

# Clownfish metapopulation persistence draft

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## Introduction

Metapopulation dynamics and persistence depend on the demographic rates at each  
3 patch and the connectivity among patches (e.g. Hastings and Botsford, 2006) OTHER

CITATIONS, maybe Hanski?. Many marine species exist in metapopulations, consisting of patch populations connected through dispersal (though differing from one  
6 definition of metapopulation in that individual patches are unlikely to go extinct)  
(Kritzer and Sale, 2006). Assessing demographic parameters and levels of connectivity has been particularly challenging for marine species, where much of the mortality  
9 and movement happens at larval and juvenile stages when individuals are hard to track and have the potential to travel long distances with ocean currents (e.g. Kritzer and Sale, 2006)(CITATONS, maybe Botsford et al. 2009, Roughgarden check others,  
12 Cowen and Sponagule). A need to understand metapopulations for conservation and management, such as siting marine protected areas (CITATONS), however, has led to a large body of theory describing how marine metapopulations might persist.

15 For any population to persist, individuals must on average replace themselves during their lifetimes. In non-spatially structured populations, we use criteria such as the average number of recruiting offspring contributed by each individual during  
18 its life (called  $R_0$  when the population is age-structured and density-independent) or the growth rate of the population (such as the dominant eigenvalue  $\lambda$  of an age-structured Leslie matrix) (Caswell, 2001; Burgess et al., 2014). To assess replacement,  
21 metrics must take into account the demographic processes across the whole life cycle, including how likely individuals are to survive to the next age or stage, their expected fecundity at each stage, and the survival of any offspring produced to recruitment.

24 In a spatially-structured population, persistence still requires replacement but in addition to assessing whether the reproductive output and survival of a population is sufficient, we must also consider how the offspring are distributed across space.

27 The spread of offspring is often described using dispersal kernels, probability density  
functions that give the relative number of settlers with increasing distance from the  
origin patch (e.g. Bode et al., 2018). Connectivity can also be described using a con-  
30 nectivity matrix, where entries give the probability of dispersing from one patch to  
another, either found by discretizing the dispersal kernel or through direct estimates  
of pairwise exchange among patches (CITATION). A long-held paradigm suggested  
33 that marine larvae were well-mixed and dispersed far on ocean currents (Roughgar-  
den et al., 1988), suggesting widespread connectivity. With the ability to estimate  
connectivity through natural tags such as otolith microchemistry or genetics and the  
36 realization that larvae can alter their dispersal through behavior (e.g. Morgan et al.,  
2009), the paradigm is shifting and local persistence of marine populations is seeming  
more possible.

39 When we consider both the demographic processes within patches and the con-  
nectivity among them, a metapopulation can persist in two ways: 1) at least one  
patch can achieve replacement in isolation, or 2) patches receive enough recruit-  
42 ment to achieve replacement through loops of connectivity with other patches in the  
metapopulation (Hastings and Botsford, 2006; Burgess et al., 2014). In the first case  
(termed self-persistence), enough of the reproductive output produced at a patch is  
45 retained at the patch for the patch, and therefore the metapopulation as a whole, to  
persist. In the second (network persistence), closed loops of connectivity among at  
least some of the patches - where individuals from one patch settle at another and  
48 eventually send offspring back to the first in a future generation - provide the patch  
with enough recruitment to persist in the network. Though it has been challeng-

ing to estimate the parameters necessary to understand how actual metapopulations  
51 persist, a large work of theory developed to guide marine protected area helps pre-  
dict when each type of persistence is likely to occur (i.e. large patches relative to the  
mean dispersal distance are likely to be self-persistent Botsford et al., 2001).

54 New ways of identifying individuals and determining their origins, such as otolith  
microchemistry and genetic parentage analysis (e.g. Wang, 2004, 2014), however, are  
making it increasingly possible to estimate both the demographic [ADD EXAMPLE  
57 CITATIONS] and the connectivity (e.g. Hameed et al., 2016; Almany et al., 2017)  
parameters necessary to assess persistence in real metapopulations. We might expect  
that populations on isolated islands are the most likely to be self-persistent and  
60 Salles et al. (2015) find that the population of orange clownfish (*Amphiprion percula*)  
at isolated Kimbe Island in Papua New Guinea can likely persist without outside  
immigration. In contrast, a metapopulation of bicolor damselfish (*Stegastes partitus*)  
63 across four isolated islands in the Bahamas does not appear able to persist without  
outside input (Johnson et al., 2018). For populations that exist in patches along  
a continuous coastline, rather than on separate islands, however, it is still an open  
66 question of how patches interact and the scale of metapopulation persistence.

We further our understanding of metapopulation dynamics in a network of patches  
along a coastline through a study of yellowtail clownfish (*Amphiprion clarkii*) in the  
69 Philippines. We assess persistence for all patches of habitat within a 30 km stretch  
of coastline, which exceeds estimates of the dispersal spread for this species (Pinsky  
et al., 2010), suggesting the network is likely to operate as a contained metapopula-  
72 tion. With seven years of sampling data, we are able to estimate persistence metrics

and replacement over the longer term, rather than just capturing a snapshot of the population dynamics. Our annual sampling also enables us to estimate abundance each year and investigate dynamics through time to compare with the replacement-based persistence metrics. Here, we use a long-term data set from habitat patches on a continuous set of coastline to understand persistence within a local network.

## Methods

### Study system

We focus on a tropical metapopulation of yellowtail clownfish (*Ampiprion clarkii* in the Philippines. Like many clownfish species, yellowtail clownfish have a mutualistic relationship with anemones, where small colonies of fish live (Buston, 2003; Fautin et al., 1992). Yellowtail clownfish are protandrous hermaphrodites and maintain a size-structured hierarchy; within an anemone, the largest fish is the breeding female, the next largest is the breeding male, and any smaller fish are non-breeding juveniles. The fish on an anemone maintain a strict social and size hierarchy (Buston, 2003), with fish moving up in rank to become breeders only after the larger fish have died. In the tropical patch reef habitat of the Philippines, yellowtail clownfish spawn once per lunar month from November to May, laying clutches of benthic eggs that the parents protect and tend (Ochi, 1989). Larvae hatch after about six days and spend 7-10 days as pelagic larvae before returning to reef habitat to settle in an anemone (Fautin et al., 1992).

Clownfish are particularly well-suited to metapopulation studies due to their lim-

ited movement as adults and clearly patchy habitat. Once fish have settled, they tend to stay within close proximity of their anemones [XX meters, CITATION]. This  
 96 makes fish easier to relocate for mark-recapture studies and simplifies the exchange between patches to only the dispersal during the larval phase. Patches, whether considered to be the reef patch or the anemone territory of the fish, are clearly discrete and easily delineated, which makes determining the spatial structure of the  
 99 metapopulation clear. Additionally, clear patches make it easier to assess how much of the site has been surveyed. These simplifying characteristics in habitat and fish  
 102 behavior make clownfish and other similarly territory-based reef fish useful model systems for studies of metapopulation dynamics and persistence (e.g. Buston and DAloia, 2013; Salles et al., 2015; Johnson et al., 2018).

## 105 **Field data collection**

We focus on a set of seventeen patch reef sites spanning approximately 30 km along the western coast of Leyte island in the Philippines (MAP FIGURE). The sites  
 108 consist of rocky patches of coral reef and are separated by sand flats. Previous work using genetic isolation by distances estimated that yellowtail clownfish larvae have a dispersal spread of about 10 km (range 4-27 km Pinsky et al., 2010), so our sites were  
 111 selected to cover and exceed that range. On the north edge, the sites are isolated from nearby habitat with no additional reef habitat for at least 20 km.

TO ADD: Figure 1: map of study sites, picture of clownfish [(Add figure with  
 114 map of study sites and a picture of a clownfish(?).]

Since 2012, members of the team have sampled fish and habitat at most of the

sites annually. During sampling, divers using SCUBA and tethered to GPS readers  
117 swim the extent of each site. Divers visit each anemone inhabited by yellowtail  
clownfish, tagging the anemone to be able to track anemones through time. At each  
anemone, the divers attempt to catch all of the yellowtail clownfish 3.5 cm and larger,  
120 taking a non-lethal tail fin-clip from each for use in genetic analysis, measuring the  
fork length, and noting the tail color (as an indicator of life stage). Starting in  
the 2015 field season, fish 6.0 cm and larger are tagged with a passive integrated  
123 transponder (PIT) tag, unless already tagged. Divers also looked for eggs around  
each anemone and measured and photographed any clutches found. In total, we took  
fin clips from XX fish and PIT-tagged XX fish across all years and sites combined,  
126 with an average of XX fish clipped and XX fish tagged per year.

### **Genotyping and parentage analysis**

[Add in brief overview of genetic methods, with citations to papers with relevant  
129 methods and to Katrina's connectivity paper. Include number of fish genotyped.]

