

# Clownfish metapopulation persistence draft

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## Introduction

Metapopulation dynamics and persistence depend on the demographic rates at each

<sup>3</sup> patch and the connectivity among patches (e.g. Hastings and Botsford, 2006; Han-

ski, 1998). Metapopulations exist along a continuum, with persistence driven by the balance of extinction and colonization of local patches at one extreme and dynamics focused on the balance of immigration and emigration at constantly-occupied local patches at the other extreme (Kritzer and Sale, 2006). Terrestrial metapopulations often show extinction/colonization dynamics (e.g. Hanski, 1998), while marine metapopulations tend to exhibit immigration/emigration dynamics, with local extinction uncommon and dispersal connecting patches through delivery of larvae (Kritzer and Sale, 2006). Assessing levels of connectivity and demographic parameters has been particularly challenging for marine species, where much of the mortality 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; Cowen and Sponaugle, 2009; Roughgarden et al., 1988). A need to understand metapopulations for conservation and management, such as siting marine protected areas (e.g. Botsford et al., 2001; White et al., 2010), however, has led to a large body of theory describing how marine metapopulations might persist.

For any population to persist, individuals must on average replace themselves during their lifetimes. Assessing replacement 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. In a spatially-structured population, 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. Marine larvae were once thought to be well-mixed and dispersed far on ocean currents (e.g.

<sup>27</sup> Roughgarden et al., 1988), suggesting widespread connectivity among patches. Recent advances in estimating connectivity through natural tags and genetics, however, suggest that dispersal may be more limited (e.g. D'Aloia et al., 2013; Hameed et al.,  
<sup>30</sup> 2016; Almany et al., 2017), and local persistence of marine populations is seeming more possible.

Considering both the demographic processes within patches and the connectivity  
<sup>33</sup> among them, a metapopulation can persist in two ways: 1) at least one patch can achieve replacement in isolation, or 2) patches receive enough recruitment to achieve replacement through multi-generational loops of connectivity with other patches in  
<sup>36</sup> 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 retained at the patch for the patch to persist. If one patch persists,  
<sup>39</sup> the metapopulation persists. 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 eventually send offspring back to the first in a future generation  
<sup>42</sup> - provide the patch with enough recruitment to persist in the network. Though it has been challenging to estimate the parameters necessary to understand how actual metapopulations persist, a large work of theory developed in part to guide  
<sup>45</sup> marine protected area design helps predict 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).

<sup>48</sup> New ways of identifying individuals and determining their origins, such as otolith microchemistry and genetic parentage analysis (e.g. Wang, 2004, 2014) are making

it increasingly possible to estimate both the demographic [ADD EXAMPLE 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 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 set of reef patches of bicolor damselfish (*Stegastes partitus*) 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 question of how patches interact and what the scale of metapopulation persistence is. Flow differences along extended coastlines compared to isolated islands likely change the patterns of connectivity and ability of larvae to stay close to their natal site. (NEED CITATIONS, EXPLANATION OF FLOW).

When assessing persistence, we want to XXXX, rather than capturing short-term interannual variability. Though the number of studies estimating demographic rates and connectivity in marine metapopulations is growing (EXAMPLES), most use data from one or few years. SOMETHING ABOUT WHY LONGER DATA SETS ARE GOOD AND HOW THEY CAN AVERAGE OVER SOME OF THE 69 INTERANNUAL VARIABILITY. Additionally, sampling over many years provides the possibility of comparing abundance trends to persistence metrics to see if they tell a consistent story.

72 Here, 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 Philippines. We assess persistence for all patches of habitat within  
75 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 metapopulation. With seven years of annual sampling data, we are able  
78 to estimate persistence metrics and replacement over the longer term and investigate abundance through time to compare with the replacement-based persistence metrics.  
We use a long-term data set from habitat patches on a continuous set of coastline to  
81 understand persistence within a local network.

## Methods

### Persistence theory and metrics

84 For a population to persist, individuals must be able to replace themselves on average at low abundance (CITATIONS?). In non-spatially structured populations, we use criteria such as the average number of recruiting offspring each individual produces during 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).  
87  
90 For spatially-structured populations, we must also consider the spatial spread of offspring, often represented through a dispersal kernel or connectivity matrix (CITATIONS). At least one patch needs to achieve replacement, where the number of  
93 individuals entering the population balances those lost to mortality or emigration,

for a metapopulation to persist (Burgess et al., 2014; Hastings and Botsford, 2006).

We consider three primary metrics to assess whether and how the population  
96 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  
99 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.

### Lifetime production of recruits

102 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)  
105 by multiplying the total number of eggs a recruit-sized individual will produce in its  
lifetime (lifetime egg production: LEP) by the estimated survival from egg to recruit  
 $S_e$ :

$$\text{LRP} = \text{LEP} * S_e. \quad (1)$$

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

## Self-persistence

A patch is able to persist in isolation (self-persistent) if individuals produce enough  
114 offspring (LRP) that disperse back to the natal patch and survive to recruitment to  
be able to replace themselves (LR):  $\text{LRP} \times \text{LR} \geq 1$  (Burgess et al., 2014, modified  
so that egg-to-recruit survival is included in the LEP term instead of the probability  
117 of dispersing component of LR). We include survival from egg to recruit ( $S_e$ ) sep-  
arately from the probability of dispersal to assess whether a particular patch  $i$  is  
self-persistent:

$$SP_i = \text{LEP} \times \frac{\text{recruits}}{\text{egg}} \times \frac{p_{i,i} \times \# \text{ recruits from patch } i}{\frac{\text{recruits}}{\text{egg}} \times \# \text{ eggs produced by patch } i} \quad (2)$$

$$SP_i = \text{LRP} \times p_{i,i}.$$

120 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).

## 123 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. 3) over the distance between each set of sites.  
126 We then create a realized connectivity matrix  $C$  by multiplying the dispersal proba-  
bilities 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  
129 are the same sites, are the values of self-persistence we calculate above.

Network persistence requires that the largest real eigenvalue of the realized connectivity matrix  $\lambda_C$  be greater than 1:  $NP = \lambda_C > 1$  (e.g. Hastings and Botsford, 132 White et al., 2010; Burgess et al., 2014).

### Defining recruit and census stage

When assessing persistence, it is important to consider mortality and reproduction 135 that occurs across the entire life cycle to determine whether an individual is replacing itself with an individual that reaches the same life stage (Burgess et al., 2014). We define a recruit to be a juvenile individual that has settled on the reef within the 138 previous year; LEP assesses how many offspring an individual recruit is likely to 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 (Fig. 1). In theory, it 141 should not matter exactly how we define recruit so long we use that definition in our 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- 144 recruit survival to allow different definitions of recruit: we do not have enough tagged 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 147 size of a recruit ( $size_{recruit}$ ) and test sensitivity to different sizes within the range of sizes that the recruit stage covers (Table 1).

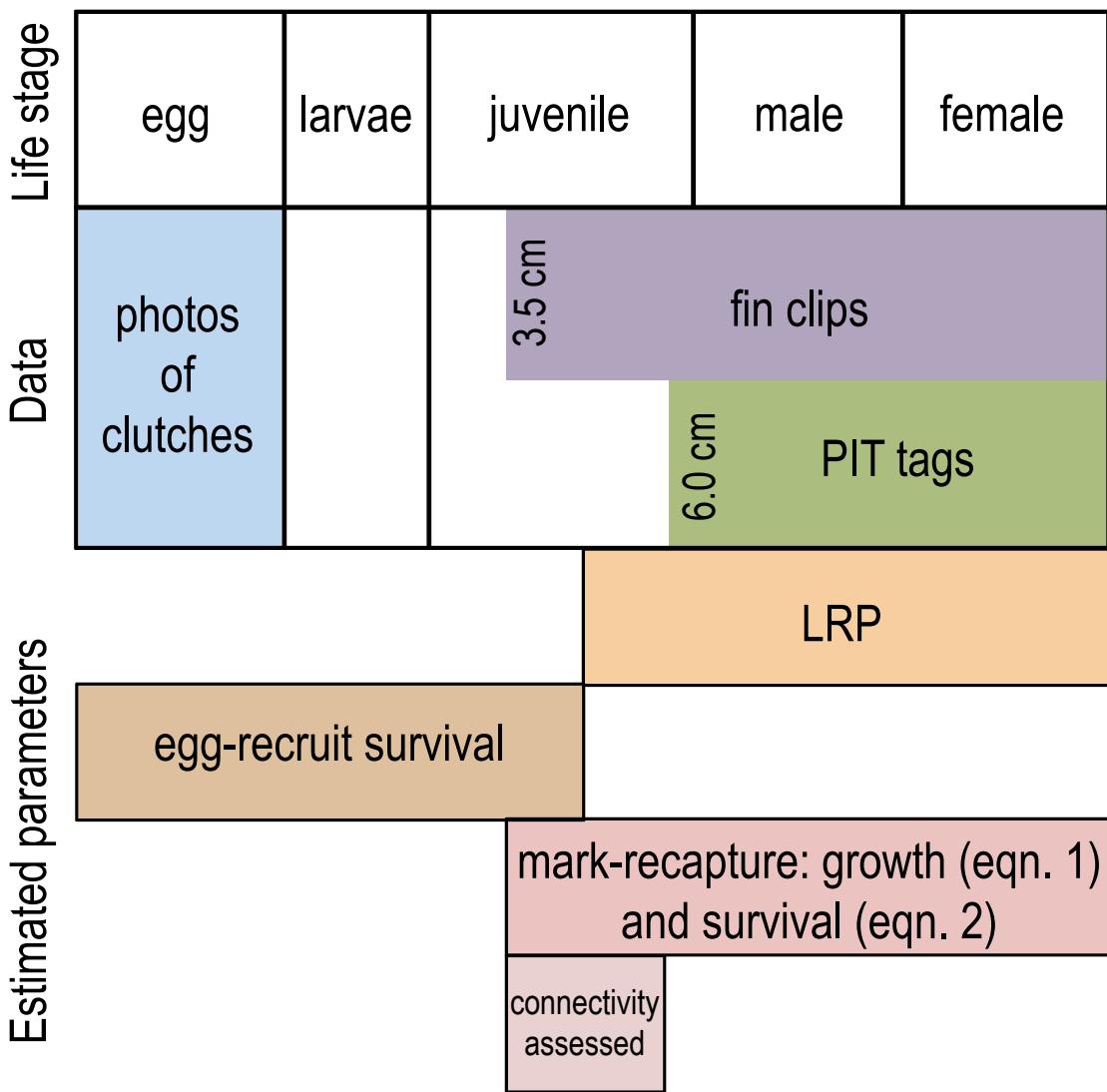


Figure 1: Here, we show the data collected for fish at each life stage (life stage boxes are not scaled by length of stage) and how the empirical data fit into our parameter and metric calculations.

## Study system

We focus on a tropical metapopulation of yellowtail clownfish (*Ampiprion clarkii*, Fig. 2c) 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 or left. 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; Holtswarth et al., 2017). Larvae hatch after about six days and spend 7-10 days in the water column 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 limited 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 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 metapopulation clear. Additionally, clear patches make it easier to assess how much

<sup>171</sup> of the site has been surveyed. These simplifying characteristics in habitat and fish behavior make clownfish and other similarly territory-based reef fish useful model systems for studies of metapopulation dynamics and persistence (e.g. Buston and <sup>174</sup> DAloia, 2013; Salles et al., 2015; Johnson et al., 2018). Our focal species of yellow-tail clownfish tends to behave more like larger reef fishes, with territories that can extend beyond single anemones (CITATION) and strong enough swimming skills <sup>177</sup> that movement between patch reefs is possible though unusual (CITATION), than the smaller clownfish *A. percula* commonly used in previous metapopulation studies (e.g. Buston et al., 2011; Salles et al., 2015).

<sup>180</sup> **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 (Fig. 2a). The sites consist of <sup>183</sup> rocky patches of coral reef and are separated by sand flats (Fig. 2b). 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 <sup>186</sup> selected to cover and exceed that range. On the north edge, the sites are isolated from nearby habitat with no substantial reef habitat for at least 20 km.

