this fishery.

While global and Australian assessments of seabird conservation status against the International Union for the Conservation of Nature criteria do not currently consider the flesh-footed shearwater a threatened species (Garnett *et al.*, 2011; *Birdlife International*, 2019), monitoring the risk of fishery impacts on listed and protected species in WA is a key requirement of Ecosystem-Based Fisheries Management (Fletcher *et al.*, 2016). These risk assessments would benefit greatly from the application of recognized quantitative approaches to examine the ability of the flesh-footed shearwater population in WA to sustain fishery bycatch mortalities. While demographic models have been applied to assess fishery impacts on this species in eastern Australia and New Zealand (Baker and Wise, 2005; Dillingham and Fletcher, 2011), the potential impact of purse seine fishing on flesh-footed shearwaters in WA has not yet been examined. For populations with relatively limited demographic information, estimating the potential biological removals (PBR; e.g. Richard and Abraham, 2015) that can likely be sustained has been recognized as a valuable means to assess the risk of incidental bycatch mortalities while accounting for uncertainty (Williams *et al.*, 2008; Lonergan, 2011).

This study aimed to determine the temporal (intra-annual) pattern of flesh-footed shearwater bycatch mortalities in King George Sound using fishery-dependent data from the SCPSF, identifying contributions from changes in the mortality rate per fishing trip as well as the number of trips (fishing effort). Corroboration of this temporal pattern was attempted by comparing it with known life histories of both flesh-footed shearwaters (i.e. the timing of trans-equatorial migrations and stages of the breeding cycle) and sardines in WA, to confirm the peak period identified for focusing independent bycatch monitoring and mitigation. A second objective was to implement an independent bycatch observer program designed to estimate the total annual number of flesh-footed shearwater mortalities from purse seine bycatch during 2016/2017 and 2017/2018, including cryptic mortality (i.e. unobserved and not readily detectable), which can be significant for non-target species (Gilman *et al.*, 2013). Finally, the annual estimates of bycatch mortality were compared to estimates of PBR for flesh-footed shearwaters in WA to assess the sustainability risk associated with SCPSF bycatch.

Methods

Description of fishery and study area

The SCPSF is a limited entry, small-scale fishery using purse seine gear in single-vessel fishing operations to take small pelagic fish, predominantly sardines, on the southern coast of WA (Figure 1; Norriss and Webster, 2019). Annual retained catches have been

reported since the mid-1970s and were highest in the 1980s and 1990s, peaking at 8100 tonnes. Since 2005, the fishery has been managed by an annual catch quota, set at 5683 tonnes for the 2016/2017 and 2017/2018 quota years (1 July to 30 June), although annual catches in the last decade have ranged only from 1500 to 2700 tonnes. More than half of the SCPSF catch is taken in King George Sound (Zone 1 of the SCPSF, Figure 1), where flesh-footed shearwaters are taken as bycatch (Lavers, 2015). Only two bycatch mortalities have been reported by the SCPSF outside King George Sound. The SCPSF has implemented a range of voluntary bycatch mitigation strategies in King George Sound since 2006, including a moratorium on dawn fishing during a Special Management Period encompassing the assumed peak period for flesh-footed shearwater bycatch in March and April.

Located adjacent to the port city of Albany, King George Sound is the most prominent embayment on WA's south coast at ~200 km² and depths to ~50 m. The proximity of the purse seine fleet to the fishing grounds enables vessels to complete two or infrequently three fishing trips (and unloads) within a 24-hour period, with fishing occurring during both daylight and at night. There is usually a single net deployment on each trip, although up to four have been recorded. From 2009/2010 to 2017/2018 the SCPSF fishing effort in King George Sound has ranged between 389 and 877 fishing trips each quota year. During 2016/2017 and 2017/2018 five to six purse seine vessels fished in King George Sound, ranging in length from 11.1 to 19.4 m. Purse seine nets for the five most active vessels ranged in size from 220 m × 35 m to 380 m × 90 m with mesh sizes not <19 mm. Net hanging ratios, defined as the length of float line on which a horizontal section of net is mounted divided by the length of that section of net when fully stretched horizontally (Prado, 1990), ranged from 0.02 to 0.18 for those five vessels when measured in November 2017. Vessels use one or two powered rollers to retrieve the net and concentrate the catch inside the net pocket, which is then tautly fastened alongside the vessel. Fish are scooped from the net pocket with a brail net and brought on board. Not all fishing trips result in the purse seine net being deployed and the catch may be released if fish are not the desired size or species composition.

Overview of bycatch data sources and analyses

Described in more detail in the sections below, two sources of bycatch data from King George Sound were analysed:

- interactions recorded by fishers between 2009/2010 and 2017/2018 (fishery-dependent), and
- records from independent observers accompanying vessels on a proportion of fishing trips during March and April (the peak period for bycatch, see Results) of 2007, 2008, 2017, and 2018.

While the independent data were considered to provide more reliable information of interactions with flesh-footed shearwaters, implementing bycatch-monitoring programmes for relatively low-value fisheries in regional areas of WA is costly and thus the observer coverage focused only on the period in which the majority of interactions have been recorded. As a consequence, analyses of the fishery-dependent data were necessary to determine the temporal variation in bycatch mortalities within each year, enabling mortality estimates from the observer programme in the peak period to be appropriately scaled up to annual estimates.



Figure 1. Map of the south coast of Western Australia including Zone 1 of the South Coast Purse Seine Fishery encompassing King George Sound.

The fishery-dependent data were first used to examine the temporal (inter-annual) pattern in the rate of bycatch mortalities per fishing trip across 24 half-months and to justify what has historically been considered the peak period for interactions. A second analysis was then undertaken to estimate the ratio of bycatch mortality rates per trip between the peak and off-peak periods, which was necessary to estimate the total annual bycatch mortalities, described below.

The estimate of total annual bycatch mortalities was comprised of peak and off-peak period components. Estimates of bycatch mortality rate per trip in the peak period were calculated from the independent observer data and adjusted for cryptic mortality. The off-peak bycatch mortality rate estimate was then calculated using the estimate for the peak period and the estimated ratio of the off-peak to peak period bycatch mortalities (based on the fishery-dependent data, described above). The total number of bycatch mortalities was then estimated, for the peak and off-peak period, by multiplying the estimated mortality rates per trip with the estimated total number of trips with net deployments.

Temporal patterns in bycatch mortalities

The first component of this study focused on examining available fishery-dependent data to determine any temporal (intra-annual) patterns in bycatch mortalities of flesh-footed shearwaters in King George Sound. Since 1 July 2009, the number of interactions with flesh-footed shearwaters on each fishing trip has been recorded by purse seine fishers on Catch and Disposal Records

(CDRs) compulsorily lodged with the fishery authority when landing any small pelagic fish. Although the fate of each shearwater was recorded as unharmed, injured, or dead, this study conservatively counted the very small number injured (six in the fishery-dependent dataset and one independently observed) as mortalities. The number of interactions for each net deployment on the trip (if more than one) was not recorded on CDRs, so the unit for quantifying and extrapolating fishing effort in this study was the number of trips rather than the number of net deployments. As the main purpose of the CDR is to track fish catches against quota entitlement, fishers are only required to submit CDRs for trips where fish are landed, including trips when the net is not deployed, but the vessel receives a transfer of fish from another vessel while at sea. The CDR data therefore exclude interactions that might have occurred during trips when the net was deployed, but no fish were caught, or when catches were released. However, the data should reflect temporal (intra-annual) patterns in the rate of bycatch mortalities per trip.