## Estimating inputs from empirical data

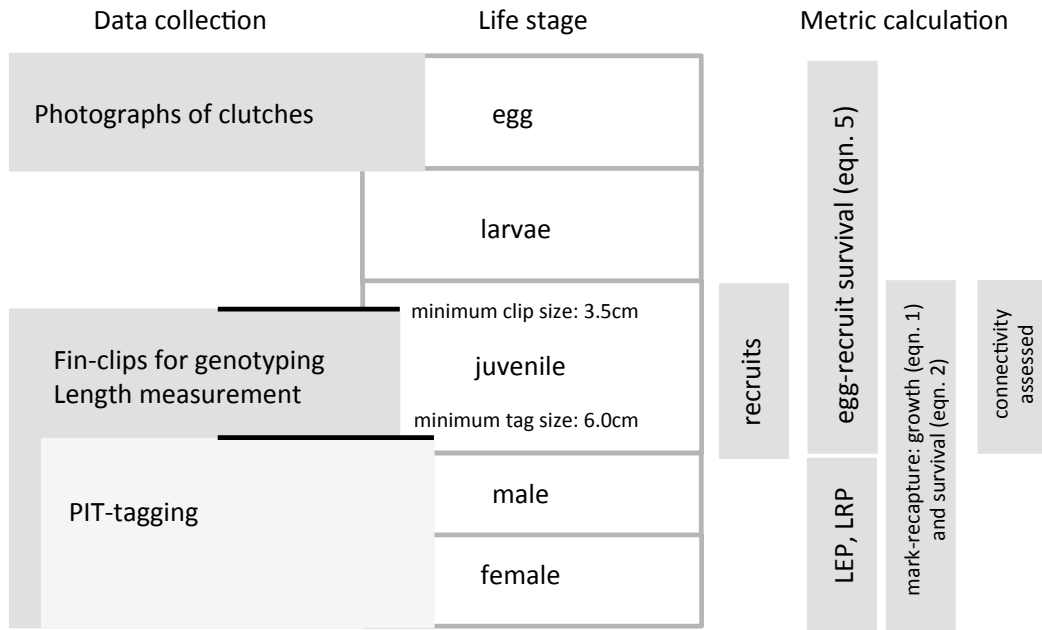


Figure 1: Here, we show the data collected for fish at each life stage (life stage boxes are not scaled by length of stage) and how the empirical data fit into the metric calculations.

### Growth and survival: mark-recapture analyses

132 We mark fish through both genetic samples and PIT tags, allowing us to estimate growth and survival through mark-recapture. After matching up recaptures of the



same fish identified by genotype or tag, we have a set of encounters of XX marked  
 135 fish that includes size and stage at each capture time.

For growth, we estimate the parameters of a von Bertalanffy growth curve (Fabens,  
 1965) in the growth increment form relating the length at first capture  $L_t$  to the  
 138 length at a later capture  $L_{t+1}$  (Hart and Chute, 2009), where  $L_\infty$  is the average  
 asymptotic size across the population and  $K$  controls the rate of growth:

$$\begin{aligned} L_{t+1} &= L_t + (L_\infty - L_t)[1 - e^{(-K)}] \\ &= e^{(-K)}L_t + L_\infty[1 - e^{(-K)}]. \end{aligned} \tag{1}$$

We see from eqn. 1 that we would expect the first length  $L_t$  and the second length  
 141  $L_{t+1}$  to be related linearly (Hart and Chute, 2009). From the slope  $m = e^{(-K)}$  and  
 y-intercept  $b = L_\infty[1 - e^{(-K)}]$ , we can estimate the von Bertalanffy parameters, such  
 that  $K = -\ln m$  and  $L_\infty = \frac{b}{(1-m)}$ . We use the first and second capture lengths for  
 144 fish that were recaptured after a year (within 345 to 385 days) to estimate  $L_\infty$  and  $K$ .  
 We have some fish that were recaptured multiple times so we randomly select only  
 one pair of recaptures from each to use in estimating the parameters, then repeat  
 147 this process 1000 times to generate a distribution (Fig. 3b, B.1d).

We use the full set of fish encountered multiple times to estimate annual survival  
 $\phi$  and probability of recapture  $p_r$  using the mark-recapture program MARK imple-  
 150 mented in R (Laake, 2013). We consider several models with year, size, and site  
 effects on the probability of survival and year and size effects on the probability of  
 recapturing a fish on a log-odds scale (see full list in Table A1. For fish that are not  
 153 recaptured at a particular time point, we estimate their size using our growth model

(eqn. 1) and the size recorded or estimated in the previous year. Because fish are not well-mixed at our sites and instead stay quite close to their home anemones, we  
156 need to swim near an anemone to have a reasonable chance of capturing the fish on it. Therefore, we also consider a distance effect on recapture probability; we use the GPS tracks of divers to estimate the shortest distance a diver got to the anemone for  
159 each tagged fish in each sample year and include it as a factor in some of the models.

The best-fit model using model selection with AICc has an effect of fish size on survival and additive effects of fish size and shortest distance to anemone on the  
162 probability of recapture:

$$\log\left(\frac{\phi}{1-\phi}\right) = b_{\phi} + b_a \text{size} \quad (2)$$

$$\log\left(\frac{p_r}{1-p_r}\right) = b_{p_r} + b_1 \text{size} + b_2 d. \quad (3)$$

## Fecundity

We use a size-dependent fecundity relationship, determined using photos of egg  
165 clutches and females (Yawdoszyn, in prep), where the number of eggs per clutch ( $E_c$ ) is exponentially related to the length in cm of the female ( $L$ ) with size effect  $\beta_{\text{size}} = 2.388$ , intercept  $b = 1.174$ , and egg age effect  $\beta_e = -0.6083$  dependent on if  
168 the eggs are old enough to have visible eyes:

$$\ln(E_c) = \beta_l \ln(L) + b_e [\text{eyed}] + b. \quad (4)$$

To get total annual fecundity  $f$ , we multiply the number of eggs per clutch by the number of clutches per year  $c_e = 11.9$ , using the estimate from Holtswarth et al.

171 (2017).

We only consider reproductive effort once the fish has reached the female stage. Though the size at which a fish transitions to become a breeding female  $L_f$  will  
174 depend on the size hierarchy in each particular colony [CITATION], we use the average size recaptured fish were first observed as female for the best estimate.

### Lifetime egg production

177 We use an integral projection model (IPM) (e.g. Rees et al., 2014) to estimate the total number of eggs produced by one individual (lifetime egg production: LEP), starting at the recruit stage, when individuals have settled and survived to a size we  
180 can sample.

In an IPM, the state of the population at time  $t$  is described by the distribution of the population over a continuous trait  $z$ , for which we use size:  $n(z, t)$ . The total  
183 number of individuals in the population at time  $t$  is the integral of the size distribution over size from the lower size bound  $L$  to the upper size bound  $U$ :  $\int_L^U n(z, t) dz$ . The population is projected forward with probability density functions, called the kernel,  
186 that describe the survival, growth, and reproductive output of existing individuals into the next time step.

We initialize the IPM with one recruit-sized individual  $\text{size}_{\text{recruit}}$ :  $n(t = 0) =$   
189  $n(\text{size}_{\text{recruit}}, 0)$ , then use a kernel with the size-dependent survival and growth functions described above to project forward for 100 time steps. This gives us the size distribution at each time step, which represents the probability that the individual  
192 has survived and grown into each of the possible size categories. The probability

that the individual is still alive and of any size decreases as the time steps progress;  
 by using a large number of steps, we are able to avoid arbitrarily setting a maximum  
 195 age and instead let the probabilities become essentially zero.

We then multiply each size-distribution vector  $v_z$  in the matrix by the size-  
 dependent fecundity function described above (eqn. 4) to get the total number of  
 198 eggs produced at each time step. To get the total number of of eggs one individual is  
 likely to produce in its lifetime, we then sum across all time steps in the individual's  
 potential life.

$$\text{LEP} = \sum_{t=0}^{t=100} \sum_{z=L}^{z=U} v_z, t f_z. \quad (5)$$

## 201 **Survival from egg to recruit**

We estimate survival from egg to recruit  $S_e$  using the number of recruited offspring  
 we can match back to genotyped parents as surviving individuals from genetically  
 204 "tagged" eggs in a method similar to that in Johnson et al. (2018). We estimate  
 the number of eggs produced by genotyped parent fish by multiplying the number of  
 genotyped parents ( $N_g = 913$ ) by the expected lifetime egg production of a parent  
 207 fish  $LEP_p$ , using LEP calculated starting with an individual of 6 cm. We make the  
 assumption that all recruited offspring originating from the genotyped parents end  
 up in one of the sites we sample and estimate the total number of offspring that  
 210 survive to recruit  $R_t$  by dividing the number of offspring matches we find ( $R_m = 90$ )  
 by the proportion of our site habitat we sample cumulatively across all sampling  
 years  $P_h = 0.34$  and the probability of capturing a fish if we sample an anemone  $P_c$

213 (see A, A for details on  $P_c$  and  $P_h$  estimates, respectively). Our estimated survival from egg to recruit is the number of tagged recruits divided by the number of tagged eggs produced:

$$S_e = \frac{\frac{R_m}{P_h P_c}}{N_g \text{LEP}_p}. \quad (6)$$

## 216 **Defining recruit and census stage**

When assessing persistence, it is important to consider mortality and reproduction that occurs across the entire life cycle to determine whether an individual is replacing  
 219 itself with an individual that reaches its same life stage (Burgess et al., 2014). We define recruit to be a juvenile individual that has settled on the reef the previous year; lifetime egg production assesses how many offspring an individual recruit is likely to  
 222 produce in its lifetime from that point forward and egg-recruit survival gives us the fraction of those eggs that will survive to reach the recruit stage. In theory, it should not matter exactly how we define recruit so long we use that definition in our  
 225 calculations of both egg-recruit survival and LEP. In our system it is straightforward to calculate LEP from any point but it is not possible to change our estimate of egg-recruit survival to allow different definitions of recruit: we do not have enough tagged  
 228 recruits to reliably estimate survival to different recruit sizes. Instead, we choose the mean size of offspring matched in the parentage study as our best estimate of the size of a recruit ( $\text{size}_{\text{recruit}}$ ) and test sensitivity to different sizes within the range of  
 231 sizes that the recruit stage covers (Table 1).