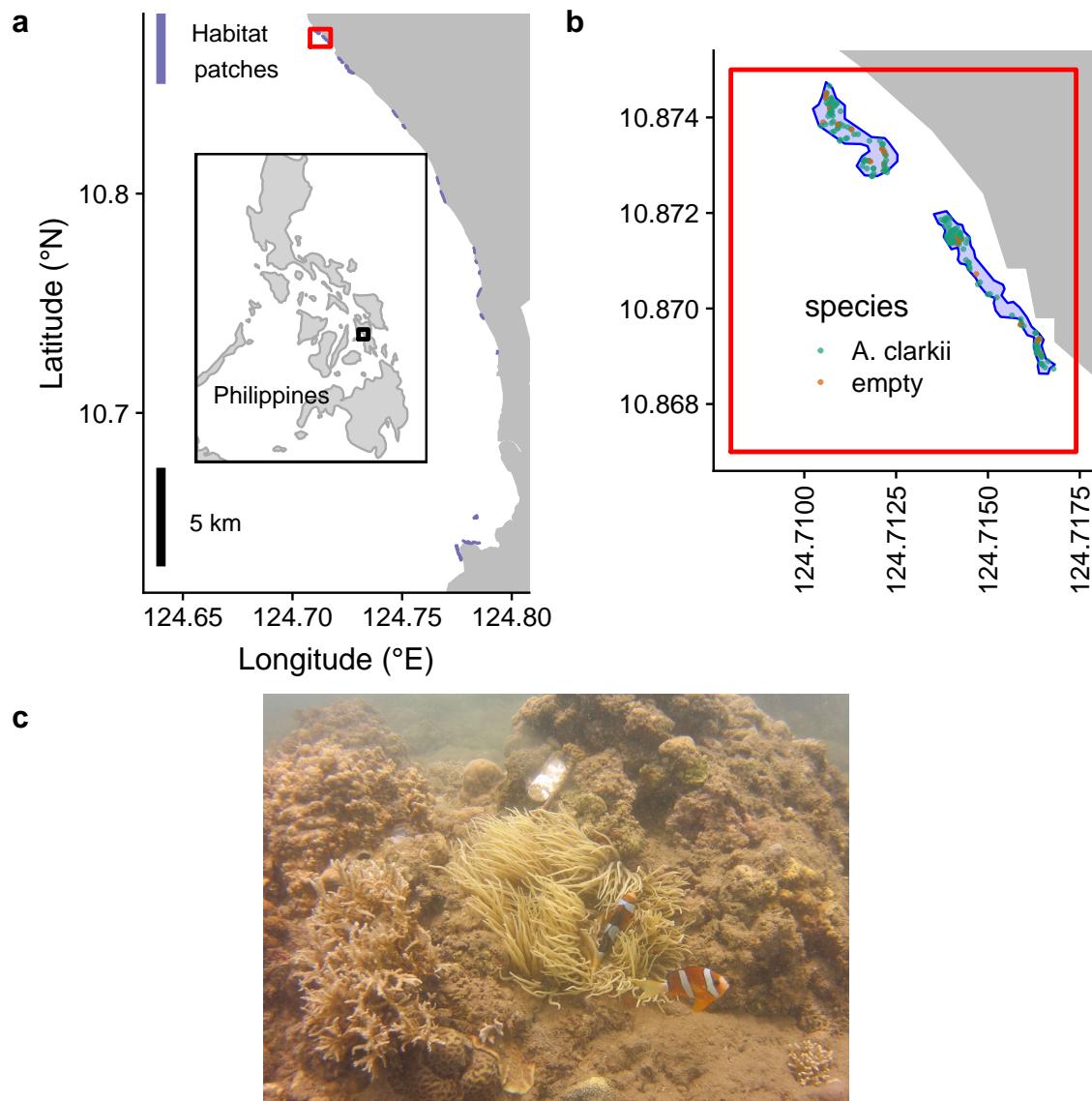


Figure 2: a) A map of the sites along the coast of Leyte in the Philippines. b) A zoomed-in map of Palanas and Wangag to show anemone arrangement for anemones occupied by *A. clarkii* (green) or unoccupied by clownfish (green). c) An example anemone occupied by *A. clarkii* in a typical habitat at the sites.

Since 2012, we have sampled fish and habitat at most of the sites annually (Table 189 A1). During sampling, divers using SCUBA and tethered to GPS readers swam the extent of each site. Divers visited each anemone inhabited by yellowtail clownfish, tagging the anemone to be able to track anemones through time. At each anemone, 190 the divers attempted to catch all of the yellowtail clownfish 3.5 cm and larger, taking a small 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 195 season, fish 6.0 cm and larger were also tagged with a passive integrated transponder (PIT) tag, unless already tagged. Divers also looked for eggs around each anemone and measure and photographed any clutches found. In total, we took fin clips from 198 XX fish and PIT-tagged XX fish across all years and sites combined, with an average of XX fish clipped and XX fish tagged per year.

### Parentage analysis and dispersal kernel

201 We digested extracted genomic DNA from our tissue samples using the ddRAD-seq protocol (Peterson et al., 2012), filtered the sequences with the bioinformatics pipeline dDocent (Puritz et al., 2014), and called singled nucleotide polymorphisms 204 (SNPs) using the program FreeBayes (*is there a citation for this?*). In total, we genotyped XX fish. We used the SNPs to identify parent-offspring matches with the software program COLONY2 (Wang, 2012) (details on genotyping and parentage 207 analysis in Catalano et al., in prep).

Using the method described in (Bode et al., 2018), we fit a distance-based dispersal kernel (Catalano et al., in prep), where the relative dispersal is a function of

210 distance  $d$  as measured in kilometers and parameters  $\theta$  and  $k_d$ , which control the shape and scale of the kernel:

$$p(d) = e^k e^{-(e^k d)^\theta}. \quad (3)$$

We use a Laplacian dispersal kernel with shape parameters  $\theta = 1$  and scale parameter 213  $k_d = -1.84$  (Fig. 4a, 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 216 given that a fish recruits somewhere, not the probability that a released larva will travel a particular distance. To find the probability of fish dispersing among our sites, we numerically integrate the dispersal kernel (eqn. 3) using the distance from 219 the middle of the origin site to the closest and farthest bounds of the destination site as the upper and lower bounds. 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 222  $d_2$  is the distance from the middle of A to the far edge of B, is:

$$p_{A,B}(d) = \int_{d_1}^{d_2} e^k e^{-(e^k d)^\theta} dd. \quad (4)$$

## Estimating inputs from empirical data

### Growth and survival: mark-recapture analyses

225 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 228 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  
<sub>231</sub> 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:

$$\begin{aligned} L_{t+1} &= L_t + (L_\infty - L_t)[1 - e^{(-K)}] \\ &= e^{(-K)}L_t + L_\infty[1 - e^{(-K)}]. \end{aligned} \tag{5}$$

We see from eqn. 5 that we would expect the first length  $L_t$  and the second length  
<sub>234</sub>  $L_{t+1}$  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  
<sub>237</sub> 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  
<sub>240</sub> this process 1000 times to generate a distribution.

We use the full set of marked fish to estimate annual survival  $\phi$  and probability  
<sub>243</sub> of recapture  $p_r$  using the mark-recapture program MARK implemented 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 A2). For fish that are not recaptured in particular  
<sub>246</sub> year, we estimate their size using our growth model (eqn. 5) 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 need to swim near an anemone

249 to have a reasonable chance of capturing the fish on it. Therefore, we also consider a  
250 distance effect on recapture probability; we use the GPS tracks of divers to estimate  
251 the minimum distance between a diver and the anemone for each tagged fish in each  
252 sample year and include it as a factor in some of the models (Table A2).

## Fecundity

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

$$\ln(E_c) = \beta_l \ln(L) + \beta_e[\text{eyed}] + b. \quad (6)$$

To get total annual fecundity  $f$ , we multiply the number of eyed eggs per clutch by  
257 the number of clutches per year  $c_e = 11.9$ , using the estimate from Holtswarth et al.  
258 (2017).

We only consider reproductive effort once the fish has reached the female stage  
259 and use the average size of first observation as female for recapture fish as the tran-  
260 sition size  $L_f$ .

## Lifetime egg production

We use an integral projection model (IPM) (e.g. Rees et al., 2014) to estimate the  
261 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 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 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, 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 ( $\text{size}_{\text{recruit}}$ ):  $n(t = 0) = n(\text{size}_{\text{recruit}}, 0)$ , 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 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 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. 6) to get the total number of eggs produced at each time step. To get the total number of eggs one individual is likely to produce in its lifetime, we then sum across all time steps in the individual's potential life.

$$\text{LEP} = \sum_{t=0}^{t=100} \sum_{z=L}^{z=U} v_z, t f_z. \quad (7)$$

### Survival from egg to recruit

291 We estimate survival  $S_e$  from egg to recruit using the number of recruited offspring  
 we can match back to genotyped parents as surviving individuals from genetically  
 "tagged" eggs in a method similar to that in Johnson et al. (2018). We estimate  
 294 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  
 fish  $\text{LEP}_p$ , using LEP calculated starting with an individual of 6 cm. We make the  
 297 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  
 survive to recruit  $R_t$  by dividing the number of offspring matches we find ( $R_m = 90$ )  
 300 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  
 $P_c$  (see A.1, A.2 for details on  $P_h$  and  $P_c$  estimates, respectively). Our estimated  
 303 survival from egg to recruit is the number of tagged recruits divided by the number  
 of tagged eggs produced:

$$S_e = \frac{\frac{R_m}{P_h P_c}}{N_g \text{LEP}_p}. \quad (8)$$

## Estimated abundance over time

We also consider trends in abundance of breeding females at each site over time to compare to our replacement-based estimates of persistence. Similarly to as we do for offspring, we scale up the number of females caught at each site  $i$  in each sampling year  $t$  by the proportion of habitat sampled in that site and year  $P_{h_i,t}$  and by the probability of capturing a fish  $P_c$ :

$$\# \text{ females}_{i,t} = \frac{\# \text{ females captured}_{i,t}}{P_{h_i,t} P_c}. \quad (9)$$

We then fit a linear model through the time series for each site and the population overall to assess whether the slope  $m$  over time indicates growth, decline, or stability in abundance:

$$\# \text{ females} = m * \text{year} + b. \quad (10)$$

## 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 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.

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 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

324 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  
327 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  
330 pull from a normal distribution generated using the uncertainty 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  
333 both the number of offspring assigned to parents  $R_m$  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  
336 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  
339 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  
342 estimated from recapture dives across sites and sampling seasons (details in A.2).

## Results

Our estimated abundance of females at each site over time is relatively constant [add  
345 some sort of actual analysis here] (Fig. 3), suggesting that our sample populations

are stable over time.

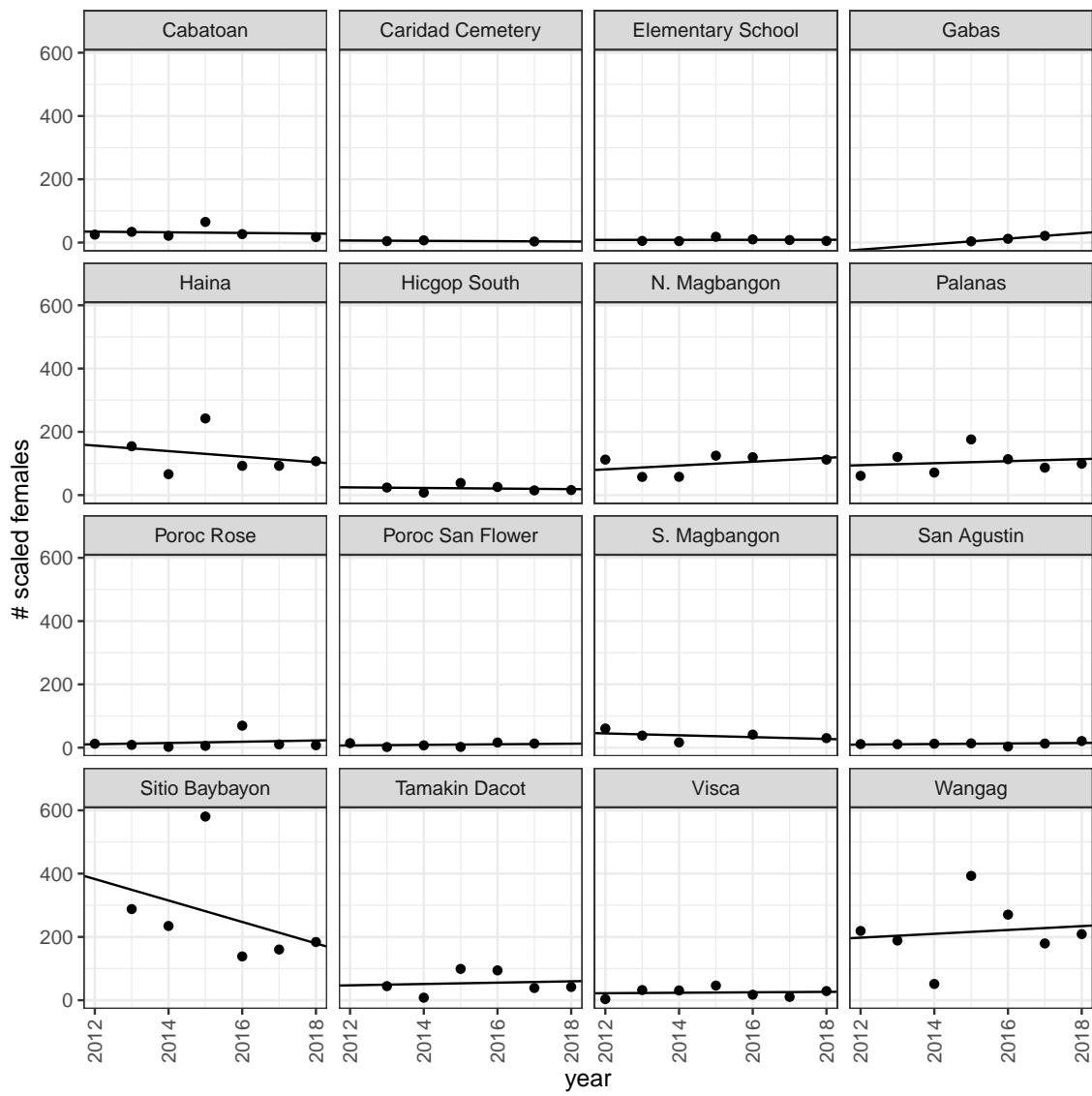


Figure 3: The estimated number of females at each site over the sampling years. The total number of females at each site was estimated by taking the number of females (fish  $> 5$  cm with the yellow pointed tail indicating female) captured at each site in each year and scaling up by the proportion of habitat sampled at that site that season (see A.1 for details) and by the average probability of capturing a fish (see A.2).