To examine the temporal patterns in the bycatch data reported by fishers in CDRs, the numbers of flesh-footed shearwater mortalities per fishing trip were calculated and assigned to 24 half-month intervals in each of nine quota years from 1 July 2009 to 30 June 2018. Half-months were defined as the 1st to the 15th day, and the 16th day to the end of the month, except for February which was defined as 1st to 14th and 15th to the end of the month. To test for any differences in the mean number of mortalities per trip among the half-months and between years, a

generalized linear model (GLM), assuming a negative binomial distribution with a log link function, was fitted to the bycatch mortality data with selected covariates quota year and half-month. The negative binomial distribution is commonly used to describe probabilities of occurrence of whole numbers greater than or equal to zero, with allowance for over-dispersion, i.e. variance larger than the mean (e.g. White and Bennetts, 1996). The distribution is described by the mean μ and dispersion θ , and the associated variance is given by

$$\sigma^2 = \mu + \mu^2/\theta.$$

The GLM was fitted to CDR data using the *glm.nb* function from the MASS library in R (R Core Team, 2019). The analyses focused on the period of consecutive half-months where one or more mortalities had been recorded (mid-December to end of May). It thus excluded the period in each quota year when flesh-footed shearwaters were absent from the south coast of WA (Powell et al., 2007) and no mortalities had been recorded (June to mid-September), as well as mid-September to mid-December when just 11 mortalities had been recorded. The fitted model is described by:

$$N_{mi} \sim NB(\mu_i, \theta), \quad i = 1, \dots, n,$$

$$\log_e(\mu_i) = \text{QuotaYear}_i + \text{HalfMonth}_i,$$

where N_{mi} is the number of mortalities on the i th trip and n is equal to 3414 trips. The covariates included are the quota year (categorical with 9 levels) and half-month (categorical with 11 levels). A vessel/skipper effect was not included in the analyses due to unbalanced data; however, an exploration of data for individual vessels with skippers that fished consistently throughout the sampling period suggested that including this effect would not significantly influence the results. Results of the GLM analysis were compared to known life history information for flesh-footed shearwaters in WA, i.e. the timing of trans-equatorial migrations and stages of the breeding cycle (Warham, 1958; Powell, 2004; Powell et al., 2007; Lavers et al., 2019), as well as to the temporal variability in fishing effort of the SCPSF, to identify the period of greatest risk to the flesh-footed shearwaters.

To determine the peak and off-peak periods for bycatch mortalities, pairwise comparisons of marginal means (on the log scale) were undertaken to identify differences in bycatch mortality rates per trip between half-months, based on the $\alpha = 0.05$ significance level. The comparisons were undertaken using the *emmeans* and *clm* functions from the *emmeans* and *multcomp* libraries, respectively, in R, with p -values adjusted for multiple comparisons using the Tukey method. A second GLM was fitted to derive a ratio of mortality rates between the identified off-peak and peak periods, γ_o , required for estimating total annual mortalities. The fitted model is described by:

$$N_{mi} \sim NB(\mu_i, \theta), \quad i = 1, \dots, n,$$

$$\log_e(\mu_i) = \text{QuotaYear}_i + \text{Period}_i,$$

where N_{mi} is the number of mortalities on the i th trip. The covariates included are the quota year (categorical with 9 levels) and

period (categorical with 2 levels). As the model utilized treatment contrasts, the (log-transformed) ratio of mortality rates (γ_o , defined below) was given by the fitted coefficient for the off-peak period.

Independent bycatch observation

To improve the understanding of flesh-footed shearwater bycatch in the SCPSF, independent observers have accompanied purse seine vessels fishing in King George Sound during the peak period for flesh-footed shearwater bycatch (March and April, see below) in 2007 and 2008, and more recently in 2017 and 2018. Data from observed trips in 2007 and 2008 were kindly provided by the Western Australian Fishing Industry Council and have previously been summarized by Baker and Hamilton (2016). Six of the seven active vessels in 2007 and all eight active vessels in 2008 were monitored, with the large majority (>90%) of fishing trips having occurred during daylight hours. For each trip in 2007 and 2008, observers recorded the number of flesh-footed shearwater entanglements and mortalities, and whether the net was deployed on each trip, but they often did not record whether fish were caught.

The more recent bycatch observation programme in 2017 and 2018 was based on a statistically robust design, supported by a power analysis for sample size estimation, to derive estimates of the total annual flesh-footed shearwater mortalities in King George Sound for the 2016/2017 and 2017/2018 quota years. Observers accompanied all five SCPSF vessels that fished both day and night during March and April, with vessel priority selected at random for each day. Flesh-footed shearwater bycatch was defined as those trapped or entangled in the purse seine net requiring human intervention to be extricated, as well as dead or injured birds floating within 100 m of the deployed net. This definition was considered more objective than the earlier observer programme, where records of “entanglements” may have included birds that freed themselves without human intervention. Observers in 2017 and 2018 also recorded whether the net was deployed, if flesh-footed shearwaters were visible during deployment, if fish were caught, and if they were landed. Observed trips not resulting in net deployment were excluded from all results and analyses, assuming zero potential for bycatch.

Bycatch mortality estimates for 2016/2017 and 2017/2018

The total annual number of bycatch mortalities for the 2016/2017 and 2017/2018 quota years (1 July to 30 June) was estimated from independent observer data recorded during the peak period for bycatch (March and April, see Results) in 2017 and 2018, respectively. The temporal patterns of bycatch mortalities and fishing effort reported by fishers between 2009/2010 and 2017/2018 were used to extrapolate observer results across each year. The off-peak period for bycatch was therefore considered to extend from May to February (inclusive) but excluded the period from June to early September (inclusive) when flesh-footed shearwaters were absent due to their annual trans-equatorial migration and no bycatch mortalities were recorded by fishers. Annual mortality estimates could not be generated from the 2007 and 2008 observer data due to inadequate information on the capture and landing of fish on observed trips, which was necessary to extrapolate from the proportion of fishing effort observed to total effort.

Cryptic, i.e. unobserved and not readily detectable components of fishing mortality, can be significant for non-target species

(Gilman *et al.*, 2013) and is routinely included in estimates of seabird bycatch in New Zealand fisheries (Richard and Abraham, 2015). Two sources of cryptic mortality were therefore considered in this study to generate conservative estimates of total annual bycatch mortalities of flesh-footed shearwaters in King George Sound in 2016/2017 and 2017/2018. As methods for estimating cryptic mortality of seabird bycatch in purse seine fisheries have not been published, those developed for trawl fisheries were used as the closest available proxies, as both involve seabirds becoming trapped or entangled in nets designed to corral fish. The first cryptic multiplier (c_1) described the number of potential bycatch mortalities as a multiple of observed mortalities and was modelled as a log-normal distribution with a mean of 1.3 and a 95% confidence interval of 1.1–1.7, derived from an estimate for small diving seabirds enmeshed in trawl net wings during setting, trapped inside the net as it closes, or on the outside of the net during hauling (Richard and Abraham, 2015). As trawl nets are towed astern of a moving vessel and the cryptic mortality estimate incorporates birds falling off unobserved, the estimate of c_1 is likely more conservative when applied to purse seine vessels as they remain relatively immobile while the net is deployed. Note that the estimation of c_1 does not account for the potential that the number of undetected mortalities is related to the density of birds present at the fishing operations.