## Probability of dispersal

We use a distance-based dispersal kernel, estimated in other work using parent-offspring matches from our genetic data (Catalano et al., in prep) using the method described in Bode et al. (2018). The relative dispersal is a function of distance  $d$  as measured in kilometers and parameters  $\theta$  and  $k_d$ , which control the shape and scale of the kernel:

$$p(d) = e^k e^{-(e^k d)^\theta}. \quad (7)$$

We use a fat-tailed dispersal kernel with shape parameters  $\theta = 0.5$  and scale parameter  $k_d = -1.36$  (Fig. 3a, estimated in (Catalano et al., in prep)).

The dispersal kernel is estimated using fish that have already recruited to a population and survived to be sampled so it gives the relative amount of dispersal given that a fish recruits somewhere, not the probability that a released larvae will travel a particular distance. To find the probability of fish dispersing among our sites, we calculate the distance between the middle of each site to the closest and farthest edge of each other site, then use the distances as upper and lower bounds when integrating eqn. 7, which we do numerically. For example, the probability of dispersal from site A to B, where  $d_1$  is the distance from the middle of A to the closest edge of B and  $d_2$  is the distance from the middle of A to the far edge of B, is:

$$p_{A,B}(d) = \int_{d_1}^{d_2} e^k e^{-(e^k d)^\theta} dd. \quad (8)$$

## 249 **Persistence metrics**

For a metapopulation to persist, at least one patch needs to achieve replacement, where the number of individuals entering the population balances those lost to mortality or emmigration (Burgess et al., 2014). In our focal system, adults do not move among patches so we do not need to consider emmigration and only need to assess whether fish produce enough offspring that survive to recruitment to be able to replace themselves and where those offspring travel within the metapopulation. We consider three primary metrics to assess whether and how the population is persistent: 1) lifetime production of recruits, to assess whether the population has enough surviving offspring to achieve replacement 2) self-persistence, to assess whether any individual patches would be able to persist in isolation without any input from other patches, and 3) network persistence, to assess whether the metapopulation is persistent as a connected unit. We explain each metric below in detail.

### **Estimated abundance over time**

*[Add brief section here.]*

## 264 **Lifetime production of recruits**

To assess whether individuals at our focal patches produce enough offspring that survive to become recruits themselves, we find the estimated number of recruits an individual recruit will produce over its lifetime (lifetime recruit production: LRP)

by multiplying LEP by the estimated survival from egg to recruit  $S_e$ :

$$LRP = LEP * S_e. \quad (9)$$

If  $LRP \geq 1$ , the population has the possibility for replacement; individuals produce  
 270 enough surviving offspring, before taking into account the probability of dispersal  
 and settlement. If  $LRP < 1$ , the individuals are not replacing themselves and the  
 population cannot persist without input from outside patches .

### 273 **Self-persistence**

A patch is able to persist in isolation (self-persistent) if individuals produce enough  
 offspring (LEP) that disperse back to the natal patch and survive to recruitment  
 276 to be able to replace themselves (LR):  $LEP \times LR \geq 1$  (Burgess et al., 2014). Our  
 dispersal kernel represents the probability that a recruit disperses a distance given  
 that it recruits somewhere, rather than the probability of a larvae dispersing and  
 279 recruiting to a particular patch, which implicitly encompasses mortality from egg to  
 recruitment. We modify the equation to fit our data and include survival from egg  
 to recruit to whether a particular patch  $i$  is self-persistent:

$$SP_i = LEP \times \frac{\text{recruits}}{\text{egg}} \times \frac{p_{i,i} \times \# \text{ recruits from site}}{\frac{\text{recruits}}{\text{egg}} \times \# \text{ eggs produced by patch } i} \quad (10)$$

$$SP_i = LEP \times S_e \times p_{i,i}.$$

282 A patch is self-persistent if  $SP \geq 1$ . If at least one patch is self-persistent, the  
 metapopulation as a whole is persistent as well (Hastings and Botsford, 2006; Burgess  
 et al., 2014).



## 285 **Realized connectivity matrix and network persistence**

We find the probabilities of a recruit dispersing between each set of sites ( $p_{i,j}$ ) by integrating the dispersal kernel (eqn. 7 over the distance between each set of sites. We  
288 then create a realized connectivity matrix  $C$  by multiplying the dispersal probabilities by the expected number of recruits an individual produces:  $C_{i,j} = \text{LRP} \times p_{i,j}$  (Burgess et al., 2014). The diagonal entries of  $C$ , where the origin and destination are the  
291 same sites, are the values of self-persistence we calculate above.

Network persistence requires that the largest real eigenvalue of the realized connectivity matrix be  $\lambda_C$  be greater than 1:  $\text{NP} = \lambda_C > 1$  (e.g. Hastings and Botsford,  
294 2006; White et al., 2010; Burgess et al., 2014).

## **Incorporating uncertainty**

To represent the uncertainty in our estimates of the parameters that go into calculating our persistence metrics, we calculate each metric 1000 times, pulling each  
297 parameter from a distribution or range. In our results, we show the range of values of each persistence metric as well as the value with our best estimate of each parameter.

300 For the dispersal kernel, we keep the shape parameter  $\theta$  constant and pull the scale parameter  $k_d$  from a set capturing the 95% confidence intervals, which was produced during kernel estimation in (Catalano et al., in prep). To capture uncertainty in the  
303 size of a recruit  $\text{size}_{\text{recruit}}$ , and therefore the transition of mortality being captured by egg-recruit survival to being captured by LEP, we pull from a uniform distribution over the range of fish sizes (3.5 - 6.0 cm) considered as offspring in the parentage

analyses (Catalano et al., in prep). We include uncertainty in the size of transition to a breeding female  $L_F$  by pulling from the set of sizes observed in the data for fish at their first recapture as a female. For the von Bertalanffy growth parameters  $L_\infty$  and  $K$ , we pull from the full set of estimates using different combinations of recapture pairs for fish recaptured more than twice. For uncertainty in adult survival, we pull from a normal distribution generated using the standard error estimated in the mark-recapture analysis for both the intercept  $b_\phi$  and the size effect  $b_a$ .

To incorporate uncertainty in egg-recruit survival, we consider uncertainty in both the number of offspring assigned to parents during the parentage analysis and the probability of capturing a fish  $P_c$ , which affects how the captured assigned offspring are scaled up to account for fish uncaught. For the number of assigned offspring, we generate a set of values of number of assigned offspring using a random binomial, where the number of trials is the number of genotyped offspring (XX) and the probability of success on each trial is the assignment rate XX of offspring from the parentage analysis (Catalano et al., in prep). To represent uncertainty in the probability of capturing a fish, we pull values from a beta distribution with parameters  $\alpha_{P_c}$  and  $\beta_{P_c}$ , found using the mean and variance of capture probabilities estimated from recapture dives across sites and sampling seasons (details in A).

## Results

Our estimated abundance of females at each site over time is relatively constant [*add some sort of actual analysis here*] (Fig. 2, suggesting that our sample populations are persistent over time.