From the mark-recapture analysis of tagged and genotyped fish, we estimate mean  
348 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. 4b,  
Table 1). For juvenile and adult (post-recruitment) survival on a log-odds scale, the  
351 best-fit model has a coefficient  $b_a = 0.74 \pm 0.060$  SE for the effect of size and an inter-  
cept  $b_\phi = -4.83 \pm 0.340$  SE. These results suggest that larger fish have higher annual  
survival, which is similar to survival estimates in other clownfish species (check Bus-  
ton paper). The accompanying best-fit model for log-odds recapture probability has  
354 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  
357 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  
360 the recapture probability plots, like the survival one in Fig. 4, 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  
363 female capture of recaptured fish (Fig. 4d). [*Contextualize these values.*]

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

---

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	$\pm 0.340$ standard error	
$b_a$	size effect for adult survival	0.74	$\pm 0.060$ standard error	
$b_{p_r}$	intercept for recapture probability from mark-recapture analysis	17.93	$\pm 0.858$ standard error	not used in persistence estimates
$b_1$	size effect for re-capture	-1.816	$\pm 0.080$ standard error	not used in persistence estimates
$b_2$	distance effect for recapture	-0.171	$\pm 0.021$ standard error	not used in persistence estimates
$\text{size}_{\text{recruit}}$	size (cm) of recruited offspring	mean of size of offspring in parentage analysis = 4.4 cm	3.5 - 6.0 cm	
$b_e$	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 relationship	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 distribution with parameters $\alpha_{P_c} = 1.44$ and $\beta_{P_c} = 1.13$	details in A.2

Table 1:

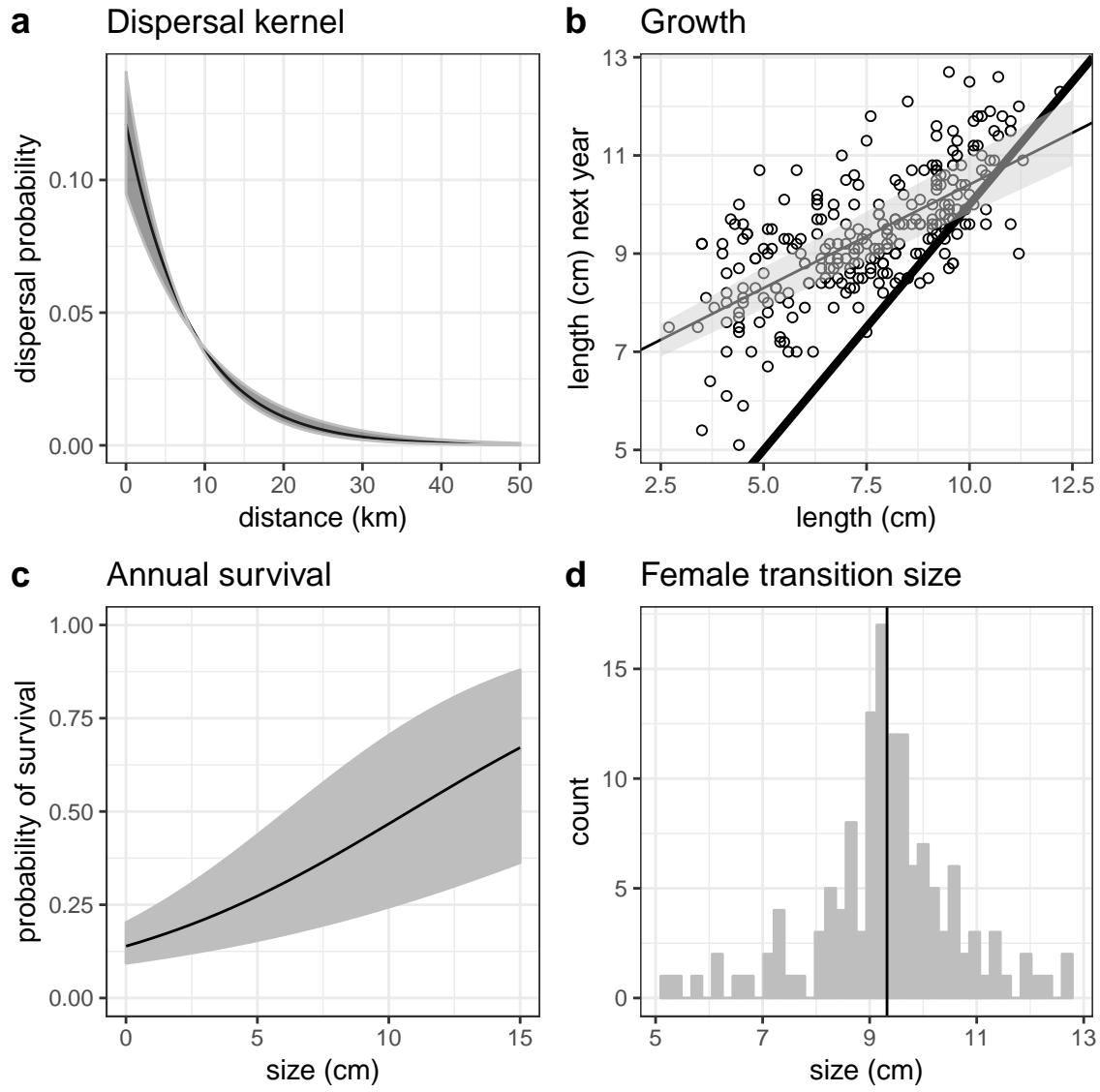


Figure 4: Best estimates (solid black line) and range included for uncertainty (gray) for dispersal (a), growth (b), post-recruit survival (c), and size at female transition (d) parameters.

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

<sup>369</sup> of LEP for 10876, ranging from XX to XX when we consider uncertainty in the inputs  
<sup>370</sup> (Fig. 5a). The size at recruitment - the census point between egg-recruit survival  
and LEP - has the most effect on the value of LEP (Fig. B.4), with higher values of  
<sup>371</sup> LEP the higher the size of recruitment as less mortality is included before reaching  
reproductive sizes.

We estimate egg-recruit survival  $S_e$  to be 1.82e-05, ranging from XX to XX  
<sup>375</sup> when we include uncertainty in the number of offspring assigned to parents and  
the probability of catching a fish (Fig. 5b). Uncertainty in the size of transition  
to breeding female  $L_f$  has the largest effect on egg-recruit survival (Fig. B.7); we  
<sup>378</sup> only consider reproduction from females, to avoid double-counting, so the larger  
the transition size to female, the fewer tagged eggs we estimate were produced by  
genotyped parents and the higher egg-recruit survival.

<sup>381</sup> We estimate lifetime recruit production, the product of LEP and  $S_e$ , to be 0.20,  
below the value of 1 necessary for replacement. This suggests that even without  
considering connectivity, the individuals at our sample populations do not produce  
<sup>384</sup> enough offspring that survive to recruitment to replace themselves. When we consider  
uncertainty in our parameter estimates, we do see a few cases where  $LRP > 1$ , but  
the majority are well below the threshold for replacement.

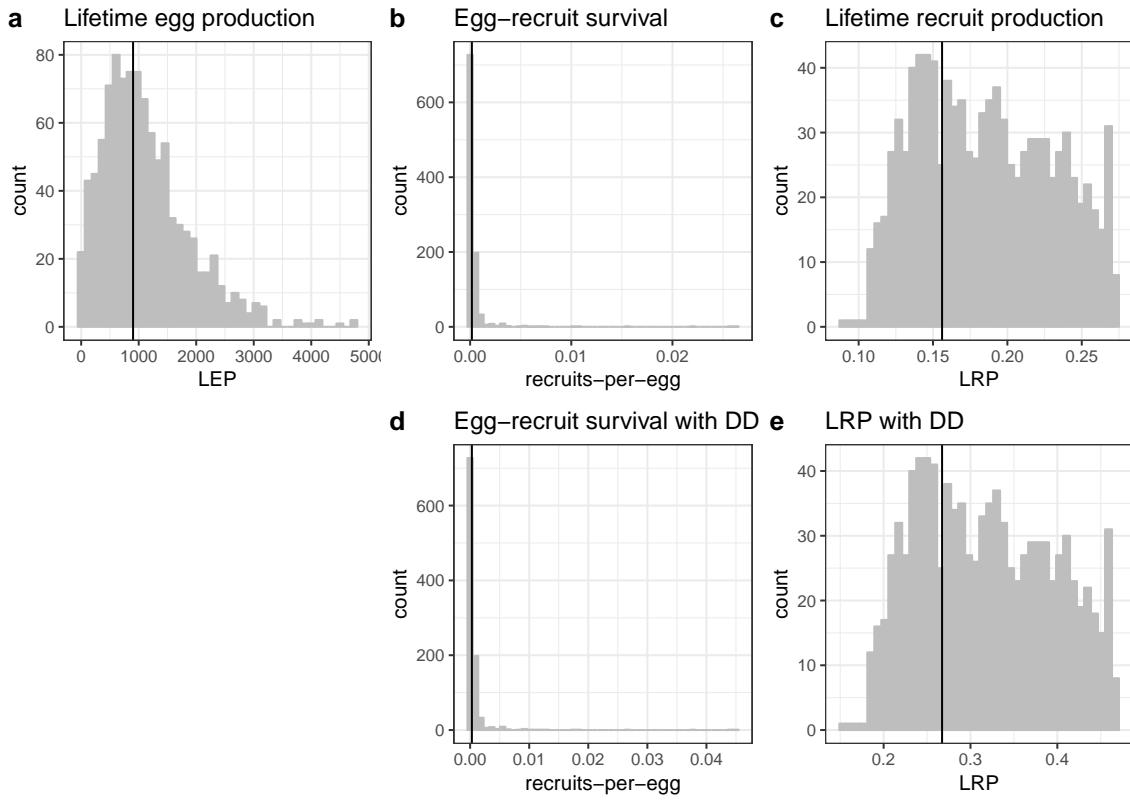


Figure 5: Estimates of a) LEP, b) egg-recruit survival, and c) LRP, showing the best estimate (black solid line) and range of estimates considering uncertainty in the inputs.

387 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  
 390 makes sense. We see the highest values of self-persistence at Haina ( $SP = 0.024$ ) and  
 Wangag ( $SP = 0.010$ ), our two widest sites.