Second, the proportion of flesh-footed shearwaters recorded by observers as released alive and unharmed and subsequently die as a result of the fishery interaction (c_2) was assumed to have a mean value of 0.01, modelled as a Beta distribution with a *cv* of 0.2, derived from Richard and Abraham’s (2015) estimate from aerial collisions with the warp cable of trawlers by small fast-flying birds, which included flesh-footed shearwaters. Richard and Abraham (2015) cite Watkins *et al.*’s (2008) observation that such strikes “usually had little apparent impact on birds”. This level of impact was assumed to be equivalent to the release of flesh-footed shearwaters, judged by observers to be alive and unharmed, following human intervention to extricate them from the purse seine net. The different, less objective definition of birds released alive and unharmed applied by observers in 2007 and 2008 meant cryptic mortality was not estimated for those years.

The total number of annual flesh-footed shearwater mortalities (N_m) resulting from purse seine bycatch in King George Sound was estimated as

$$N_m = \mu_p T_p + \mu_o T_o,$$

where μ_p and μ_o denote the mean mortality rates (per fishing trip) during the peak and off-peak periods, respectively, and T_p and T_o represent the fishing effort (number of fishing trips with net deployments) during those respective periods. Uncertainty around N_m was considered by re-sampling values for mortality rates and fishing effort from their estimated distributions.

For each year, the mean mortality rate per trip during the peak period, μ_p , was estimated from the observer data as

$$\mu_p = \mu_m c_1 + (\mu_b - \mu_m) c_2,$$

where μ_m and μ_b are the estimated mean mortality rate per trip and mean total bycatch rate (including flesh-footed shearwaters released alive and unharmed) per trip, respectively, and c_1 and c_2 are the cryptic mortality parameters. Estimates of μ_m and μ_b were calculated assuming a negative binomial distribution, as previously used to describe the fishery-dependent bycatch data. The distribution was

fitted using a (null) GLM model via the *glm.nb* function in R. The confidence limits (CLs) for μ_m and μ_b were constructed by back-transforming the CLs of the parameter estimates on the log scale. As no observer data were available for the off-peak period, the mean mortality rate for this period was estimated as

$$\mu_o = \gamma_o \mu_p,$$

where γ_o is the ratio of the mortality rate during the off-peak period to that in the peak period, estimated from the fisher-reported bycatch mortality data (see above).

The total number of fishing trips in which the net was deployed during the peak period T_p in the 2016/2017 and 2017/2018 quota years was estimated from the number of trips resulting in lodgement of a CDR (i.e. fish were landed), $n_{p,c}$ and the frequency of observer trips with and without net deployment and CDRs as

$$T_p = f(n_{p,c}, \mathbf{N}_b).$$

The \mathbf{N}_b matrix contains the frequencies of trips in the observer data with net deployment and CDRs during the peak period, given by

$$\mathbf{N}_b = \begin{bmatrix} b_{c,s} & b_{nc,s} \\ b_{c,ns} & b_{nc,ns} \end{bmatrix},$$

where $b_{c,s}$ is the number of observer trips with CDRs and net deployment, $b_{c,ns}$ is the number of observer trips with CDRs and no net deployment (received at-sea transfer of fish from another vessel), $b_{nc,s}$ is the number of observer trips with no CDRs but with net deployment, and $b_{nc,ns}$ is the number of observer trips with no CDRs and no net deployment. Furthermore we denote the number of observer trips with CDRs as $b_c = b_{c,s} + b_{c,ns}$, the number of observer trips without CDRs as $b_{nc} = b_{nc,s} + b_{nc,ns}$, and the total number of observer trips as $b_T = b_c + b_{nc}$.

In a similar manner, the number of fishing trips in the off-peak period was estimated as

$$T_o = f(n_{o,c}, \mathbf{N}_b),$$

where $n_{o,c}$ was the number of trips resulting in lodgement of a CDR during the off-peak period, and \mathbf{N}_b defined as above. The function f included three parameters, namely the numbers of trips with CDRs and net deployment ($n_{c,s}$), the number of trips with no CDRs (n_{nc}), and the number of trips with net deployment but no CDR ($n_{nc,s}$). Assuming binomial distributions for the probabilities of observing the relative numbers of trips in the observer data, the likelihood of the model combined three components: (i) the likelihood that a trip with a CDR also has net deployment, (ii) the likelihood that a trip involves a CDR, and (iii) the likelihood that a trip with no CDRs will involve net deployment. The combined likelihood is

$$\lambda = \binom{b_c}{b_{c,s}} (\pi_{c,s})^{b_{c,s}} (1 - \pi_{c,s})^{b_c - b_{c,s}} + \binom{b_T}{b_{c,s}} (\pi_c)^{b_c} (1 - \pi_c)^{b_T - b_c} + \binom{b_{nc}}{b_{nc,s}} (\pi_{nc,s})^{b_{nc,s}} (1 - \pi_{nc,s})^{b_{nc} - b_{nc,s}},$$

where the associated probabilities are given by $\pi_{c,s} = \frac{n_{c,s}}{b_c}$, $\pi_c = \frac{n_{c,s}}{b_c}$, and $\pi_{nc,s} = \frac{n_{nc,s}}{b_{nc}}$. Penalties were used to ensure that the

number of trips with net deployment and CDRs did not exceed the number of trips with CDRs, and similarly that the number of trips with no CDRs was at least as great as the number of observer trips with no CDRs. Maximum likelihood estimation was used to estimate the parameters of the model using the *optim* function in R from the *stats* package, which were then used to calculate the number of trips that involved net deployment ($n_T = n_c + n_{nc}$) in separate analyses for the peak and off-peak periods, i.e. for estimates of T_p and T_o .

Bycatch risk to the flesh-footed shearwater population

The ability of the WA flesh-footed shearwater population to sustain incidental mortalities by the purse seine fishery in King George Sound was explored using the PBR approach, which was initially developed to assess bycatch impact on marine mammal populations in the United States (Wade, 1998) and has also been extensively applied to seabirds, including flesh-footed shearwaters (Zydalis et al., 2009; Richard and Abraham, 2015). The PBR is defined as the number of mortalities in addition to natural mortality that a population is likely to sustain while remaining above half the carrying capacity (Dillingham and Fletcher, 2008). It is estimated from four demographic parameters: the age at first breeding (A), adult annual survival (S_a), proportion of adults breeding each year (P_b), and the number of breeding pairs (N_b). Estimates of these parameters for flesh-footed shearwaters in WA were sourced from published literature, with uncertainty accounted for by re-sampling from specified distributions for each of the parameters (Table 1). For each parameter, 5000 random values were drawn from the assumed distribution and used to calculate PBR.