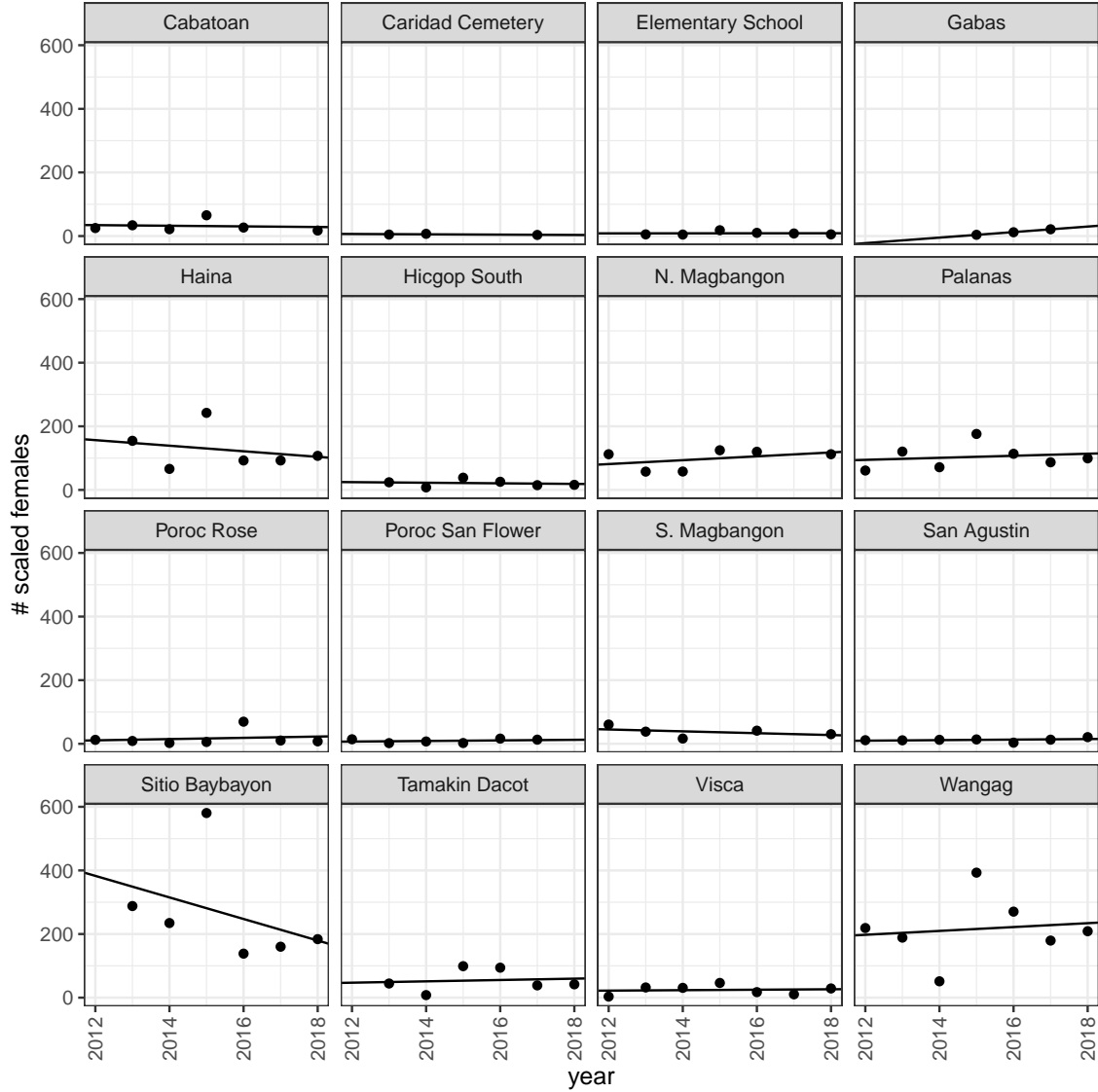


Figure 2: The estimated number of females at each site over the sampling years. The total number of females at each site was estimated by taking the number of females (fish  $\geq 5$ cm with the yellow pointed tail indicating female) captured at each site in each year and scaling up by the proportion of habitat sampled at that site that season (see A for details) and by the average probability of capturing a fish (see A).

From the mark-recapture analysis of tagged and genotyped fish, we estimate mean values of  $L_\infty = 10.58\text{cm}$  (range of estimates 10.39 - 10.75 cm) and  $K = 0.928$  (range of estimates 0.854 - 1.025) for the von Bertalanffy growth curve parameters (Fig. 3b, Table 1). For juvenile and adult (post-recruitment) survival on a log-odds scale, the best-fit model has a coefficient  $b_a = 0.74 \pm 0.060$  SE for the effect of size and an intercept  $b_\phi = -4.83 \pm 0.340$  SE. These results suggest that larger fish have higher annual survival, which is similar to survival estimates in other clownfish species (check Buston paper). The accompanying best-fit model for recapture probability has intercept  $b_{pr} = 17.93 \pm 0.858$  SE, size effect  $b_1 = -1.816 \pm 0.080$  SE, and effect of diver distance from the anemone  $b_2 = -0.171 \pm 0.021$  SE. The negative effect of both size and distance suggest that divers are less likely to recapture larger fish and those at anemones far from areas sampled, with the chance of recapturing an average-sized fish falling below 5% if a diver stays farther than XX from its home anemone [add the recapture probability plots, like the survival one in Fig. 3, to the appendix and reference here.]

We set the transition size to breeding female  $L_f$  at 9.32 cm, the mean size of first female capture of recaptured fish (Fig. 3d). [*Contextualize these values.*]

[*Not sure where to put this - kind of a methods/results hybrid, or if it should exist, but seems like it might be helpful - not fully filled out yet. Need to clarify somewhere what kind of distributions are going into the uncertainty runs (drawn from data, uniform across a range, 95% confidence bounds, etc.)*]

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Parameter	Description	Best estimate	Range in uncertainty runs	Notes
$k_d$	scale parameter in dispersal kernel	-1.36	-2.03 to -0.96	estimated using methods in Bode et al. (2018) in Catalano et al. (in prep)
$\theta$	shape parameter in dispersal kernel	0.5	NA	estimated using methods in Bode et al. (2018) in Catalano et al. (in prep)
$L_\infty$	average asymptotic size in von Bertalanffy growth curve	10.58 cm	10.39 to 10.75 cm	
$K$	growth coefficient in von Bertalanffy growth curve	0.928	0.854 to 1.025	

$b_\phi$	intercept for adult survival	-4.83	$\pm 0.340$ stan- dard error	
$b_a$	size effect for adult survival	0.74	$\pm 0.060$ stan- dard error	
$b_{pr}$	intercept for recapture prob- ability from mark-recapture analysis	17.93	$\pm 0.858$ stan- dard error	not used in persis- tence estimates
$b_1$	size effect for re- capture	-1.816	$\pm 0.080$ stan- dard error	not used in persis- tence estimates
$b_2$	distance effect for recapture	-0.171	$\pm 0.021$ stan- dard error	not used in persis- tence estimates
size <sub>recruit</sub>	size (cm) of re- cruited offspring	mean of size of off- spring in parentage analysis = 4.4 cm	3.5 - 6.0 cm	
$S_e$	egg-recruit sur- vival			
$b_e$	coefficient for eyed eggs	-0.608		Yawdoszyn et al. (in prep)

$b_l$	size effect in eggs-per-clutch relationship	2.39		Yawdoszyn et al. (in prep)
$b$	intercept in eggs- per-clutch rela- tionship	1.17		Yawdoszyn et al. (in prep)
$L_f$	size at transition to female	9.32cm	5.2 - 12.7cm	
$P_c$	probability of capturing a fish	0.56	drawn from beta distri- bution with parameters $\alpha_{P_c} = 1.44$ and $\beta_{P_c} = 1.13$	details in A

Table 1:

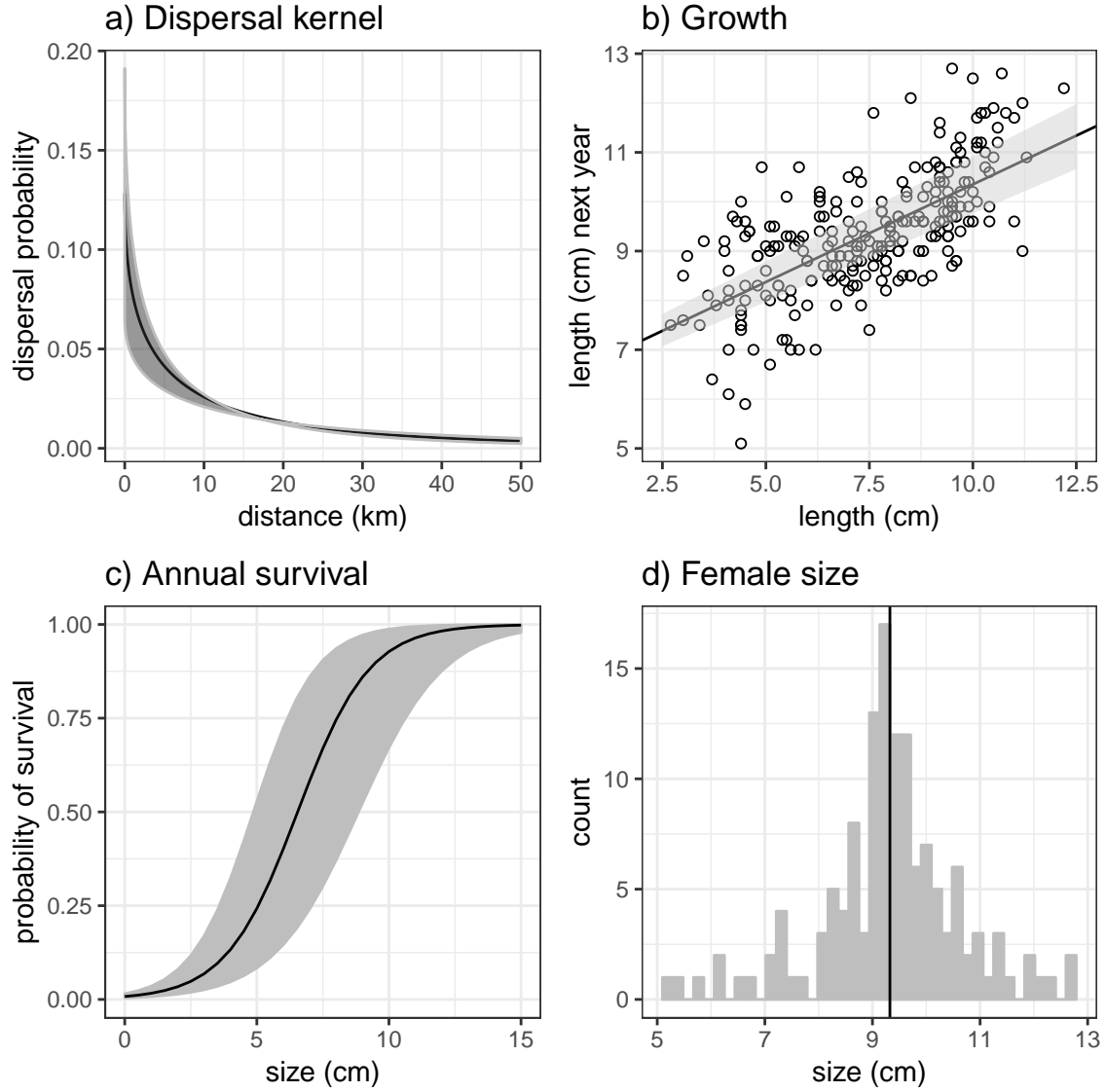


Figure 3: Best estimates (solid black line) and range included for uncertainty (gray) for dispersal (a), growth (b), post-recruit survival (c), and size at female transition (d) parameters.