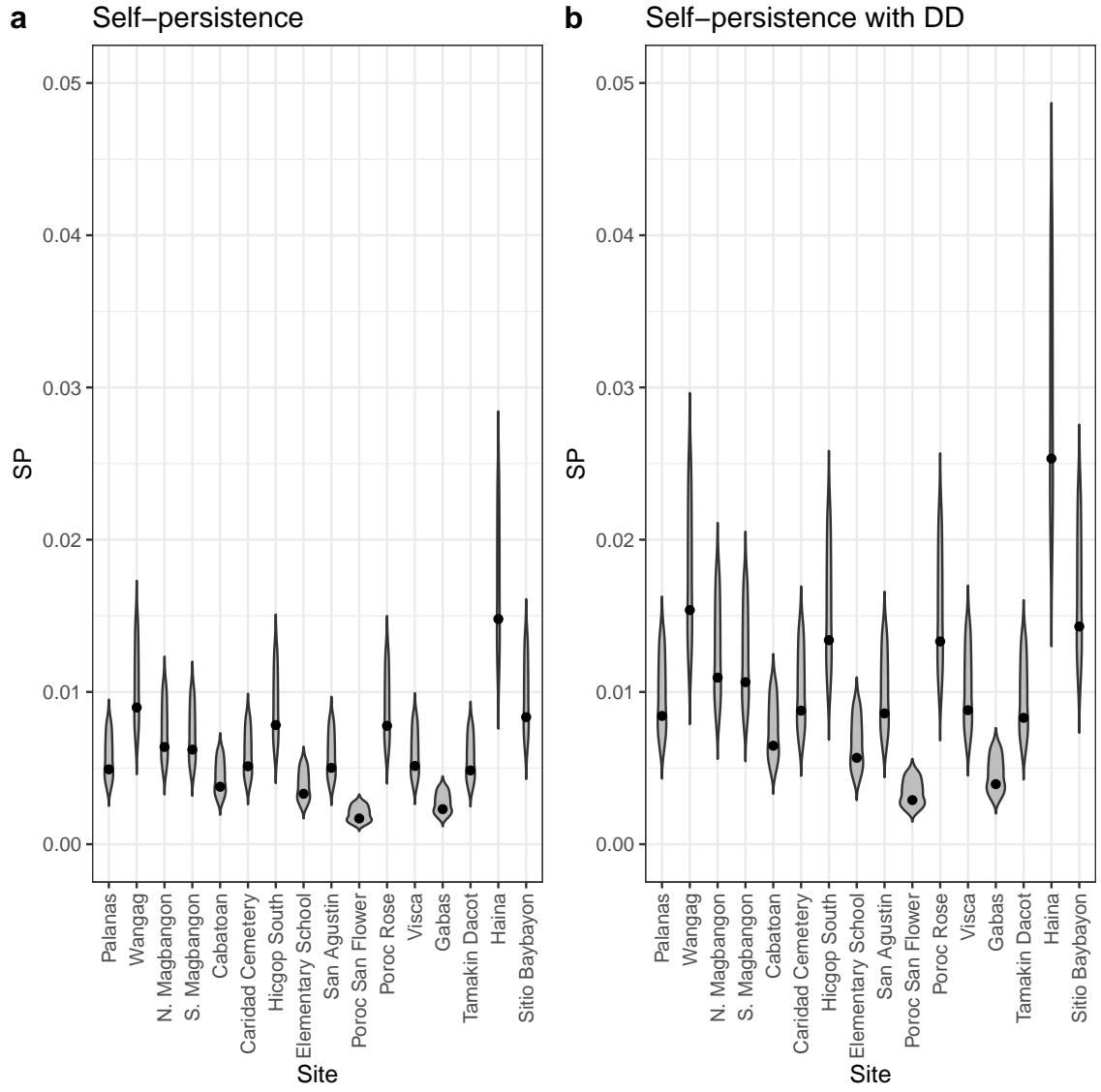


Figure 6: Values of self-persistence at each site, showing the best estimate (black point) and range of estimates considering uncertainty in the input parameters. No site reaches a value of  $SP > 1$ , necessary to be self-persistent.

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

<sup>393</sup> the realized connectivity matrix  $\lambda_c$  is 0.034, well below the value of 1 that indicates network persistence (Fig. 7a). We see that most of the connectivity occurs among the sites in the northern part of our sample area, from Palanas to Caridad Cemetery.

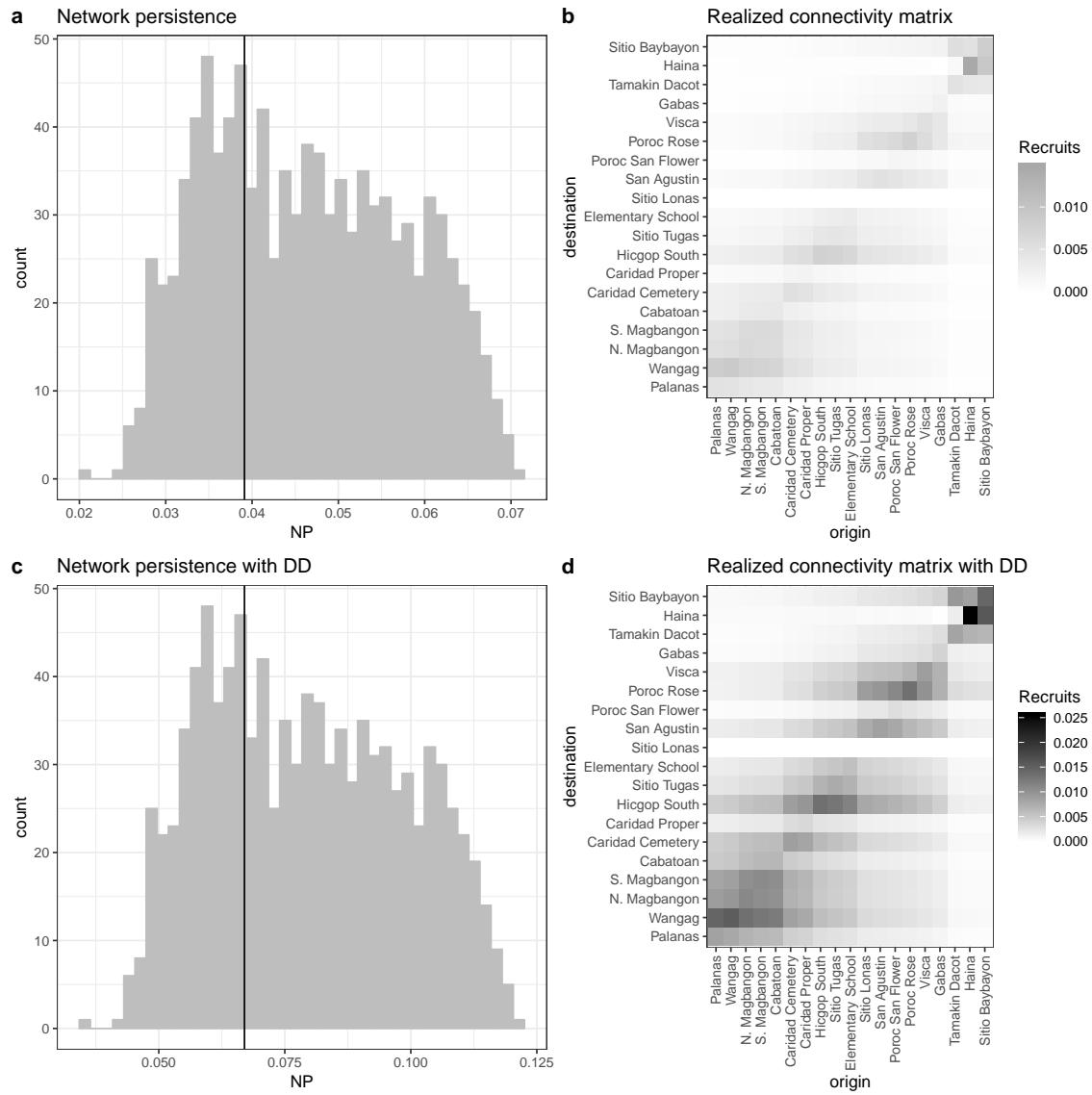


Figure 7: a) Network persistence values, showing the best estimate (black solid line) and range of estimates considering uncertainty. b) The realized connectivity matrix  $C$ , with sites arranged from north (Palanas) to south (Sitio Baybayon).

396

Based on our estimates of LRP, SP, and NP, we do not expect that our set of sites

is able to persist in isolation as a closed system. To explore what would be required for persistence, we consider a hypothetical scenario in which we consider the system  
399 closed and assume that all of the recruits arriving at our sites came from adults at our sites. In this case, we find a value of  $LRP = 1.21$ , above the value of 1 necessary for replacement (Fig. B.1a). When we add in the connectivity, we see a higher  
402 value of  $\lambda_c$  in our best estimate ( $NP = 0.20$ ) but still not high enough to indicate network persistence (Fig. B.1b). We see more of the distribution of estimates above 1, however, suggesting that network persistence is within our range of uncertainty  
405 in this case, though not likely. With our site configuration and dispersal kernel estimate, we would need a value of LRP of XX (an egg-recruit survival of XX with our estimated value of LEP or a value of LEP of XX with our estimated value of  
408 egg-recruit survival), to  $\lambda_c = 1$  and network persistence.

## Discussion

We do not see evidence for persistence in our metric estimates, either self-persistence  
411 where an individual site could persist alone or network persistence with exchange among sites. The abundances through time at our sites are relatively constant, however, suggesting that the population at our sites is stable but relies on input of  
414 recruits from outside sites to persist. The portion of coastline we sampled is likely a portion of a larger metapopulation.

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

- So we don't see persistence in our metrics, either self-persistence or network

420 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.

- 423
- How does dispersal spread (estimated to be within our sites) interact with scale  
of a self-contained metapopulation? How do we reconcile this in our system,  
where we don't estimate dispersal that far but don't see network persistence  
426 in an area range that spans the estimated spread? (This point might change,  
depending on mean dispersal distance from the new kernels)

- Sensitivity - how would our parameters need to change to see persistence?

429 Egg-recruit survival is a big one. Discuss limitations of how we calculated it  
(offspring going outside our pops not included - though we might change this),  
what we see for persistence when estimate recruits/recruits instead. Context-  
432 tualize this with what other studies have found for these parameters, how  
reasonable it would be to get better estimates in the field.

Persistence criteria, such as those detailed in Hastings and Botsford (2006) and  
435 Burgess et al. (2014), ask whether a population at low abundance can grow and  
recover rather than going extinct. Density-dependence is assumed to not exist at  
low abundances (CITATIONS, with the exception of xx density-dependence, like the  
438 allee effect) so is not explicitly considered in persistence metrics. In real populations,  
however, it can be challenging to estimate density-independent demographic rates,  
as density-dependence is occurring in the population as it is sampled. In *A. clarkii*,

441 density-dependence is likely most important in early life stages, as for many fish  
442 species, but could play an important role throughout the life history due to the  
443 social hierarchies in colonies of clownfish (CITATIONS). In other species of clownfish,  
444 individuals on the same anemone maintain strict size spacing, restricting their food  
445 intake and growth to avoid encroaching on the position of another fish and being  
446 attacked or evicted (CITATIONS). This suggests that while fish are in the pre-  
447 reproductive queue, density-dependence may lower growth rates compared to the  
448 growth of fish alone on an anemone, as would be the case in a population at low  
449 abundance. We attempt to account for the primary effect of density-dependence  
450 on our estimate of egg-recruit survival but other estimates, particularly growth and  
451 survival, would also likely be higher in the absence of density-dependence, which  
452 would increase LRP.

453 Our estimates of survival probabilities are similar to those estimated for other  
454 species of clownfish, particularly our relationship with size where small fish have a  
455 low annual survival and the largest fish have a high annual survival (CITATIONS,  
456 Buston paper, also compare to Salles et al. 2015). Our fecundity estimates are lower  
457 than those for *A. clarkii* in temperate areas, almost XX times lower (CITATIONS,  
458 Ochi papers - 17,500 eggs/yr/female, from Bell 1976).

459 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  
460 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). But is it high enough?

465

- Discuss site-specific demographic rates, why we don't estimate them in our system, the importance they play in other studies, what we might need to go about resolving them, whether we would expect to see them.
- Contextualize our parameter estimates with those from other studies (esp. survival, growth, fecundity).

468

471 Broadening back out:

- What does this mean for moving forward in understanding metapopulation persistence more broadly? Stability in abundance doesn't mean the population would be able to persist in isolation. Area required seems to be much wider than dispersal kernel spread (particularly if LRP production is right around replacement). Even areas of habitat along a linear coastline seem to be drawing much of their recruitment from a larger surrounding area - even though we see some local retention, maybe broader connectivity is still the story in terms of receiving enough recruitment to persist.