Flesh-footed shearwaters first breed at ~ 7 years of age (mean $A = 6.7$ years, Barbraud et al., 2014) and each breeding pair can produce one egg per year, however, not all breed annually (Lavers et al., 2019). Although the breeding propensity of seabirds is notoriously difficult to estimate and requires long-term monitoring (Souhay et al., 2014), bycatch risk assessments in New Zealand have assumed that 10% of adult flesh-footed shearwaters omit breeding in any given year (i.e. mean $P_b = 0.9$, Richard and Abraham, 2015). The annual survival of adult flesh-footed shearwaters has been estimated from comprehensive, long-term mark-recapture data for a stable population in New Zealand ($S_a = 0.93 \text{ year}^{-1}$, Barbraud et al., 2014). Re-sampled values of A and S_a were drawn from a normal distribution based on the means and associated standard deviations (Table 1) estimated by Barbraud et al. (2014). Following the approach used by Richard and Abraham (2015), re-sampled values of P_b were derived from a logit-normal distribution (Table 1) to ensure that individual values did not exceed 1.

Two scenarios were explored to test the sensitivity of PBR estimates to the simplifying assumption that all individuals in the WA breeding population of flesh-footed shearwaters have an equal probability of interacting with purse seine vessels in King George Sound. By applying two alternative estimates of the number of breeding pairs that may be impacted by the fishery, N_b , the effect of mortalities on the overall population, or on a smaller component of that population from colonies closer to King George Sound, could be examined. For the first scenario, a conservative estimate of overall population size in WA was derived from Lavers' (2014) estimated range of 18 376–35 906 breeding pairs from nest burrow surveys between 2011 and 2014, noting

that this was based on the assumption of 100% annual breeding participation (i.e. likely to be an underestimate of breeding pair numbers). It was assumed that the mid-point of this range represented the mean estimate of breeding pairs; however, it was not clear how the range describes the uncertainty around this estimate. Based on the approach described by Richard and Abraham (2015), minimum estimates of breeding pair numbers in WA were derived by re-sampling from a log-normal distribution with a mean of 27 141 and a standard deviation (on the log scale) of 0.1 (Table 1), and only retaining values from the lower quartile of this distribution. The second scenario assumed attendance at King George Sound purse seine fishing grounds by only $\sim 50\%$ of WA breeding pairs (i.e. mean of 13 570), derived from supplementary information provided by Lavers (2015) for colonies between approximately 116°E and 119°E . This spatial scale was based on limited satellite tracking data showing flesh-footed shearwaters, released from their breeding colony in King George Sound, foraged up to 300 km from the release location (Powell, 2009).

To estimate PBR for the two scenarios, each based on 5000 re-sampled values of N_b , A , S_a , and P_b , the maximum annual growth rate of the population (λ_{\max}) under optimal conditions was first approximated from A and S_a using the allometric approach described by Niel and Lebreton (2005):

$$\lambda_{\max} = \exp \left[\left(A + \frac{S_a}{\lambda_{\max} - S_a} \right)^{-1} \right].$$

Assuming a constant fecundity and constant adult survival, the intrinsic rate of natural increase for the population (r_{\max}) was then calculated as

$$r_{\max} = \lambda_{\max} - 1.$$

For each scenario of flesh-footed shearwater breeding pair numbers (N_b), the minimum population size (N_{\min}) was estimated by the method of Richard et al. (2011):

$$N_{\min} = \frac{2N_b}{P_b} S_a^{1-A}.$$

The PBR was then calculated from estimates of r_{\max} and N_{\min} as

$$\text{PBR} = 0.5 r_{\max} N_{\min} f.$$

The parameter f is referred to as a recovery factor, set between 0.1 and 1 to reflect the quality of information and account for the possible overestimation of PBR caused by the approximation of r_{\max} and N_{\min} (Dillingham and Fletcher, 2011). As recommended for species listed as Near Threatened (e.g. Wade, 1998; Dillingham and Fletcher, 2008), the value of f for flesh-footed shearwaters was specified as 0.3. This is more conservative than the multiplier of 0.41 used by Richard and Abraham (2015) for flesh-footed shearwaters, which a simulation study indicated was sufficient to maintain the population above half the carrying capacity after 200 years (with a 95% probability), in the presence of environmental variability (Richard and Abraham, 2013).

For each population size scenario, the 5000 PBR estimates generated from the re-sampled values of each key life history parameter were used to calculate the median PBR and the lower and

Table 1. Parameter estimates and associated distributions used for estimating the PBR of flesh-footed shearwaters in WA.

Parameter	Distribution	Mean	Standard deviation	Source
Age at first reproduction, A (years)	Normal	6.7	0.8	Barbraud <i>et al.</i> (2014)
Adult survival, S_a (year ⁻¹)	Normal	0.93	0.01	Barbraud <i>et al.</i> (2014)
Proportion breeding annually, P_b	Logit-normal	0.9	0.05 ^a	Richard and Abraham (2015)
Number of breeding pairs, N_b	Log-normal	27 141 (WA) 13 570 (116–119°E)	0.1 ^a	Means derived from Lavers (2015), distribution and variance used by Richard and Abraham (2015)

The number of breeding pairs considered in each of the two scenarios (assuming that the fishery impacts the whole WA population or a smaller component from colonies between 116°E and 119°E) was used to derive a conservative PBR estimate of this parameter based on the first quartile (25th percentile) of this distribution.

^aStandard deviation on the transformed (log or logit) scale.

upper 95% CLs, which were derived from the 2.5th and 97.5th percentiles of the estimated distribution, respectively. The estimates of PBR were compared to the estimated total number of flesh-footed shearwater mortalities in King George Sound (N_m) for 2016/2017 and 2017/2018 to determine the probability that the mortalities exceeded the PBR in each year.

Results

Temporal patterns in bycatch mortalities

Between 2009/2010 and 2017/2018 purse seine fishers in King George Sound recorded 5232 fishing trips in which they landed fish, during which they reported 553 flesh-footed shearwater mortalities on CDRs. The bycatch mortality rate per fishing trip was highly seasonal, peaking in March and April (Figure 2a) and coinciding with the period of highest fishing effort between March and May, when 2647 (51%) of those trips were undertaken (Figure 2b). The concurring peaks in mortality rate and fishing effort combined to amplify overall bycatch, resulting in a mean of 92% of annual mortalities recorded in March and April and 42% during the first half of April alone. The ratio γ_o of off-peak to peak period mortality rates estimated by the fitted GLM was 0.050 (95% CLs 0.031–0.081).