Using our best estimates for growth, survival, and fecundity, we calculate a value



of LEP for 10876, ranging from XX to XX when we consider uncertainty in the inputs  
351 (Fig. 4a). The size at recruitment - the census point between egg-recruit survival  
and LEP - has the most effect on the value of LEP (Fig. B.2), with higher values of  
LEP the higher the size of recruitment as less mortality is included before reaching  
354 reproductive sizes.

We estimate egg-recruit survival  $S_e$  to be 1.82e-05, ranging from XX to XX  
when we include uncertainty in the number of offspring assigned to parents and  
357 the probability of catching a fish (Fig. 4b). Uncertainty in the size of transition  
to breeding female  $L_f$  has the largest effect on egg-recruit survival (Fig. B.4); we  
only consider reproduction from females, to avoid double-counting, so the larger  
360 the transition size to female, the fewer tagged eggs we estimate were produced by  
genotyped parents and the higher egg-recruit survival.

We estimate lifetime recruit production, the product of LEP and  $S_e$ , to be 0.20,  
363 below the value of 1 necessary for replacement. This suggests that even without  
considering connectivity, the individuals at our sample populations do not produce  
enough offspring that survive to recruitment to replace themselves.

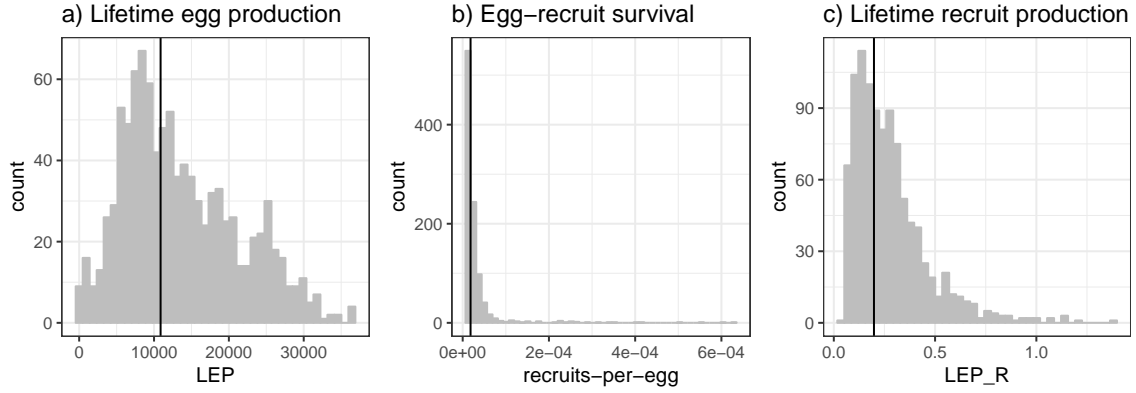


Figure 4: Estimates of a) LEP, b) egg-recruit survival, and c) LRP, showing the best estimate (black solid line) and range of estimates considering uncertainty in the inputs.

366 We do not find any sites with self-persistence values  $> 1$ , indicating that the  
 site could persist in isolation. Given that our estimate of LRP does not suggest  
 replacement and only a fraction of that recruitment stays at the natal site, this  
 369 makes sense.

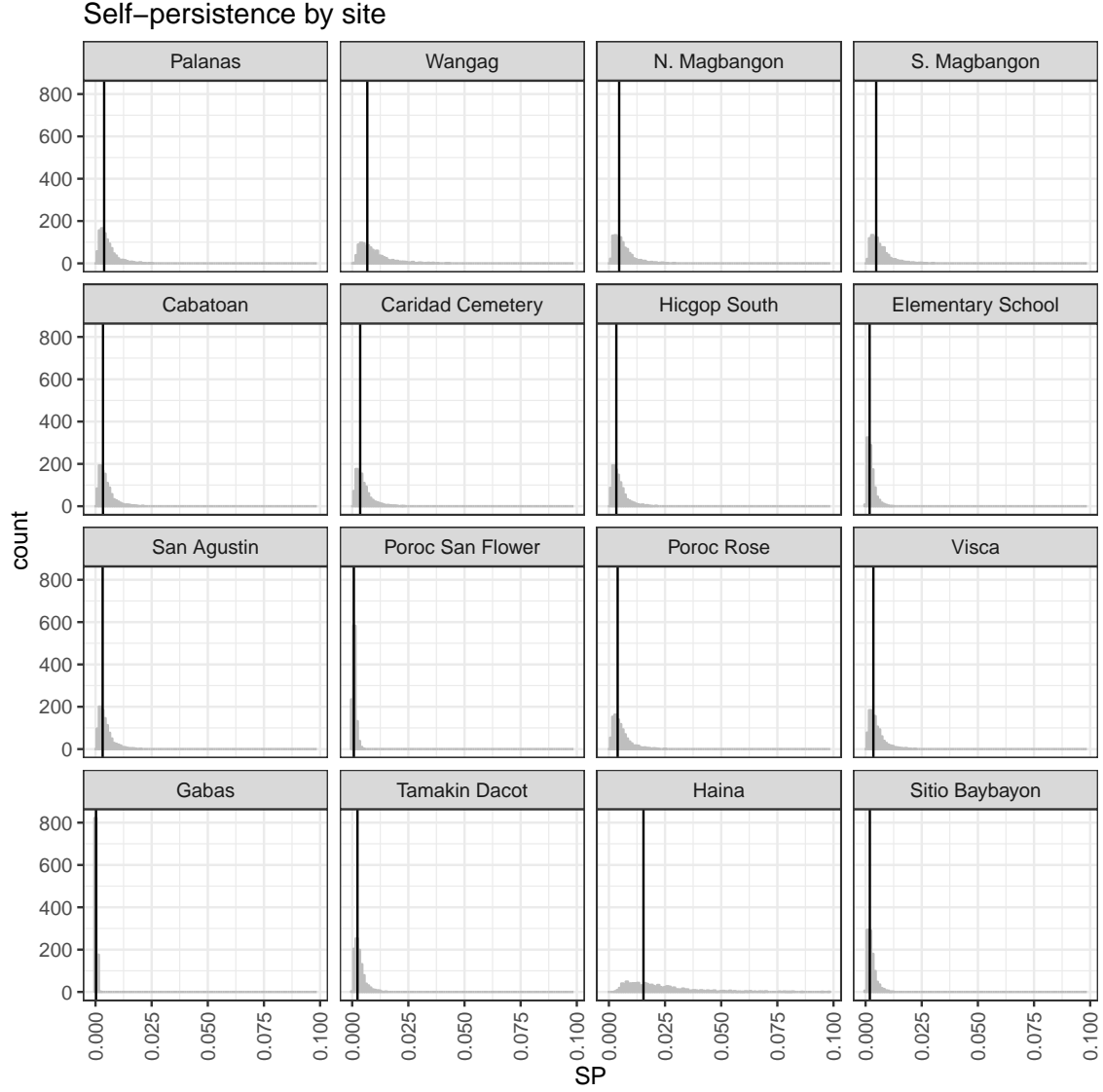


Figure 5: Values of self-persistence at each site, showing the best estimate (black line) and range of estimates considering uncertainty in the input paramters. No site reaches a value of  $SP \geq 1$ , necessary to be self-persistent.

We also do not find evidence of network persistence; the dominant eigenvalue of

the realized connectivity matrix is 0.023, well below the value of 1 needed for network  
 372 persistence.