474

477

# Appendix

## A Method details

### A.1 Proportion of habitat sampled

483 We used tagged anemones to estimate the proportion of habitat sampled at each site  
 in each year ( $P_{h_{i,t}}$ ). We tagged each anemone that is home to *A. clarkii*, with a metal  
 tag, which is relatively permanent and easy to re-sight (the anemone tag is visible  
 486 above the anemone in Fig. 2c), so we consider the total number of metal tags at each  
 site to be the total number of anemones that are habitat. We divide the number of  
 tagged anemones visited each sampling year by the total number of metal tags at  
 489 that site to get the proportion of habitat sampled. We use proportion of anemones  
 rather than proportion of total site area because anemones, and therefore habitat  
 quality, are unevenly distributed across the site; areas we did not visit are likely to  
 492 have a lower density of anemones than the areas we did sample.

For scaling the number of tagged recruited offspring to account for areas of our sites we did not sample, we use the overall proportion habitat sampled across all sites and sampling years ( $P_h$ ). We sum the metal-tagged anemones we visited across all sites and years to get the total number of metal-tagged anemones we visited while sampling. We then divide that by the number of anemones we could have sampled,  
 495 the sum of total metal-tagged anemones across all sites multiplied by the number of sampling years, to get the overall proportion habitat sampled across our sites and sampling years.

501      *Add details about how sometimes it is ↗1 if the site doesn't have metal tags?  
Mention plastic tags?*

		% Habitat surveyed							
Site	# Total anems	2012	2013	2014	2015	2016	2017	2018	
Cabatoan	26	42	58	58	65	73	0	62	
Caridad Cemetery	4	0	75	50	0	50	50	50	
Elementary School	8	0	100	38	88	88	88	100	
Gabas	9	0	0	0	44	44	67	0	
Haina	104	0	6	13	13	10	56	80	
Hicgop South	18	0	67	22	28	56	83	78	
N. Magbangon	105	5	12	40	63	63	0	5	
S. Magbangon	34	41	56	32	0	65	0	71	
Palanas	137	29	58	47	63	85	86	86	
Poroc Rose	13	100	100	69	31	23	69	69	
Poroc San Flower	11	100	82	73	73	55	82	64	
San Agustin	17	94	65	71	65	100	82	76	
Sitio Baybaon	260	0	14	30	33	30	41	80	
Tamakin Dacot	50	0	24	22	36	34	60	68	
Visca	13	100	100	23	38	62	85	62	
Wangag	296	18	32	42	34	26	49	68	

Table A1: Table showing the percent of metal-tagged anemones surveyed at each site in each sampling year.

*Add in description*

<sup>504</sup> **Proportion of dispersal kernel area sampled**

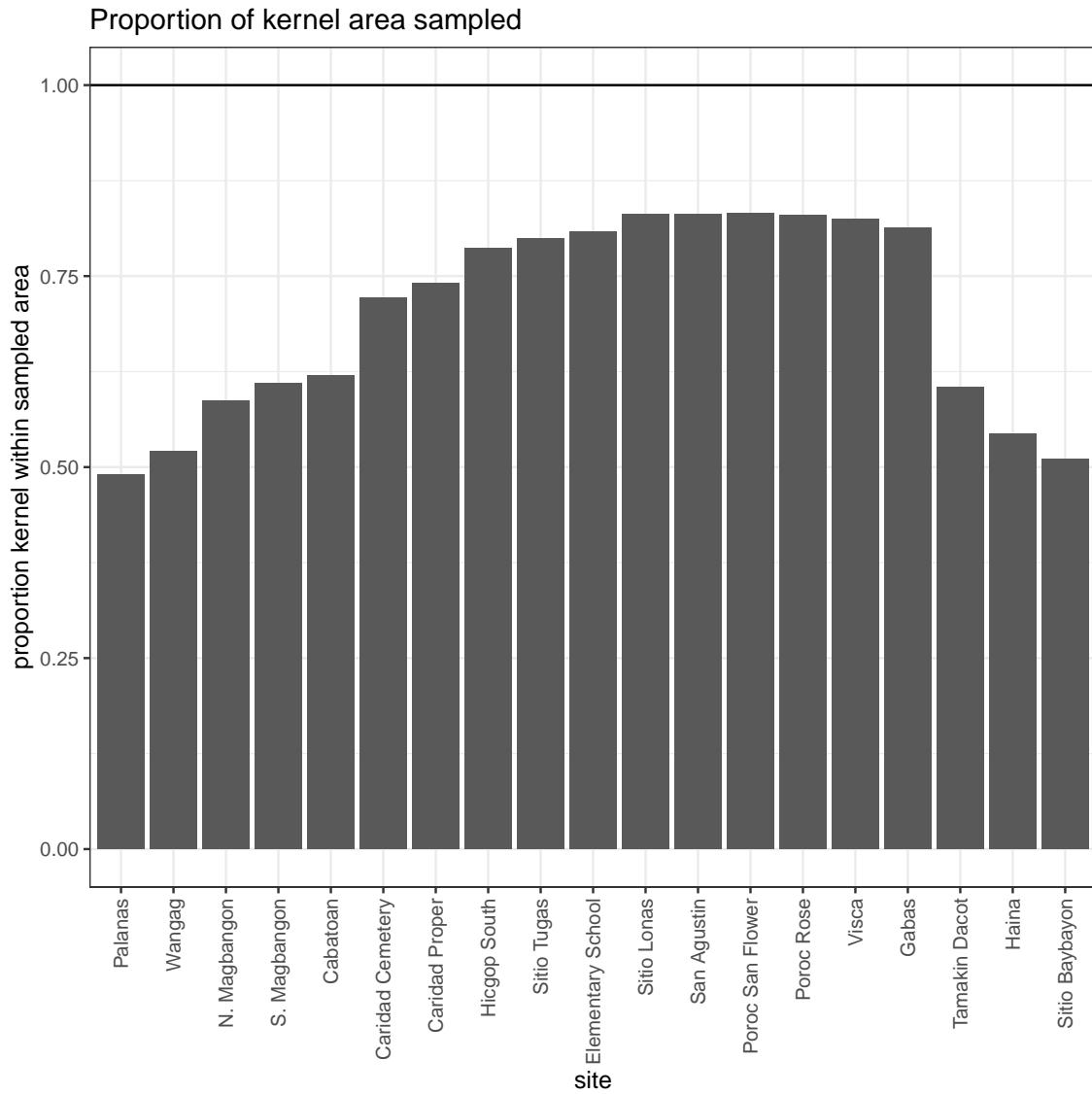


Figure A.1: Proportion of the dispersal kernel area from the center of each site covered by our sampling.

## A.2 Probability of capturing a fish, from recapture dives

We use mark-recapture data from recapture dives done within a sampling season to  
507 estimate the probability of capturing a fish. During some of the sampling years (XX),  
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  
510 dives and the recapture dives because they are so close in time and that fish do not  
change their behavior or reponse to divers, so therefore assume that the probability  
of recapturing a fish is the same as the probablity of capturing a fish on a sample dive.  
513 For each recapture dive, we use GPS tracks of the divers to identify the anemones  
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  
516  $P_c$  as the number of tagged fish caught during the capture dive  $m_2$  divided by the  
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  
519 seasons (2016, 2017, 2018), as our best estimate. Because there are so few recapture  
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  
522 pulling directly from the values calculated for each recapture dive. The distribution  
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  
525 the appropriate  $\alpha_{P_c}$  and  $\beta_{P_c}$  parameters, where

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

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

- 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  $\beta_{P_c} = 1.13$ .
- 528 We sample 1000 values from the beta distribution, then truncate the sample to only values larger than the lowest value of  $P_c$  estimated in an individual dive (0.20), to avoid extremely low values that are sometimes sampled but are unrealistically low.
- 531 We then sample with replacement from the truncated set to get a vector of values the length of the number of runs.

### A.3 Full set of MARK models

<sup>534</sup> We consider the following set of models in MARK [*Need to add in models*]:

Model	Model description	AICc	dAICc
	survival size, recapture size+distance	3348.861	0
	survival size, recapture distance	3359.998	-11.1371
	survival constant, recapture distance	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 constant	3570.908	222.04690

Table A2:

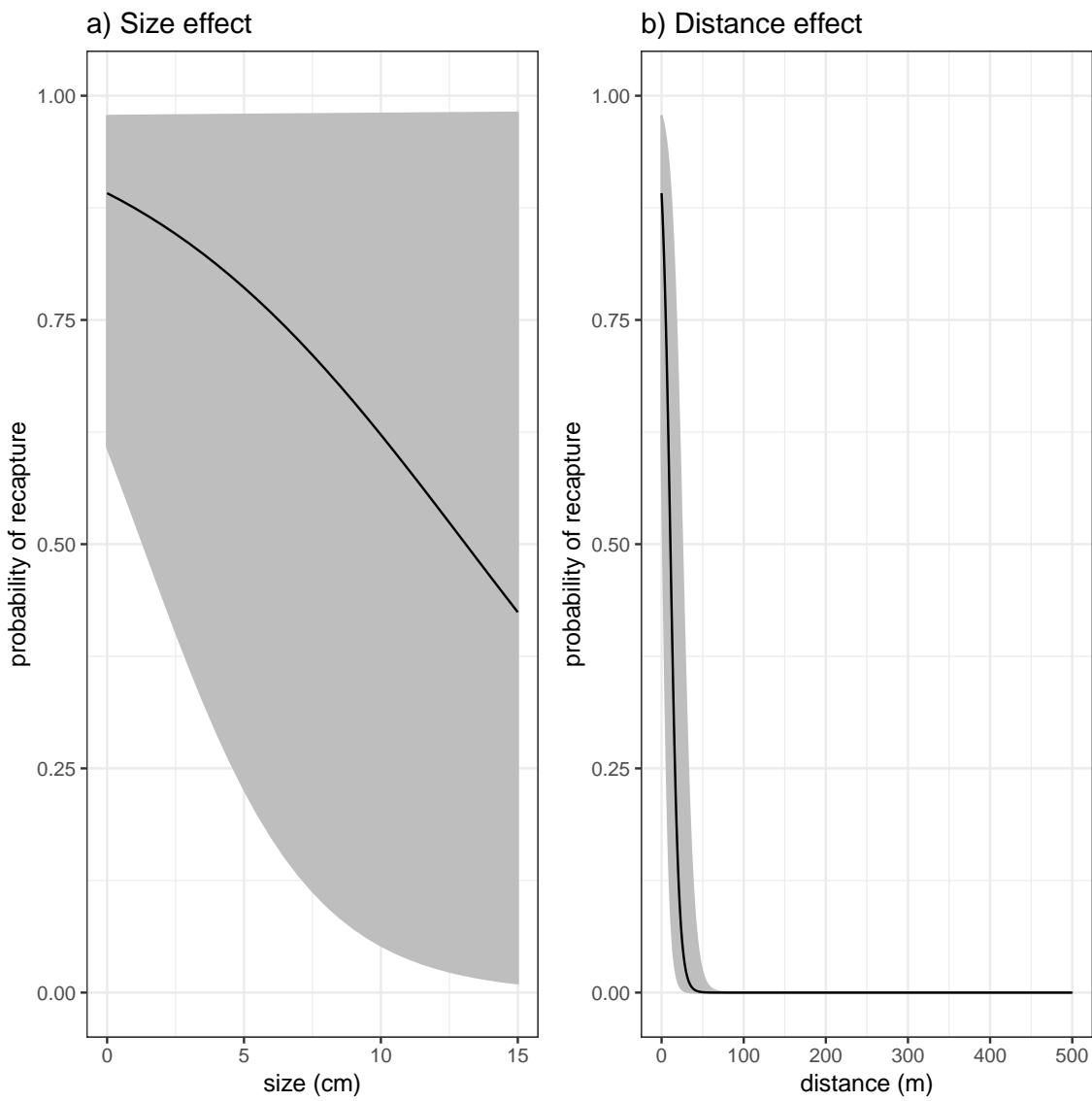


Figure A.2: Effects of a) fish size and b) minimum distance between divers and the anemone where the fish was first caught on the probability the fish will be recaptured, estimated along with survival in a mark-recapture analysis. Size has a slightly negative effect on the probability of recapture - larger fish are stronger swimmers and more likely to flee the anemone when divers approach. Distance also has a negative effect on recapture, as fish tend to stay close to their anemones and are not likely to be recaptured if divers do not get close to their anemone.

## B Uncertainty and sensitivity

### B.1 What-if analyses

537 To compare our replacement-based persistence results, which do not suggest that  
our sites make up a persistent metapopulation, with our abundance trends (Fig. 3,  
which suggest that population abundances at our site have been relatively stable  
over our sampling period, we estimate recruits arriving at our sites per recruit there,  
regardless of the origin of the arriving recruits. We repeat our metric estimates but  
use all offspring genotyped at our sites, scaled by proportion habitat sampled within  
540 our sites  $P_h$  and the probability of capturing a fish  $P_c$ , as our estimate of recruited  
tagged offspring. We see XXX, which means YYY.