The seasonal pattern of bycatch mortality rate per fishing trip described above was corroborated by the known life history stages recorded for WA flesh-footed shearwaters (Warham, 1958; Powell, 2004; Powell *et al.*, 2007) (Figure 2a). No mortalities were recorded in any half-month from June to mid-September in any year, when flesh-footed shearwaters undertake their trans-equatorial migration. From mid-September to mid-December, a period encompassing the short and synchronous phases of courtship and mating (11 days) and egg laying (16 days), only 11 mortalities had been recorded. From mid-December to mid-February, which includes the 17-day hatching phase in January, the mean mortality rates per fishing trip calculated by the GLM were relatively low, ranging between 0.01 and 0.02. Then, in close association with the chick's increasing food requirements, the mean mortality rate progressively increased from 0.05 in late February to a peak of 0.44 in early April. This peak was significantly higher than all other half-months except late March and coincides with chicks attaining peak body mass around mid-April. The mortality rate then fell rapidly with two successive and significant declines, to 0.19 in late April and to <0.01 in early May. The decline corresponded to the cessation of feeding and onset of fledging, after which fledglings feed independently of their parents. Thus, the mean mortality rate of breeding flesh-

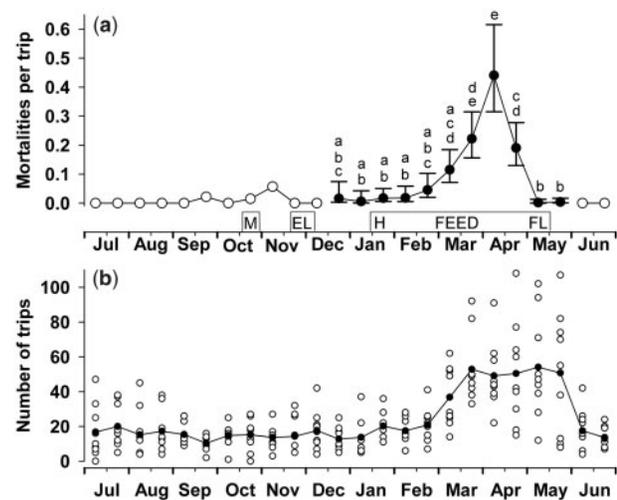


Figure 2. (a) The rate of flesh-footed shearwater mortalities per trip in King George Sound (Zone 1 of the SCPSF) recorded by purse seine fishers in each half-month from 1 July 2009 to 30 June 2018, and the approximate timing of courtship and mating (M), egg laying (EL), hatching (H), chick feeding (FEED), and fledging (FL). Black circles: mean mortality rates ($\pm 95\%$ CLs) for each half-month calculated by a GLM with the results of pairwise comparisons of significant differences ($\alpha < 0.05$) between half-months denoted by the letters above estimates; white circles: nominal mean mortalities, i.e. total mortalities divided by total number of trips. (b) The total number of fishing trips by purse seine vessels in King George Sound that landed fish in each half-month from 1 July 2009 to 30 June 2018. White circles: number of fishing trips in each year; black circles: mean.

footed shearwaters had a close temporal association with the food requirements of their chicks.

Independent bycatch observation

During March and April of 2007, 2008, 2017, and 2018, observers accompanied fishers on 222 fishing trips and recorded 171 flesh-footed shearwater bycatch mortalities (Table 2). While the proportion of trips landing fish that were observed in 2007 and 2008 is unknown, the observer coverage of such trips in 2017 and 2018 was 36 and 27%, respectively. Flesh-footed shearwaters were the only seabird species observed as bycatch in 2017 and 2018, always attending observed fishing operations in numbers estimated at up to several thousand (<5000). While their presence in numbers

Table 2. Details from flesh-footed shearwater bycatch observer programme and fishing effort used to estimate bycatch mortalities during the peak (observed) and off-peak (unobserved) periods for the South Coast Purse Seine Fishery in King George Sound (Zone 1) in four separate quota years.

Variable	2006/2007	2007/2008	2016/2017	2017/2018
Dates of observer trips	6 March–15 April	4 March–29 April	16 March–28 April	1 March–27 April
Number of observed trips with net deployment	49	70	51	52
Number of observed mortalities	54	55	30	32
Estimated mean mortality per trip μ_m (95% CLs) for peak period, excluding cryptic mortality	1.10 (0.56–1.96)	0.79 (0.34–1.58)	0.59 (0.25–1.17)	0.62 (0.33–1.05)
Number released alive and unharmed	N/A	N/A	118	130
Estimated mean mortality per trip for peak period, including cryptic mortality, μ_p (95% CLs)	N/A	N/A	0.79 (0.34–1.57)	0.82 (0.44–1.43)
Estimated mean mortality per trip for off-peak period, including cryptic mortality, μ_o (95% CLs)	N/A	N/A	0.03 (0.01–0.07)	0.04 (0.02–0.08)
Number of observed trips with fish landed	N/A	N/A	36	47
Total number of trips landing fish during peak period	N/A	N/A	99	176
Percent observer coverage during peak period	N/A	N/A	36%	27%
Estimated number of peak period trips with net deployment T_p (95% CLs)	N/A	N/A	140 (114–166)	195 (174–215)
Total number of trips landing fish during off-peak period	N/A	N/A	241	258
Estimated number of off-peak period trips with net deployment T_o (95% CLs)	N/A	N/A	340 (277–403)	285 (256–315)
Total annual mortality estimate, N_m (95% CLs)	N/A	N/A	123 (52–251)	172 (91–302)

This table includes estimates of mortality rates per fishing trip, the number of fishing trips landing fish (i.e. Catch and Disposal Record lodged), the estimated number of fishing trips with net deployment irrespective of whether fish were landed, and the estimated total annual number of mortalities. The off-peak period extends from mid-September to May (inclusive), excluding the peak period of March and April. N/A, not available due to insufficient data records.

>1000 was common on trips when no mortalities were observed, most mortalities occurred when there were more than 200 flesh-footed shearwaters present.

In all four observer programmes undertaken during the peak period for bycatch, the number of mortalities observed per fishing trip was highly skewed and well described by the negative binomial distribution (Figure 3). No concentration of mortalities on individual vessels was evident. The maximum number of bycatch mortalities recorded on a trip was 15 in both 2007 and 2008 and 8 and 10 in 2017 and 2018, respectively. In all years, between 27 and 31% of all bycatch mortalities were recorded on a single trip, yet no mortalities were observed on between 70 and 82% of trips. There were no significant differences in the estimated mean observed mortality rate per trip (μ_m and 95% CLs) among years, which ranged from 0.59 (0.25–1.17) in 2017 to 1.10 (0.56–1.96) in 2007 (Table 2).

Bycatch mortality estimates for 2016/2017 and 2017/2018

After accounting for potential cryptic mortalities undetected by observers during the 2017 and 2018 monitoring programme, the mean bycatch mortality rate estimated for each peak period (μ_p and 95% CLs) was 0.79 (0.34–1.57) and 0.82 (0.44–1.43) per trip in 2017 and 2018, respectively (Table 2). The estimated number of trips with net deployment undertaken during those peak periods (T_p and 95% CLs) was 140 (114–166) in 2017 and 195 (174 to 215) in 2018 (Table 2), resulting in the estimated total number of mortalities during the peak period of 110 (46–223) and 161 (85–280), respectively.

Based on the ratio of off-peak to peak mortality rates estimated from the fishery-dependent data, γ_o , the mean mortality rate for the off-peak (unobserved) period (μ_o and 95% CLs) was estimated as 0.03 (0.01–0.07) in 2016/2017 and 0.04 (0.02–0.08) in 2017/2018 (Table 2). The estimated numbers of fishing trips with net deployment during those off-peak periods (T_o and 95% CLs) were 340 (277–403) in 2016/2017 and 285 (256–315) in 2017/2018. The resulting estimates of off-peak bycatch mortalities for 2016/2017 and 2017/2018 were 13 (5–30) and 12 (5–23), respectively. In total, combining the peak and off-peak periods and accounting for cryptic mortality, the estimated annual numbers of flesh-footed shearwater mortalities from purse seine fishery bycatch in King George Sound (N_m and 95% CLs) were 123 (52–251) in 2016/2017 and 172 (91–302) in 2017/2018 (Table 2).