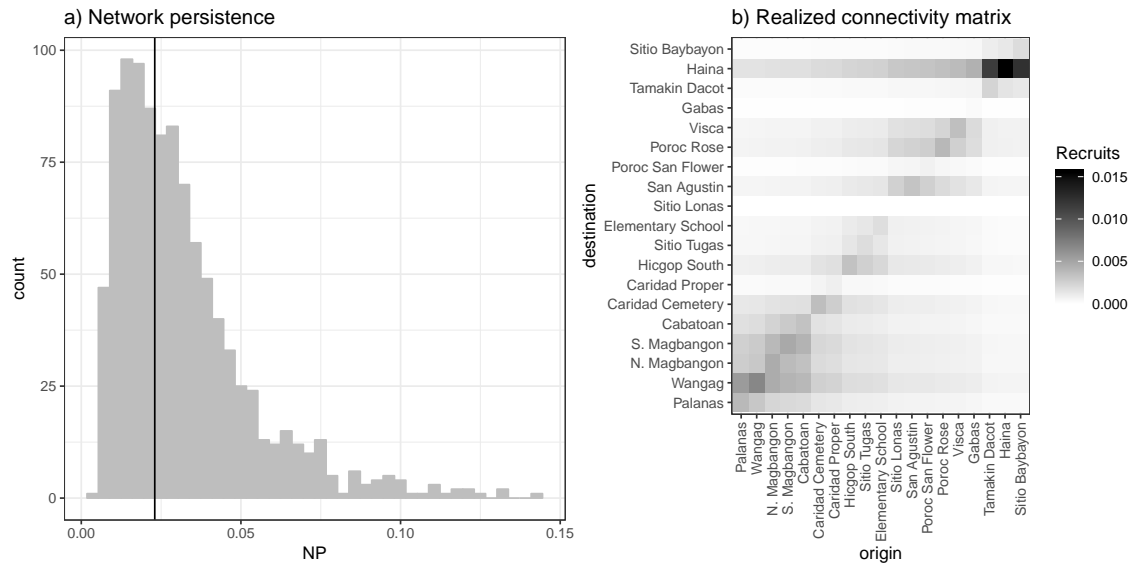


Figure 6: a) Network persistence values, showing the best estimate (black solid line) and range of estimates considering uncertainty. b) The realized connectivity matrix  $C$ .

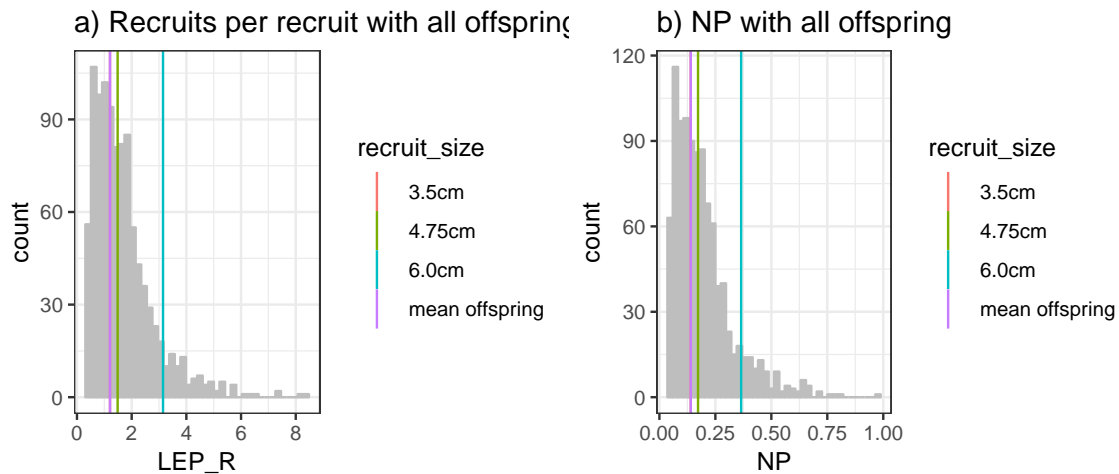


Figure 7: Range of parameter inputs for uncertainty runs with all uncertainty included. Census size is the size at fish are considered to have recruited, such that egg-recruit survival ends. Female transition is the size at which fish transition from male to female and their reproductive output is included in the estimate of lifetime egg production (LEP). FINISH LISTING PARAMS!

## Discussion

Big picture: What do our results mean for persistence in this system and our understanding of metapopulations generally?

- So we don't see persistence in our metrics, either self-persistence or network persistence but our abundances don't seem to be changing. Suggests that this is just a portion of a larger metapopulation, rather than a self-contained metapopulation. Maybe it is a sink? Persistent in terms of constant abundance but relies on outside immigration to persist.

- 381 • How does dispersal spread interact with scale of a self-contained metapopulation? How do we reconcile this in our system?
- Sensitivity - how would our parameters need to change to see persistence?
- 384 Egg-recruit survival is a big one. Discuss limitations of how we calculated it (offspring going outside our pops not included), what we see for persistence when estimate recruits/recruits instead.
- 387 More detailed discussion of our estimates, limitations, ways to move forward:
- Discuss density-dependence: not explicitly accounting for it, included in our egg-recruit survival estimate. But it's these metrics at low abundance, when
- 390 DD isn't happening, that really matter for persistence. Egg-recruit-survival is probably higher in that case than our estimate of it here (b/c larvae able to settle without being chased off by already-settled recruits).
- 393 • Discuss site-specific demographic rates, why we don't have them in our system, the importance they play in other studies, what we might need to go about resolving them.
- 396 • Contextualize our parameter estimates with those from other studies (esp. survival, growth, egg-recruit survival).

# Appendix

## 399 **A Method details**

### **Proportion of habitat sampled**

*[Need to add in the details here]*

## 402 **Probability of capturing a fish, from recapture dives**

We use mark-recapture data from recapture dives done within a sampling season to estimate the probability of capturing a fish. During some of the sampling years (XX),  
405 portions of the sites were sampled again XX-XX weeks after the original sampling dives. We assume there is no mortality of tagged fish between the original sampling dives and the recapture dives because they are so close in time and that fish do not  
408 change their behavior or reponse to divers, so therefore assume that the probability of recapturing a fish is the same as the probability of capturing a fish on a sample dive. For each recapture dive, we use GPS tracks of the divers to identify the anemones  
411 covered in the recapture dive and the set of PIT-tagged fish encountered on those anemones during the original sampling dives. We estimate the probability of capture  $P_c$  as the number of tagged fish caught during the capture dive  $m_2$  divided by the  
414 total number of fish caught on the recapture dive  $n_2$ :  $P_c = \frac{m_2}{n_2}$ .

We use the mean  $P_c$  across all 14 recapture dives, covering XX sites in 3 sampling seasons (2016, 2017, 2018), as our best estimate. Because there are so few recapture  
417 dives compared to the number of times we calculate the metrics to show the range of uncertainty, we represent the probability of capture as a distribution, rather than pulling directly from the values calculated for each recapture dive. The distribution  
420 of capture probabilities across the 14 dives is quite skewed so we represent it as a beta distribution, using the mean  $\mu_{P_c}$  and variance  $V_{P_c}$  of the set of 14 values to find the appropriate  $\alpha_{P_c}$  and  $\beta_{P_c}$  parameters, where



$$\alpha_{P_c} = \left( \frac{1 - \mu_{P_c}}{V_{P_c}} - \frac{1}{\mu_{P_c}} \right) \mu_{P_c}^2 \quad (\text{A.1})$$

$$\beta_{P_c} = \alpha_{\mu_{P_c}} \times \frac{1}{\mu_{P_c} - 1}. \quad (\text{A.2})$$

423      The mean of the individual capture probability values is  $\mu_{P_c} = 0.56$ , with variance  $V_{P_c} = 0.069$ , which gives beta distribution parameters  $\alpha_{P_c} = 1.44$  and  $\beta_{P_c} = 1.13$ .

## Full set of MARK models

<sup>426</sup> We consider the following set of models in MARK:

Model	Model description	AICc	dAICc
	survival size, recapture size+distance	3348.861	0
	survival size, recapture distance	3359.998	-11.1371
	survival constant, recapture dis- tance	3383.175	34.3141
	survival constant, recapture size+distance	3384.959	36.0981
	survival time, recapture constant	3408.342	59.4816
	survival site, recapture constant	3440.842	91.98112
	survival site, recapture size+distance	3440.842	91.98112
	survival constant, recapture time	3453.609	104.74839
	survival size, recapture size	3527.710	178.84940
	survival constant, recapture con- stant	3570.908	222.04690

Table A1:

## B Uncertainty details

### B.1 Sensitivity to parameters

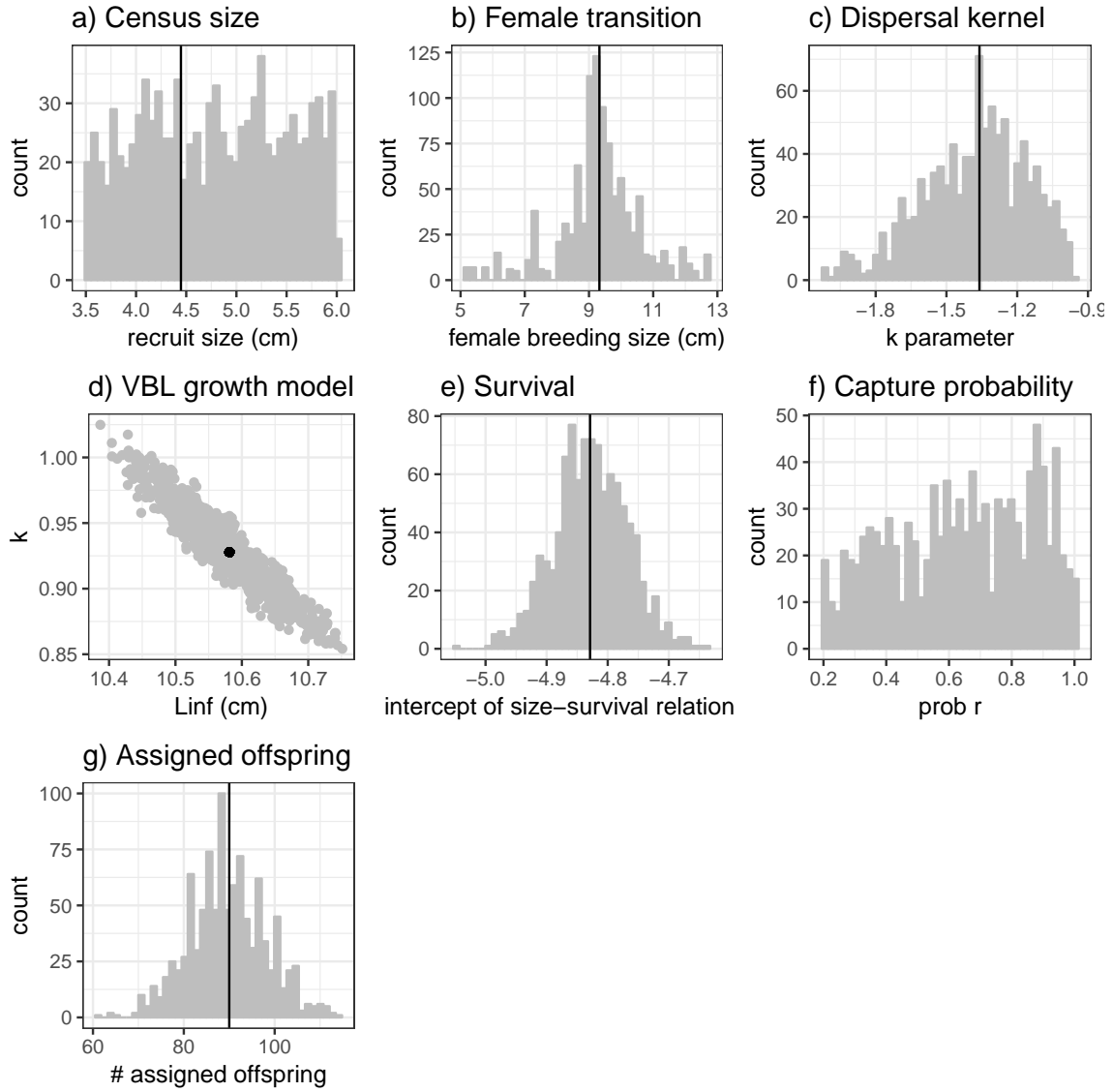


Figure B.1: Range of parameter inputs for uncertainty runs with all uncertainty included. Census size is the size at fish are considered to have recruited, such that egg-recruit survival ends. Female transition is the size at which fish transition from male to female and their reproductive output is included in the estimate of lifetime egg production (LEP). FINISH LISTING PARAMS!

## B.2 Effects of different types of uncertainty on metrics

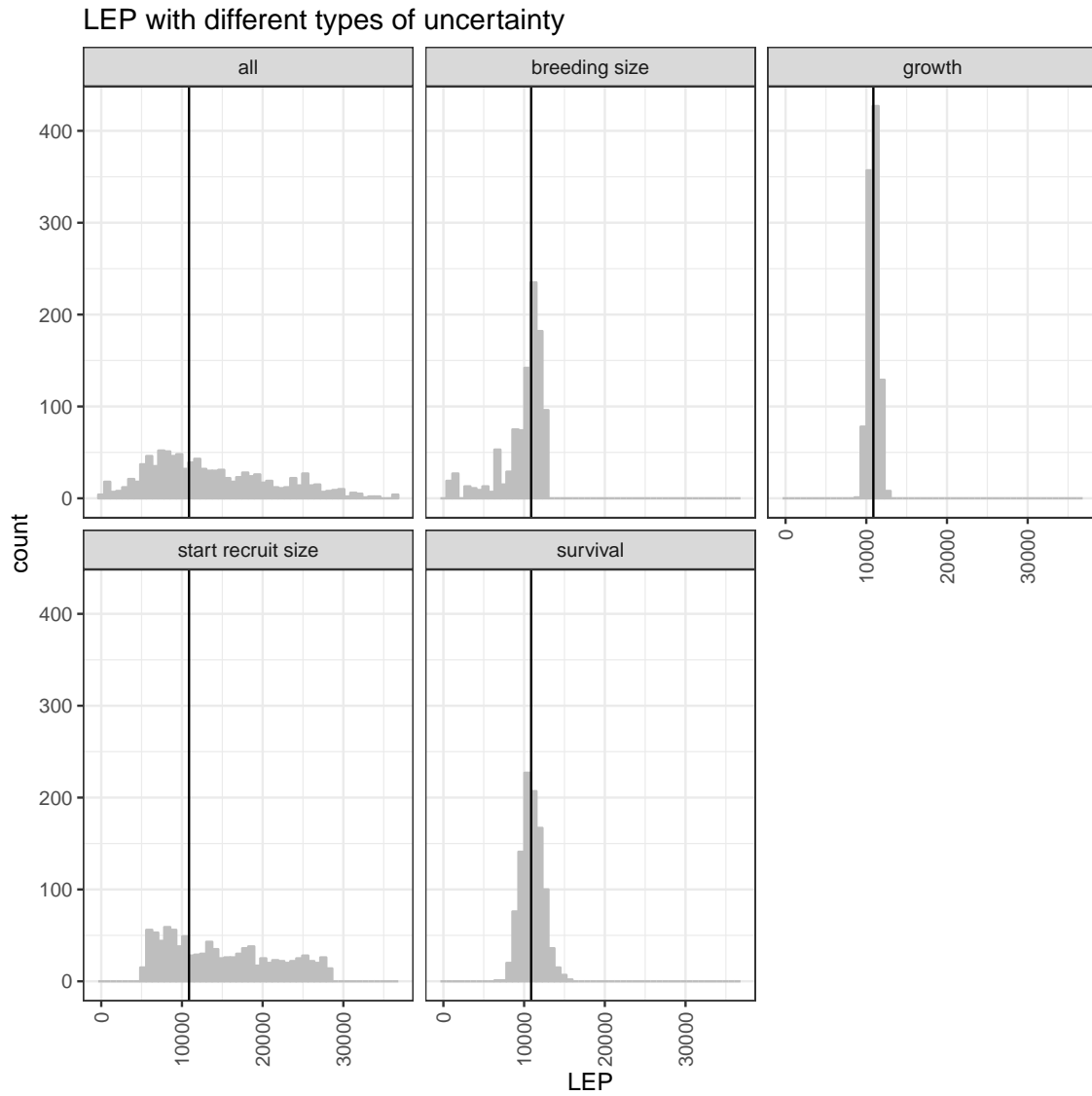


Figure B.2: WRITE A CAPTION!