### B.1.0.1 All genotyped offspring at our sites originated from our sites

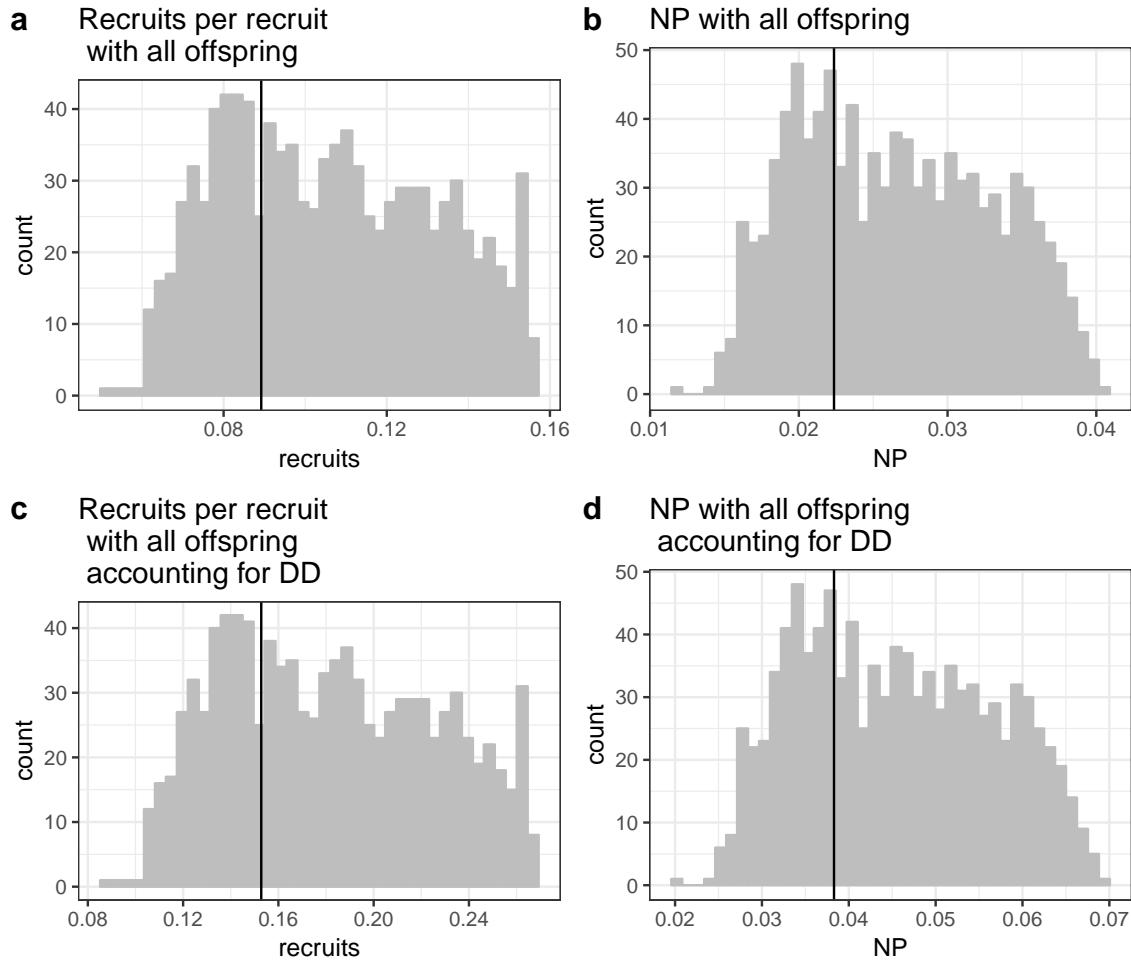


Figure B.1: a) Recruits per recruit when we consider all arriving recruits to have originated from our sites. b) Range of values of NP considering all arriving recruits to be offspring from our sites, with the best estimate in a black solid line.

<sup>546</sup> **B.2 Sensitivity to parameters**

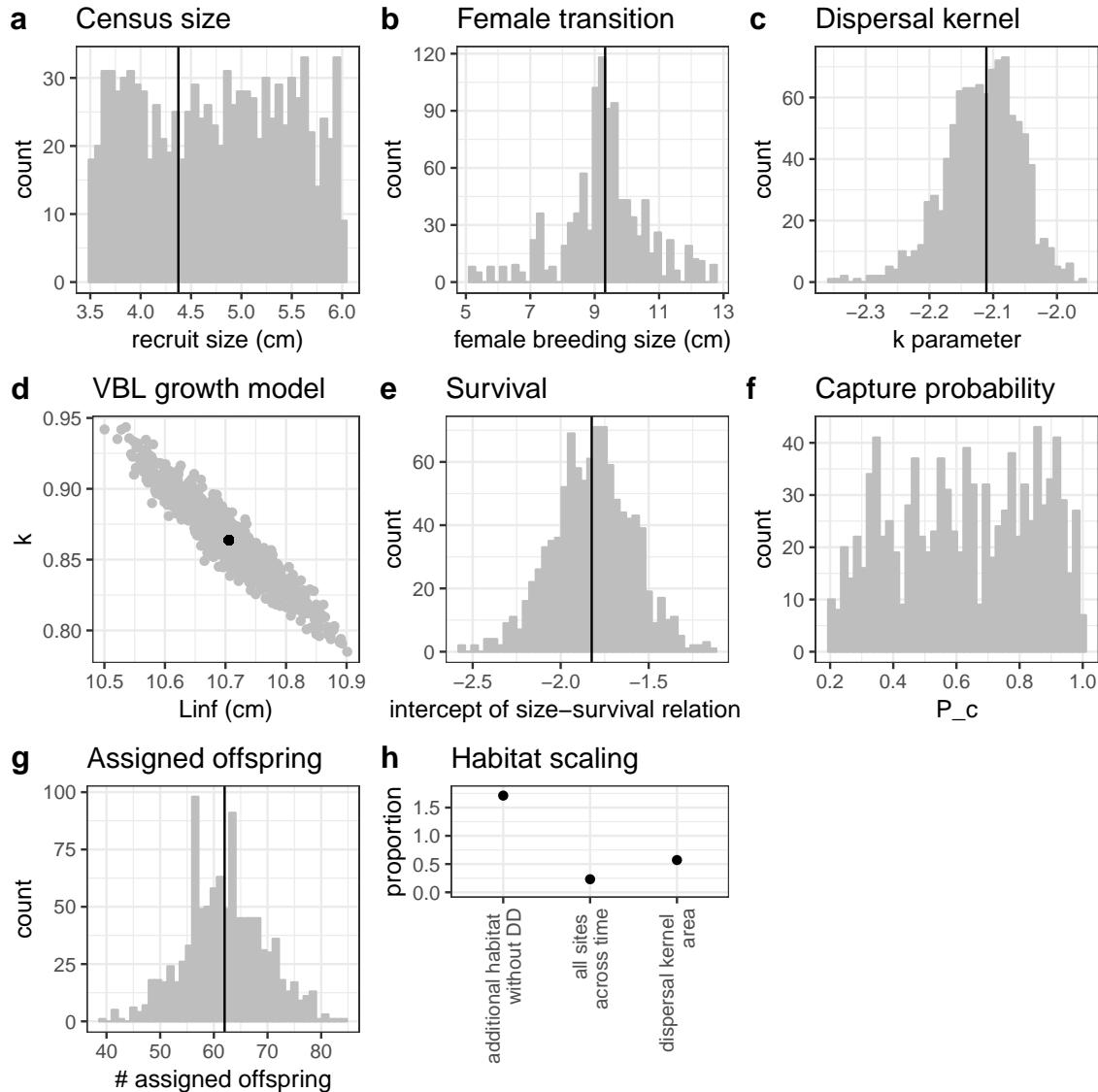


Figure B.2: Range of parameter inputs for uncertainty runs with all uncertainty included: a)  $\text{size}_{\text{recruit}}$ , the census size at which fish are considered to have recruited after egg-recruit survival occurs; b)  $L_f$ , the size at which fish transition from male to female and their reproductive output<sup>49</sup> included in the estimate of lifetime egg production (LEP); c)  $k_d$ , the scale parameter in the dispersal kernel; d) the parameters  $L_\infty$  and  $K$  of the von Bertalanffy growth model; e) the intercept  $b_\phi$  of the adult size-dependent survival relationship; f)  $P_c$ , the probability of capturing a fish; g) number of offspring assigned back to parents in the parentage analysis.

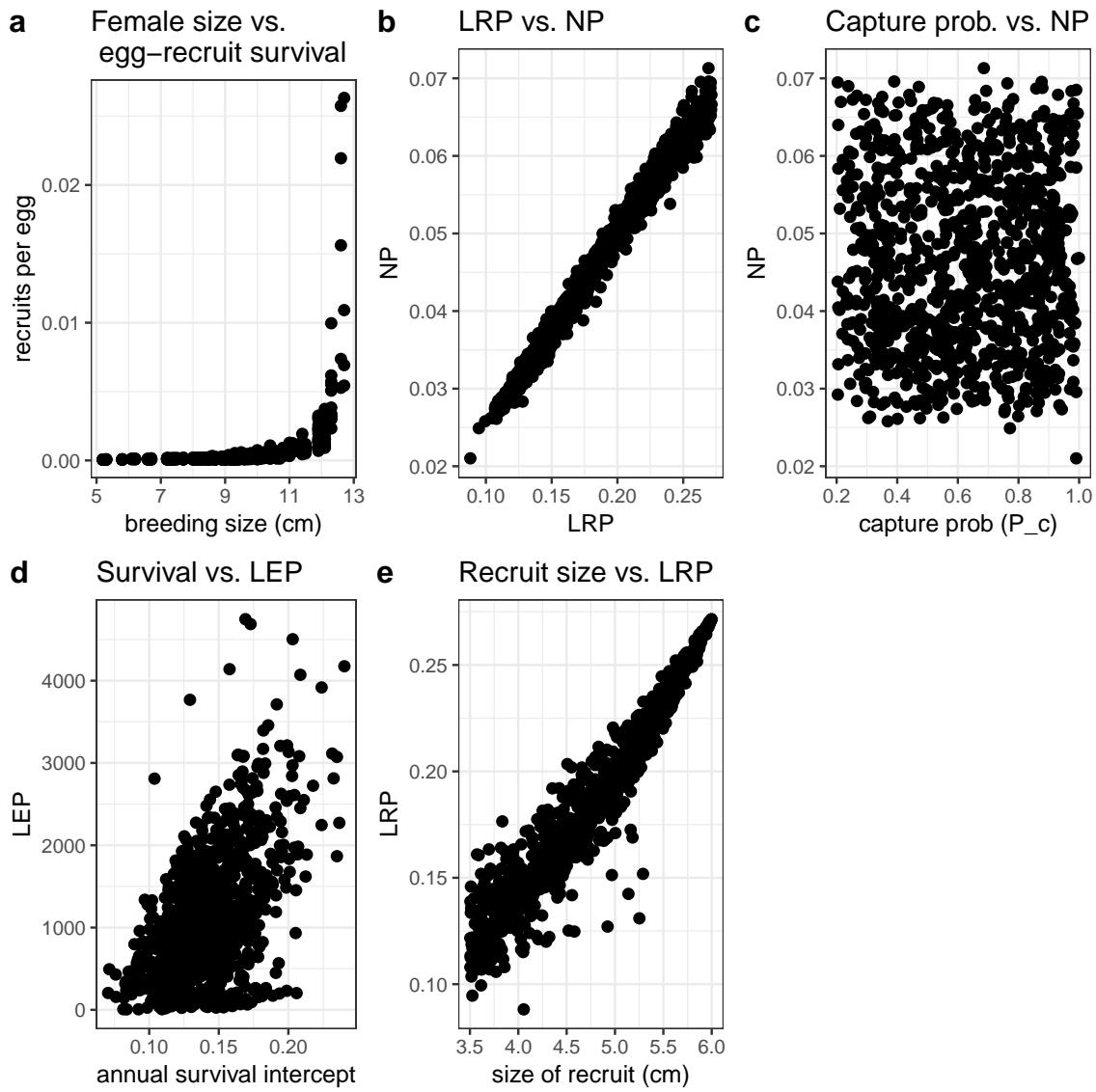


Figure B.3: Relationships among parameters and metrics. a) We only count reproductive effort by fish in the female stage so the higher the transition size to breeding female, the fewer eggs parents are considered to produce, which increases the estimated egg-recruit survival. b) LRP strongly affects NP by changing the number of potential recruits dispersed through the connectivity matrix. c) The probability of capturing a fish does not have a clear relationship to NP. d) LEP is higher with higher survival estimates because fish are more likely to survive longer as reproducing adults. e) The size we consider to be a recruit marks the transition of mortality included in egg-recruit survival to mortality being captured by annual adult survival. Because we do not have the data to change egg-recruit survival to account for

## B.3 Effects of different types of uncertainty on metrics

### B.3.0.1 Lifetime egg production (LEP)

549 Annual survival post-recruitment provides drives most of the uncertainty in LEP,  
as lower survivals keep fish from reaching and staying at large breeding sizes, with  
higher fecundity. The transition size to breeding female also drives uncertainty in  
552 LEP - the higher the transition size to female, the less time the fish has at a size  
where its reproduction is counted in LEP.