Bycatch risk to the flesh-footed shearwater population

Based on published estimates of the mean age at first reproduction and adult survival of flesh-footed shearwaters (6.7 years and 0.93 year⁻¹, respectively; Barbraud et al. 2014), the mean maximum population growth rate was estimated as 1.08 year⁻¹. Accounting for uncertainty around those two input parameters (Figure 4), the results indicate that the population under optimal conditions has the ability to increase by 7–10% (95% CLs) each year. Based on conservative estimates of breeding pair numbers in WA (within the lower quartile of the estimated distribution) and assuming that around 90% of adults breed in any given year (Figure 4), the mean minimum overall population size (including juveniles and non-breeding adults) was estimated as 82 034 individuals (95% CLs 65 569–104 068). For the second scenario, the mean number of individuals from colonies between 116°E and 119°E was estimated as 41 025 individuals (95% CLs 32 866–52 159).

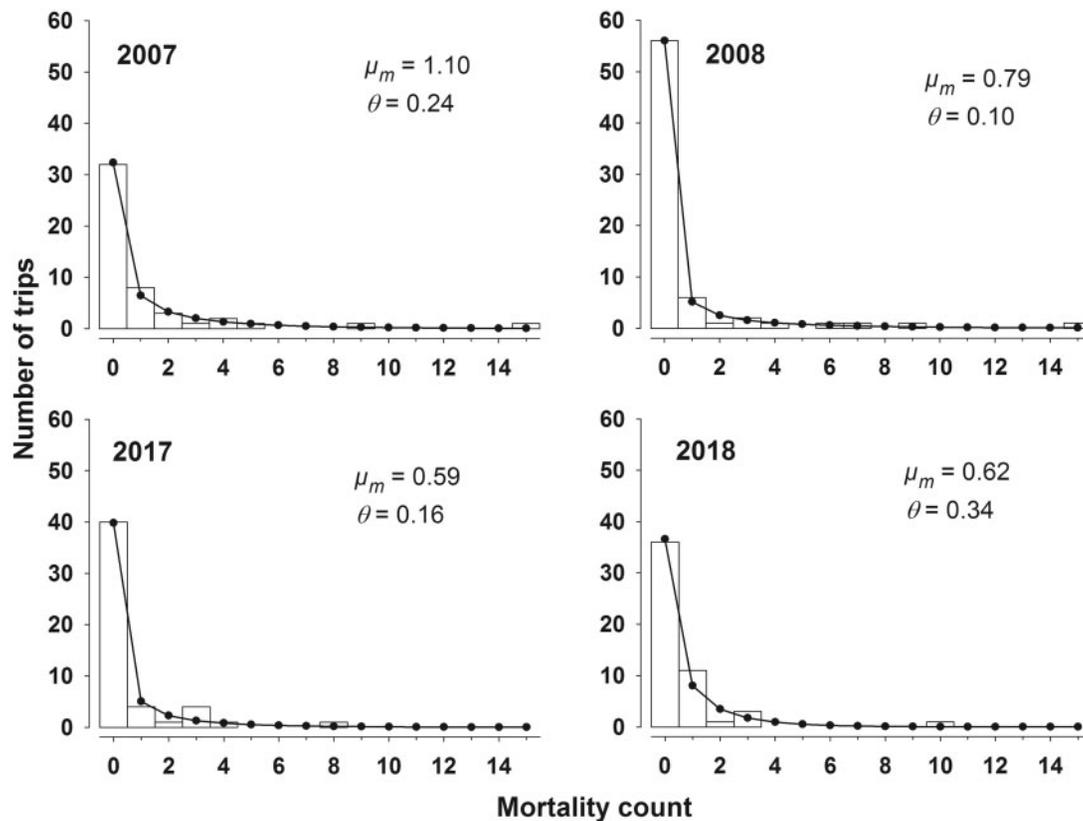


Figure 3. Frequency distribution of flesh-footed shearwater mortalities per trip recorded by observers on board South Coast Purse Seine Fishery vessels fishing in King George Sound (Zone 1) in March and April of 2007, 2008, 2017, and 2018 (bars), and the mean mortality rate per trip (μ_m), dispersion (θ), and fitted negative binomial frequency distribution (line).

As the frequency distributions for the PBR estimates were positively skewed, results have been presented as box-and-whisker plots with the median used as the preferred measure of central tendency (Figure 5). For the first scenario assuming that the purse seine fishery impacts the overall WA population of breeding flesh-footed shearwaters, the median estimate of PBR was 989 (95% CLs 742–1304). Assuming that only ~50% of this population (colonies between 116°E and 119°E) has the potential to interact with the purse seine fishery in King George Sound approximately halved the median estimate of PBR to 495 (369–660). The probability that the estimated annual bycatch mortality of flesh-footed shearwaters in the King George Sound purse seine fishery in 2016/2017 and 2017/2018 exceeded the PBR for either of the two population scenarios was <0.5%, noting that this did not consider other potential sources of anthropogenic mortalities.

Discussion

This article adds to a small number of emerging studies of seabird bycatch in purse seine fisheries, which are helping to bridge a key information gap in the understanding of the impact of seabird bycatch in fisheries globally (Pott and Wiedenfeld, 2017). The study of flesh-footed shearwater bycatch in a sardine purse seine fishery on the southern coast of WA demonstrates large temporal variability in mortalities that is closely linked to the bird's breeding cycle. As mortality events on fishing trips in King George Sound were a relatively rare occurrence for much of the year, and with most recorded during the late stage of chick provisioning in March and April, this study

highlights the importance of accounting for such temporal variation in the estimation of total annual bycatch mortalities of this species. A recently reported estimate of >880 mortalities per year from this fishery by Lavers (2015) likely represents an extrapolated overestimate, given that it was based on “up to six adult birds are killed per boat per day”. Although Lavers (2015) suggested that purse seine fisheries operating on both the south and lower west coast of WA represent a threat to flesh-footed shearwaters, there are no records of interactions on the lower west coast, which is a separately managed fishery, likely due to minimal overlap in that region with foraging flesh-footed shearwaters during their breeding season (Powell, 2009; Lavers *et al.*, 2019). On the south coast very few fishery-dependent mortalities have been recorded ($n=2$) from the comparatively low fishing effort well to the east of King George Sound. However, there has been no independent observer coverage outside the Sound.