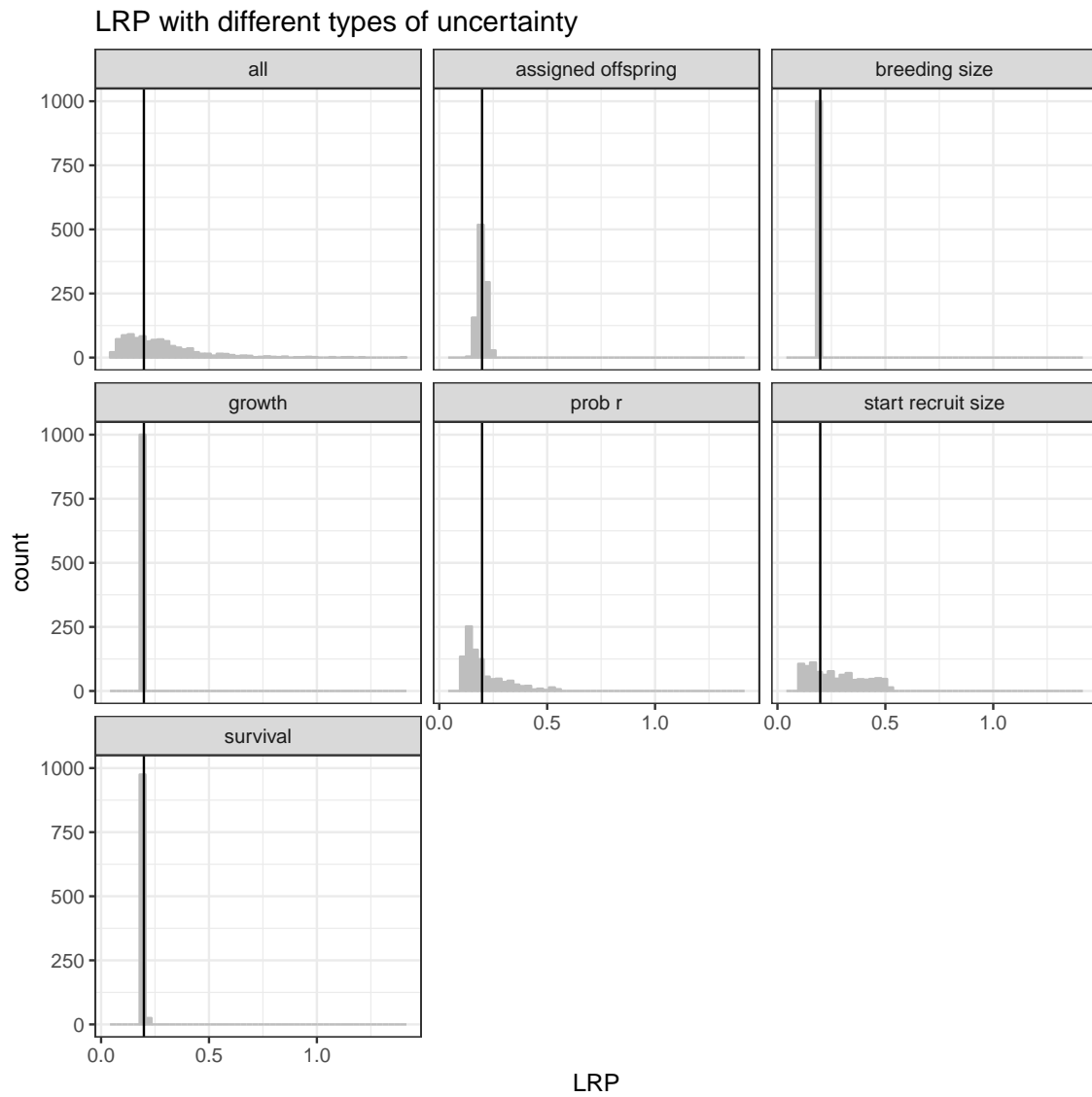


Figure B.3: WRITE A CAPTION!

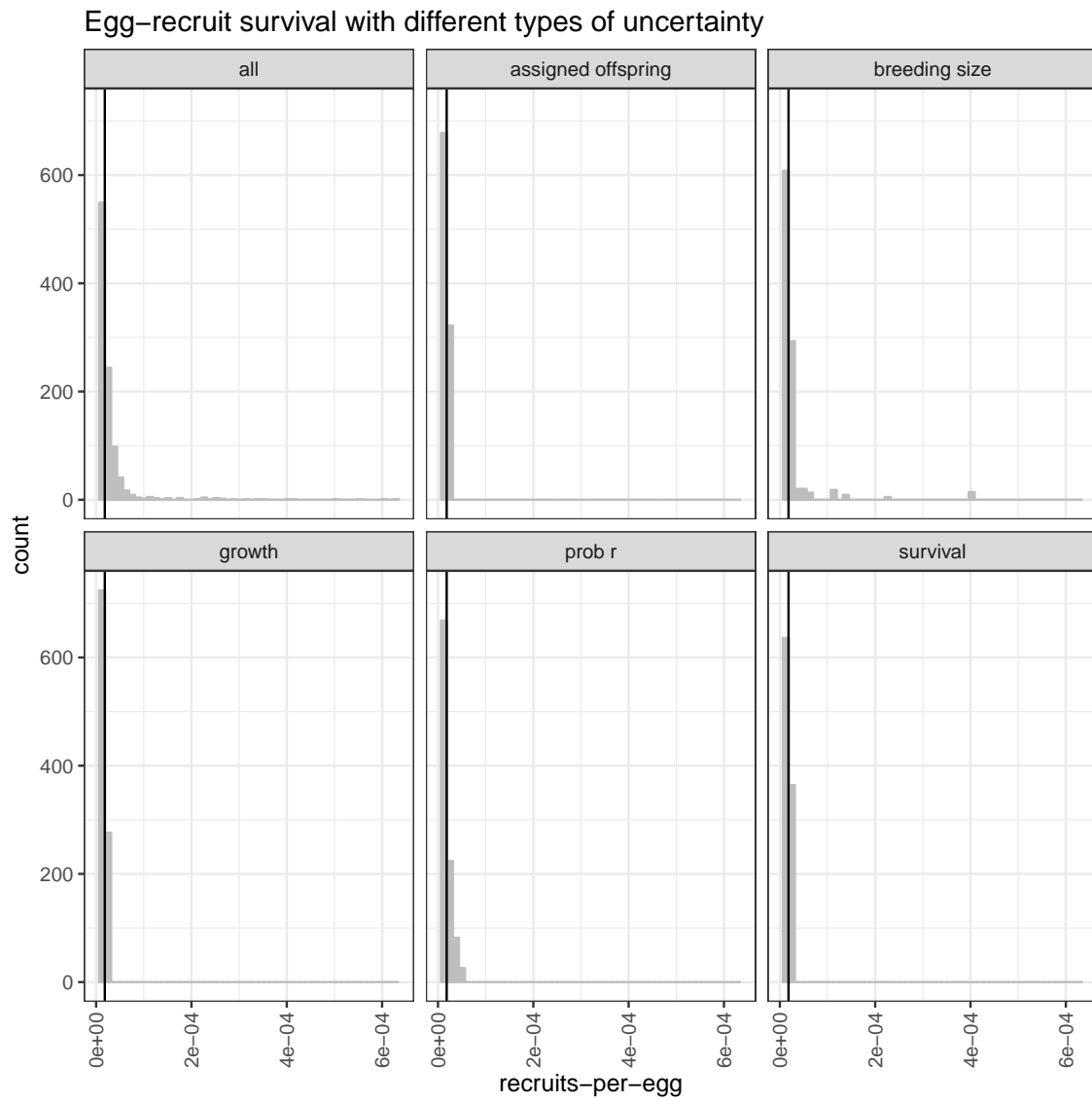


Figure B.4: WRITE A CAPTION!

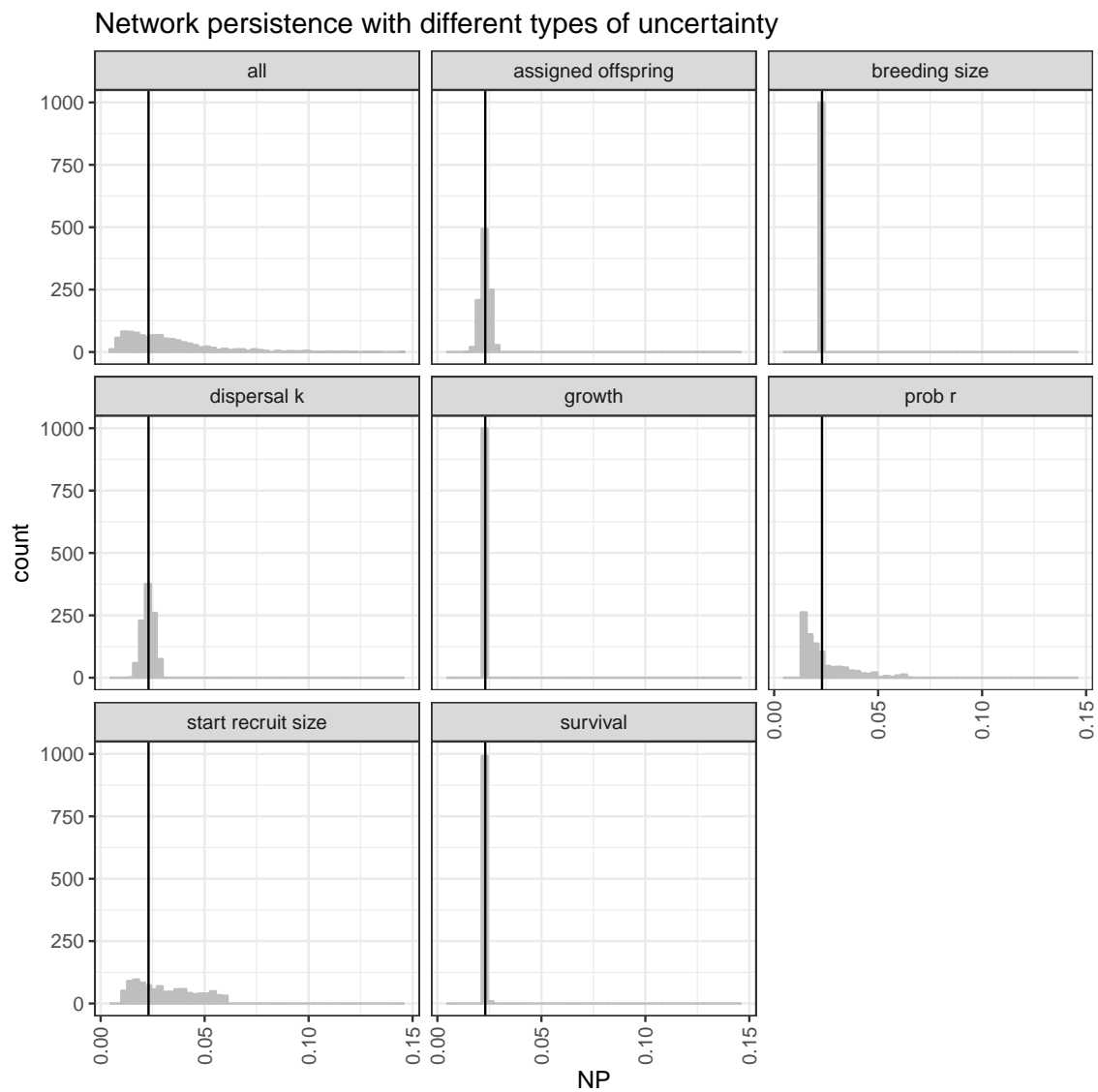


Figure B.5: WRITE A CAPTION!



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