### Uncertainty in LEP

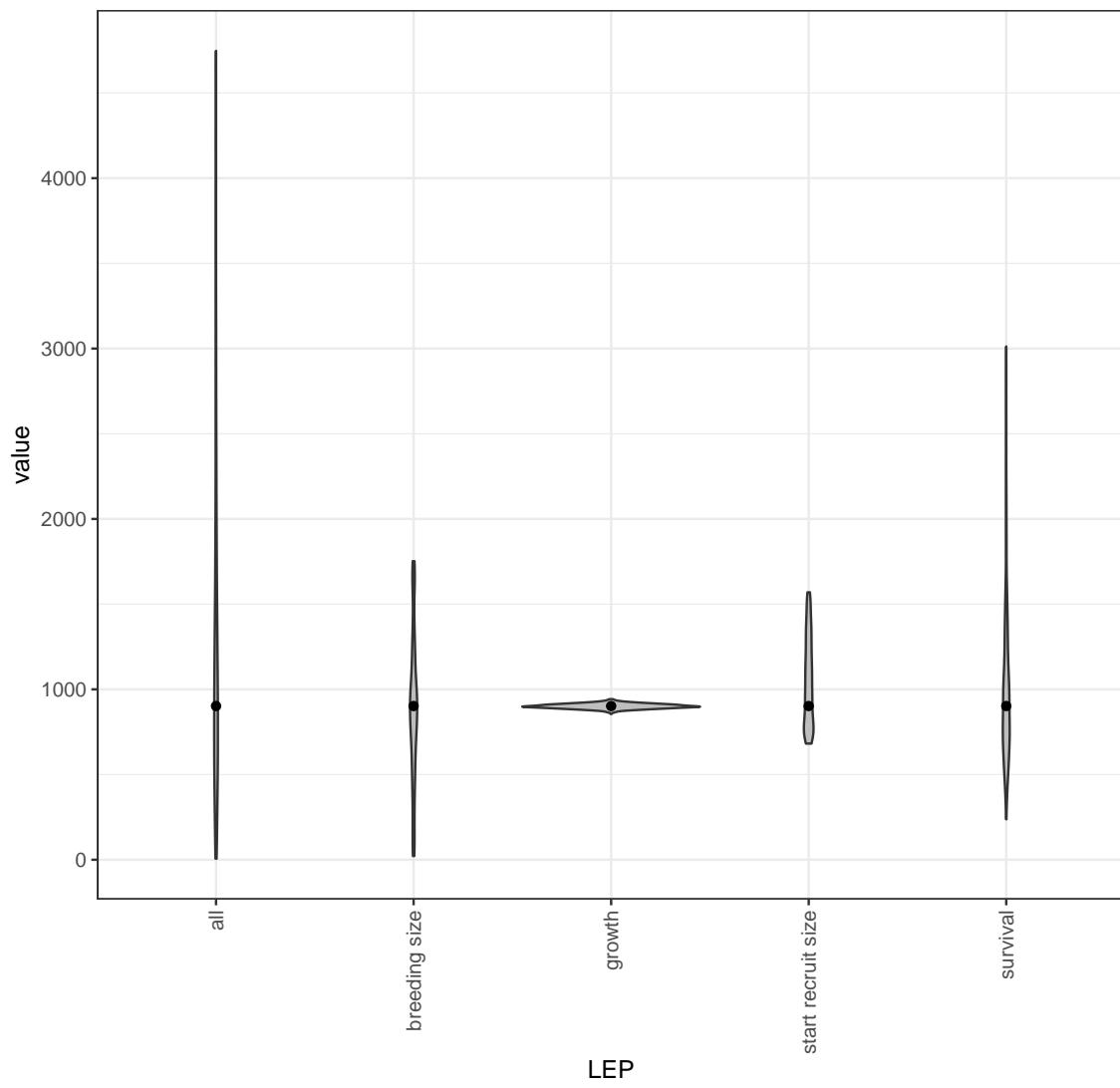


Figure B.4: The contribution of different sources of uncertainty in LEP.

### B.3.0.2 Lifetime recruit production (LRP)

555 Most of the uncertainty in LRP comes from uncertainty in the size of a recruit. This  
is an artifact of our sampling, where we are unable to estimate egg-recruit survival  
differently to account for changes in the size of a recruit, so raising the size of a recruit  
558 reduces the mortality included in LRP without increasing the mortality included in  
egg-recruit survival, as it should in an ideal situation.

### Uncertainty in LRP

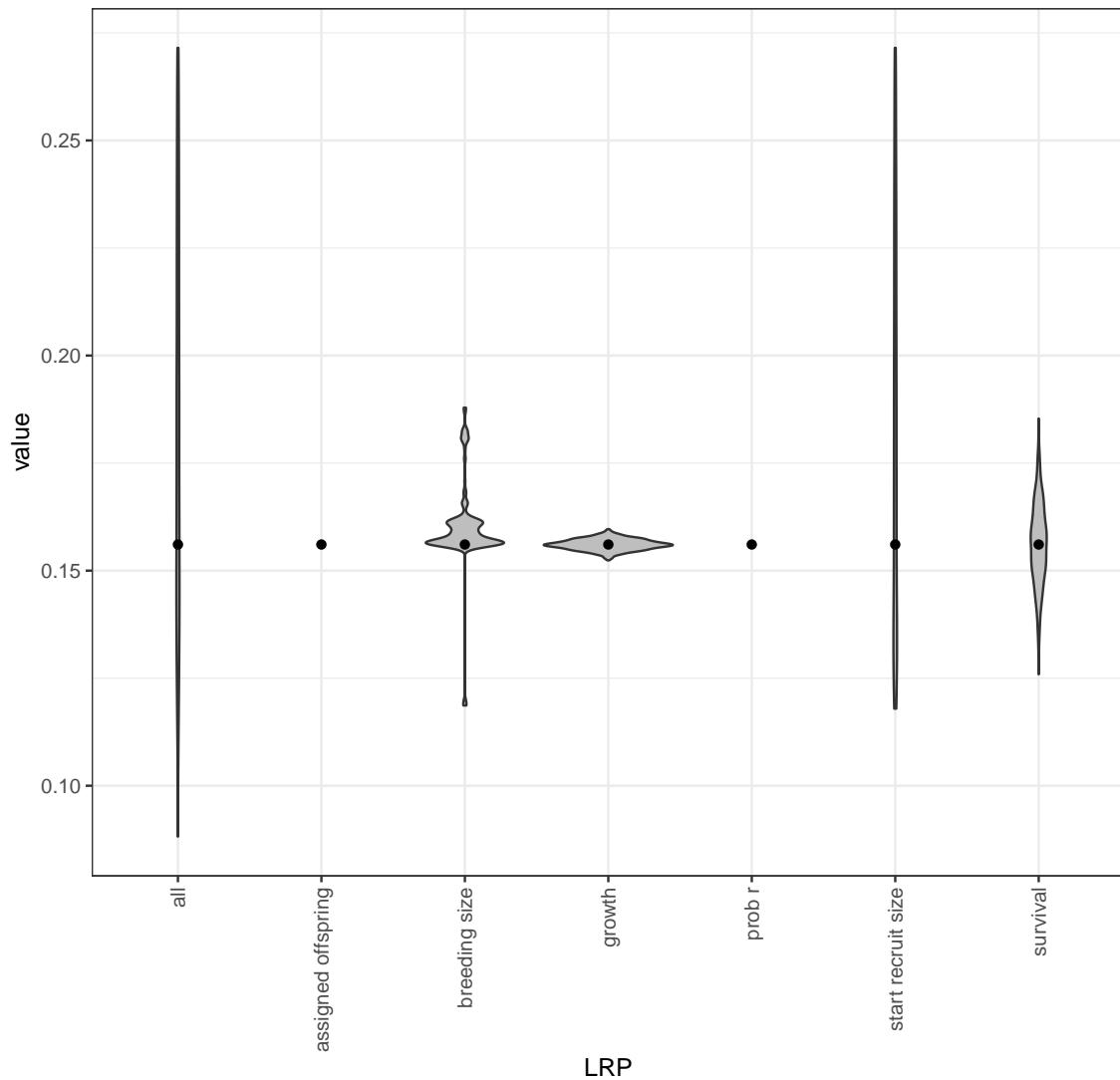


Figure B.5: The contribution of different sources of uncertainty in LRP.

### Uncertainty in LRP accounting for DD

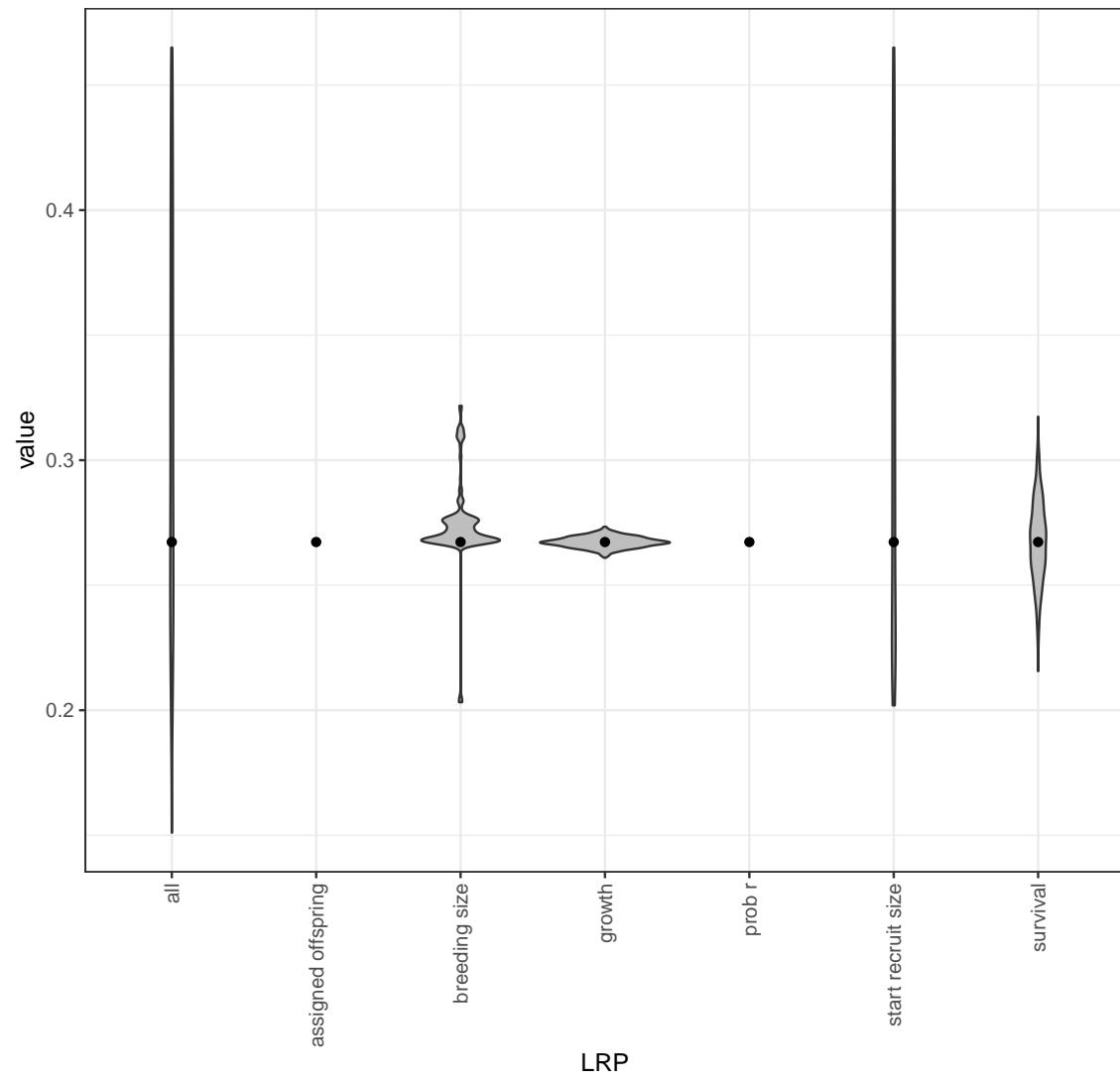


Figure B.6: The contribution of different sources of uncertainty in LRP, when we account for density-dependence in egg-recruit survival.