Temporal patterns in bycatch mortalities

The temporal pattern of flesh-footed shearwater bycatch recorded by purse seiners within King George Sound closely corresponded to documented life history and breeding biology phases for the population in WA. Although the fishery operates year round, mortalities were only recorded during the southern hemisphere phase of their life cycle. The mortality rate per fishing trip appeared closely linked to the chick's expected food requirements, peaking around early April when chicks attain peak body mass (Powell, 2004; Powell *et al.*, 2007), then rapidly declining with the onset of fledging. One explanation for this could be a

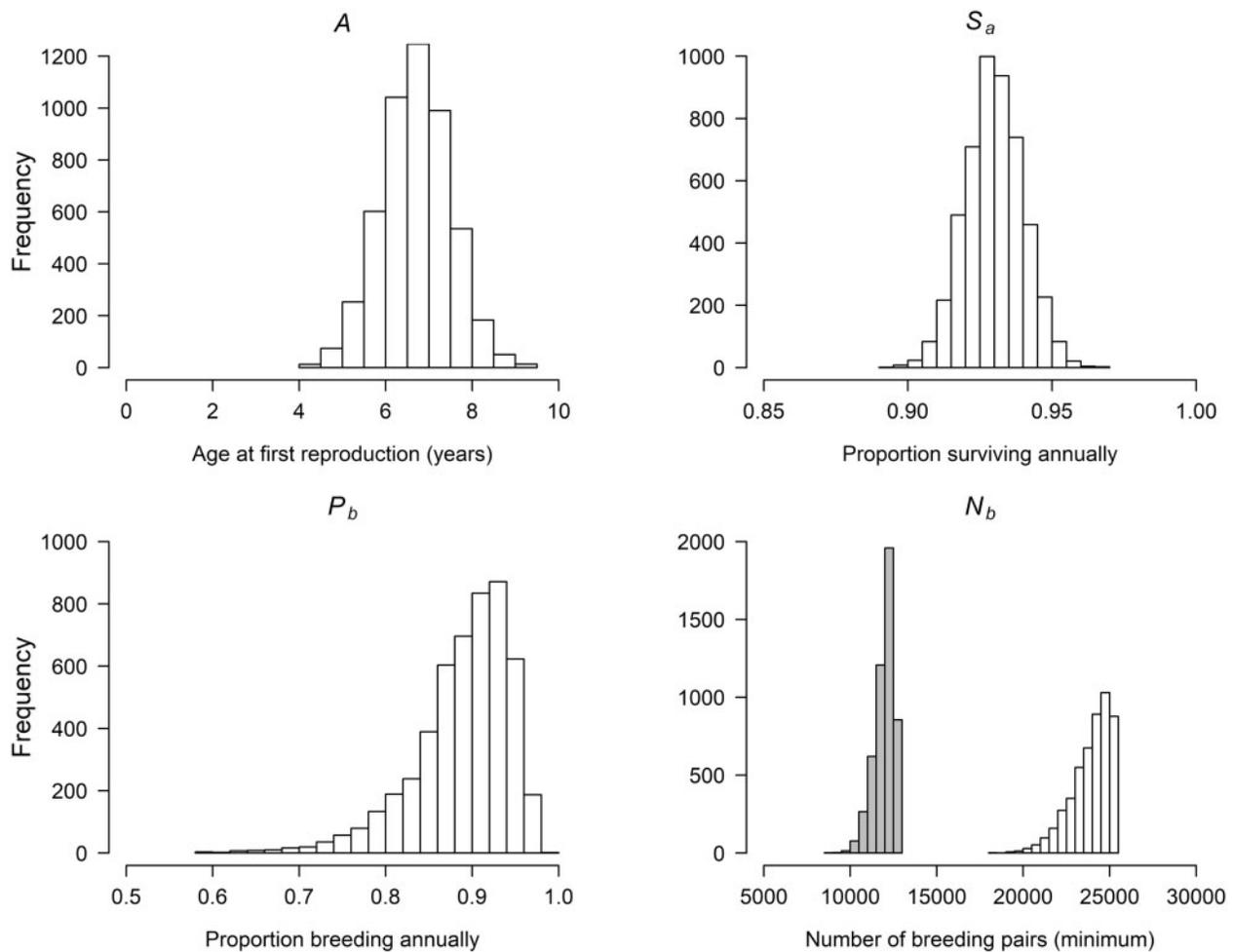


Figure 4. Distributions of re-sampled parameter estimates ($n = 5000$) used to estimate PBR for flesh-footed shearwaters in WA, including age at first reproduction A , annual adult survival S_a , proportion of adults breeding annually P_b , and the two scenarios for the number of breeding pairs N_b impacted by the purse seine fishery, shown as the whole WA population in white and a smaller component from colonies between $\sim 116^\circ\text{E}$ and 119°E in grey (see also Table 1).

stronger determination in parents to meet the increased food requirements of chicks at this time by more readily entering and remaining inside the net to pursue sardines. Such risky behaviour made more birds susceptible to entrapment and drowning if a net fold developed. This hypothesis was supported by anecdotal reports from fishers of flesh-footed shearwaters tenaciously following sardine-laden purse seine vessels almost all the way back to port only during March and April.

Another explanation for the seasonal peak in the mortality rate per fishing trip may be the simultaneous increase in the inshore abundance of sardines, including inside King George Sound, which results in increased purse seine fishing effort from March to May. Australian sardines are a key prey species for many higher trophic level predators (Goldsworthy *et al.*, 2013) including the western Australian salmon (*Arripis truttaceus*), which undertakes a westward nearshore spawning migration along the WA south coast around the same time (Malcolm, 1960). Similarly, flesh-footed shearwaters appear to have timed chick rearing to exploit the increased nearshore abundance of sardines, and may forage closer to shore and fishing operations at this time. However, this hypothesis does not explain the fine-scale temporal association of

bycatch mortalities per trip with chick's food requirements, nor the large and rapid changes in bycatch rate over as little as half a month within this period.

The rapidity of changes in the bycatch mortality rate recorded by fishers can be attributed, in part at least, to the synchronous phases of the breeding biology of flesh-footed shearwaters recorded by Powell *et al.* (2007). As the mating phase of flesh-footed shearwaters in late October occurred over only 11 days, possibly a means of avoiding conflict over nest burrow ownership among breeding pairs (Powell *et al.*, 2007), egg laying and hatching phases are also short and synchronous. Chicks, all being at a similar age, grow and develop in synchrony and so their food requirement should peak almost simultaneously in late March and early April, when the bycatch rate also peaks. The period of cessation of chick feeding at, or just before, fledging should therefore also be somewhat synchronous, which is confirmed by two successively large, significant, and rapid reductions in the mortality rate into late April and early May. Departure for the northern hemisphere commences shortly after. Thus, the bycatch rate appears linked to changes in seabird behaviour at fishing operations elicited by changing food requirements of their chicks. This process may also affect bycatch rates of other

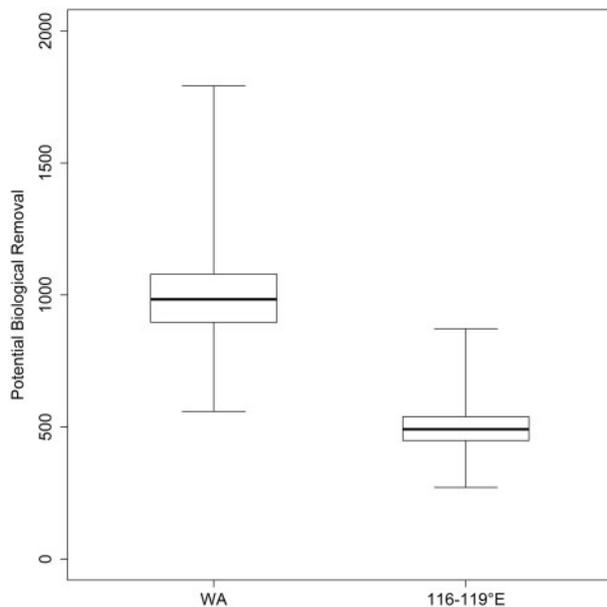


Figure 5. Estimates of PBR for flesh-footed shearwaters in WA, calculated from re-sampled values of four input parameters ($n = 5000$, see Figure 4) for two scenarios assuming that the purse seine fishing operations have the potential to interact with all adults in the WA population (left), or a smaller component ($\sim 50\%$) from breeding colonies located between $\sim 116^\circ\text{E}$ and 119°E (right). For both scenarios, the horizontal line shows the median estimate, the box represents the first and third quartiles (25th and 75th percentiles), and the whiskers show the full range of estimated values.

coastal purse seine fisheries taking small pelagic fish in the vicinity of shearwater breeding colonies, such as the closely related pink-footed shearwater (*Ardenia creatopus*) off Chile (Suazo *et al.*, 2014; Carle *et al.*, 2019).

A third possible explanation for increased bycatch rate during March and April is through longer duration and more distant foraging trips during the late chick rearing phase, as shown for flesh-footed shearwaters nesting on Lord Howe Island (Thalmann *et al.*, 2009, 2010), facilitating greater attendance at fishing operations. While limited tagging data suggest that flesh-footed shearwaters on the southern coast of WA primarily forage in waters up to 300 km from their breeding colonies (Powell, 2009), there is a possibility that flesh-footed-shearwaters from more distant colonies undertake extended foraging trips to King George Sound during the period of chick rearing. Trips >700 km during late chick rearing have been recorded for the Lord Howe Island colony (Thalmann *et al.*, 2009). As discussed below, further research on the spatial foraging patterns of this species in WA is needed to improve the current understanding of how the fishery in King George Sound impacts on the broader population.

The close temporal association of the fishery-dependent bycatch mortality rate with the chronology of the flesh-footed shearwater breeding cycle suggests that these data provide a reliable index of relative risk, and a useful guide for timing mitigation initiatives. Considering also the compounded risk from elevated fishing effort during the peak period for interactions, the findings of this study support the focus of mitigation and

observer programmes during March and April. Mortalities reported outside March and April were rare, suggesting that this off-peak period is a comparatively low risk, although this has not been confirmed by observer trips. To estimate the low off-peak mortality rates using independent observers would require a very high level of coverage over an extended period; however, this would be costly given the remote area in which this fishery operates.

Independent bycatch observation

The highly skewed frequency distribution of observed mortalities was a feature of all observer programmes, with most observed trips resulting in zero mortalities and a high proportion of mortalities resulting from very few trips. Similar results, also approximated by the negative binomial distribution, have been recorded for seabird bycatch in longline (Murray *et al.*, 1993), trawl (Bartle, 1991, assessed by Hilborn and Mangel, 1997), and gillnet fisheries (Bærum *et al.*, 2019). Weather conditions and spatio-temporal overlap between seabirds and fishers were suggested causes. As has also been shown for albatross bycatch in a longline fishery (Gilman *et al.*, 2014), the observer data from 2017 and 2018 indicated that the majority of bycatch mortalities occurred when a large number of flesh-footed shearwaters were present at the fishing observations. Flesh-footed shearwater bycatch in King George Sound arises when birds are trapped by purse seine net folds, suggesting that the frequency of the formation of such folds among trips is low. Although the large majority of net deployments run smoothly, with little risk of bycatch, the loss of net control resulting in substantial folds appears to occur sporadically despite the best effort of skilled fishers. If this occurs at a time when birds are more likely to pursue sardines inside the net to meet the increased food requirements of their chicks, an unusually high mortality count may result.

A number of bycatch mitigation measures have been voluntarily implemented by the SCPSF in recent years; however, their efficacy was not able to be assessed by this study due to the potential impact of multiple factors acting simultaneously to influence bycatch. For example, some vessels that fished in 2017 and 2018 had attached a weighted line ($0.2\text{--}0.3\text{ kg m}^{-1}$) to the net, parallel to and about 5–8 m from the float line, to maintain vertical tension and prevent net folds developing. Although the mean bycatch mortality per trip was slightly lower in both years when weighted lines were used, this was not considered significant because other differences in fishing gear among vessels may have impacted this result, e.g. net length and the number of powered rollers used to retrieve the net which determines the amount of tension that can be applied. Similarly, although the mean mortality rate was lower at night in both years, other factors, including weighted lines, may have been influential. A lower bycatch rate at night, however, is consistent with the strongly diurnal timing of foraging dives by flesh-footed shearwaters breeding on Lord Howe Island off Australia's east coast (Thalmann *et al.*, 2009) and the lower bycatch rate of that population by long-liners at night (Baker and Wise, 2005).

Bycatch risk to the flesh-footed shearwater population

The PBR approach used in this study to evaluate the risk of fisheries bycatch to flesh-footed shearwaters in WA has been widely applied to assess seabird bycatch risk in New Zealand fisheries (e.g. Richard and Abraham, 2015). For this study, it has provided a conservative estimate of the level of incidental mortalities that

the flesh-footed shearwater population in WA can likely sustain while explicitly accounting for uncertainty around estimates of key life history parameters. The finding that the 95% CLs for estimated total annual bycatch mortalities in the King George Sound purse seine fishery for 2016/2017 and 2017/2018 were below and did not overlap the 95% CLs of the most conservative PBR estimate suggests that, for those years, removals by this fishery in isolation were well below the maximum level that can be sustained. It is recognized, however, that future assessments of the flesh-footed shearwater population in WA also need to consider impacts from other fisheries including recreational, as well as anthropogenic mortalities from introduced species, plastic ingestion, mercury contamination, and climate change (Lavers, 2015). They should also consider the potential beneficial effects on the population of the enhanced food supply from the fishery, as has been demonstrated for other species (e.g. Oro, 1996).

While this study considered two alternative scenarios to examine the effect of the purse seine fleet on a smaller component of the overall WA population that included only colonies closer to King George Sound, it is recognized that the impact of bycatch mortalities on individual breeding colonies is likely to vary with distance from the fishing operations, depending on flesh-footed shearwater foraging patterns. Satellite transmitters deployed on three birds from a King George Sound colony in early March 2008 showed that they foraged up to 300 km from the release point (Powell, 2009), further than the geographical range of colonies used for the more conservative PBR estimate. The high proportion of male birds in the purse seine bycatch (Lavers, 2015) suggests a different foraging pattern to females during chick rearing. To enable more complex modelling of the fishery impacts on flesh-footed shearwaters in WA, further research on the at-sea distribution of flesh-footed shearwaters from WA colonies during chick rearing is required.

Acknowledgements

We thank the at-sea observers for collecting the bycatch data, and the purse seine fishers in King George Sound who welcomed them aboard. We are also grateful to Albany DPIRD staff for assistance with the CDR database, to Norm Hall for discussions on various statistical and modelling analyses, and to multiple reviewers of this manuscript.

Data availability

The data generated during the current study will be shared on reasonable request to the corresponding author in a form protecting the privacy of individuals due to confidentiality requirements. Data underlying this article provided by the Western Australian Fisheries Industry Council (WAFIC) will be shared on reasonable request to the corresponding author subject to WAFIC's permission.

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