### B.3.0.3 Egg-recruit survival ( $S_e$ )

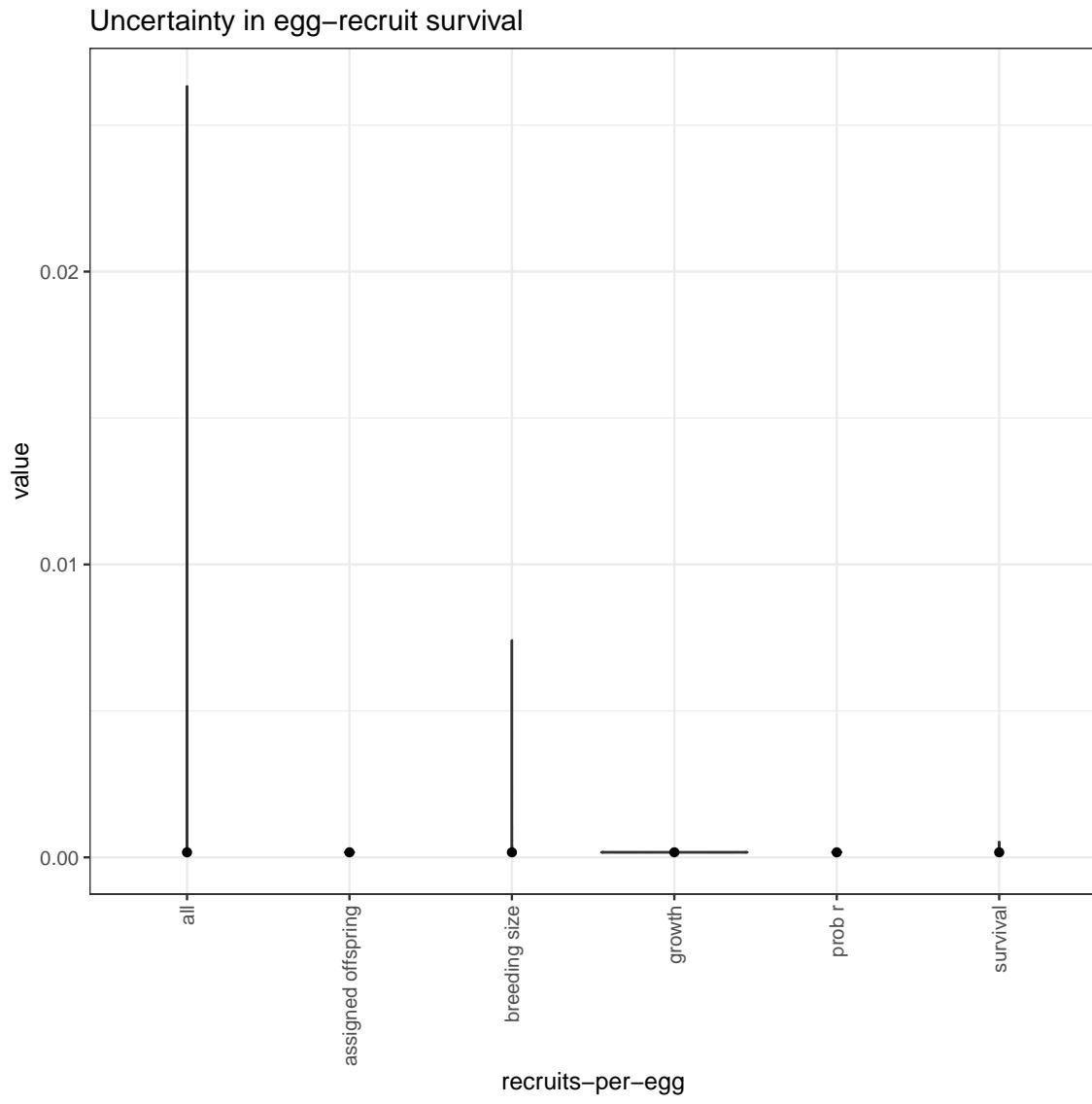


Figure B.7: The contribution of different sources of uncertainty in egg-recruit survival.

### Uncertainty in egg–recruit survival /n accounting for DD

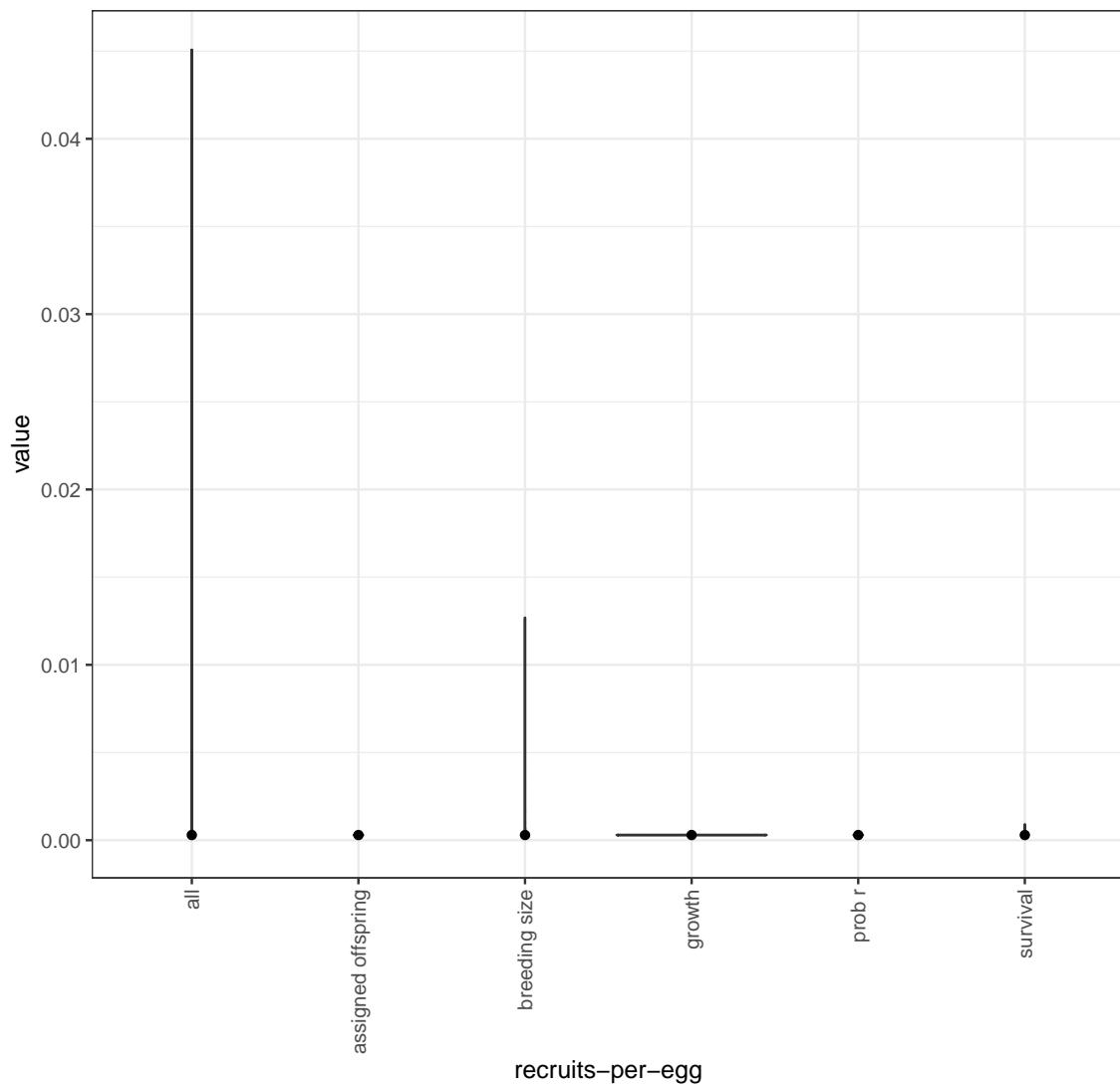


Figure B.8: The contribution of different sources of uncertainty in egg-recruit survival when we account for density-dependence in egg-recruit survival.

<sup>561</sup> B.3.0.4 Network persistence (NP)

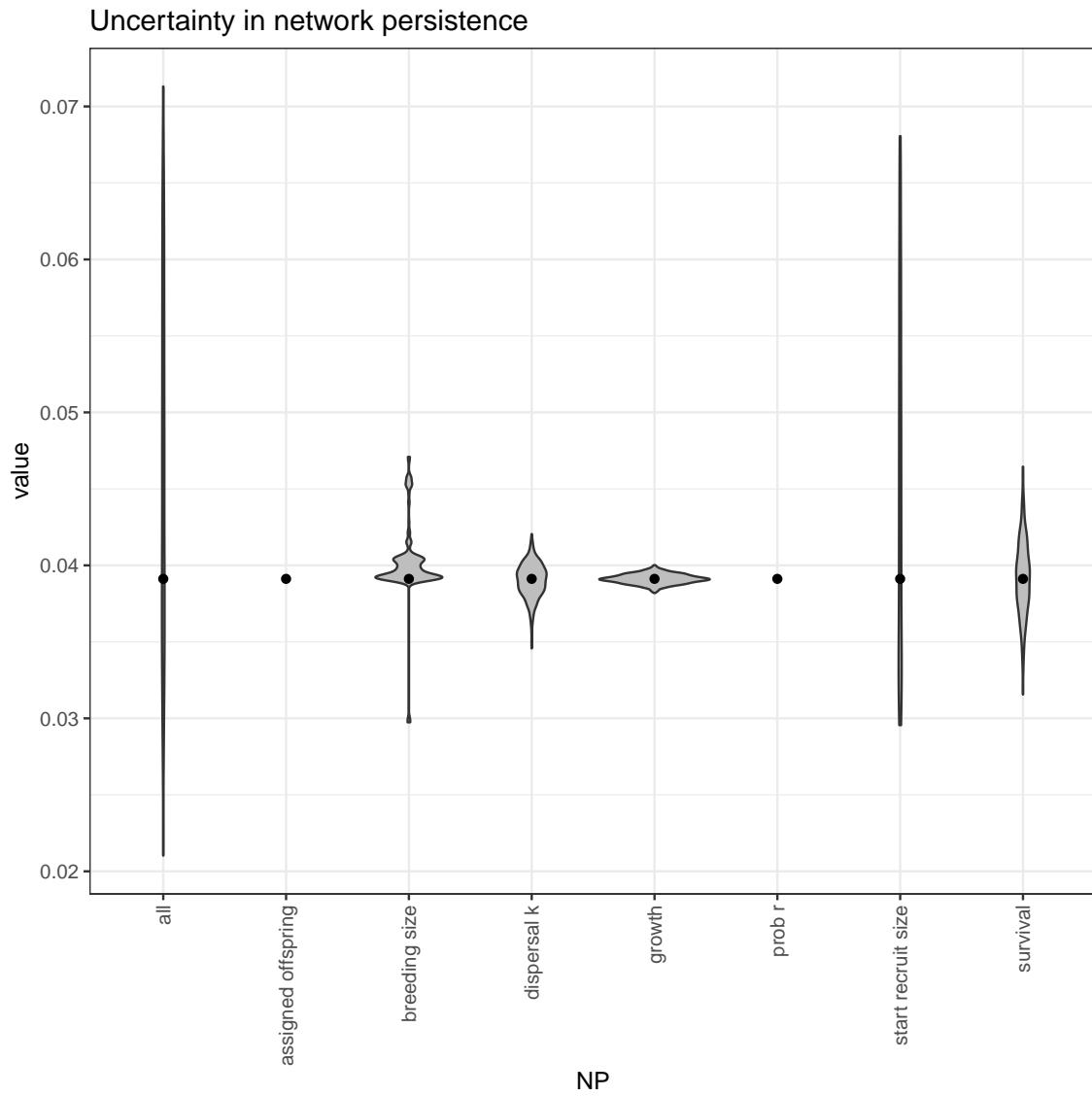


Figure B.9: The contribution of different sources of uncertainty in NP.

### Uncertainty in network persistence /n accounting for DD

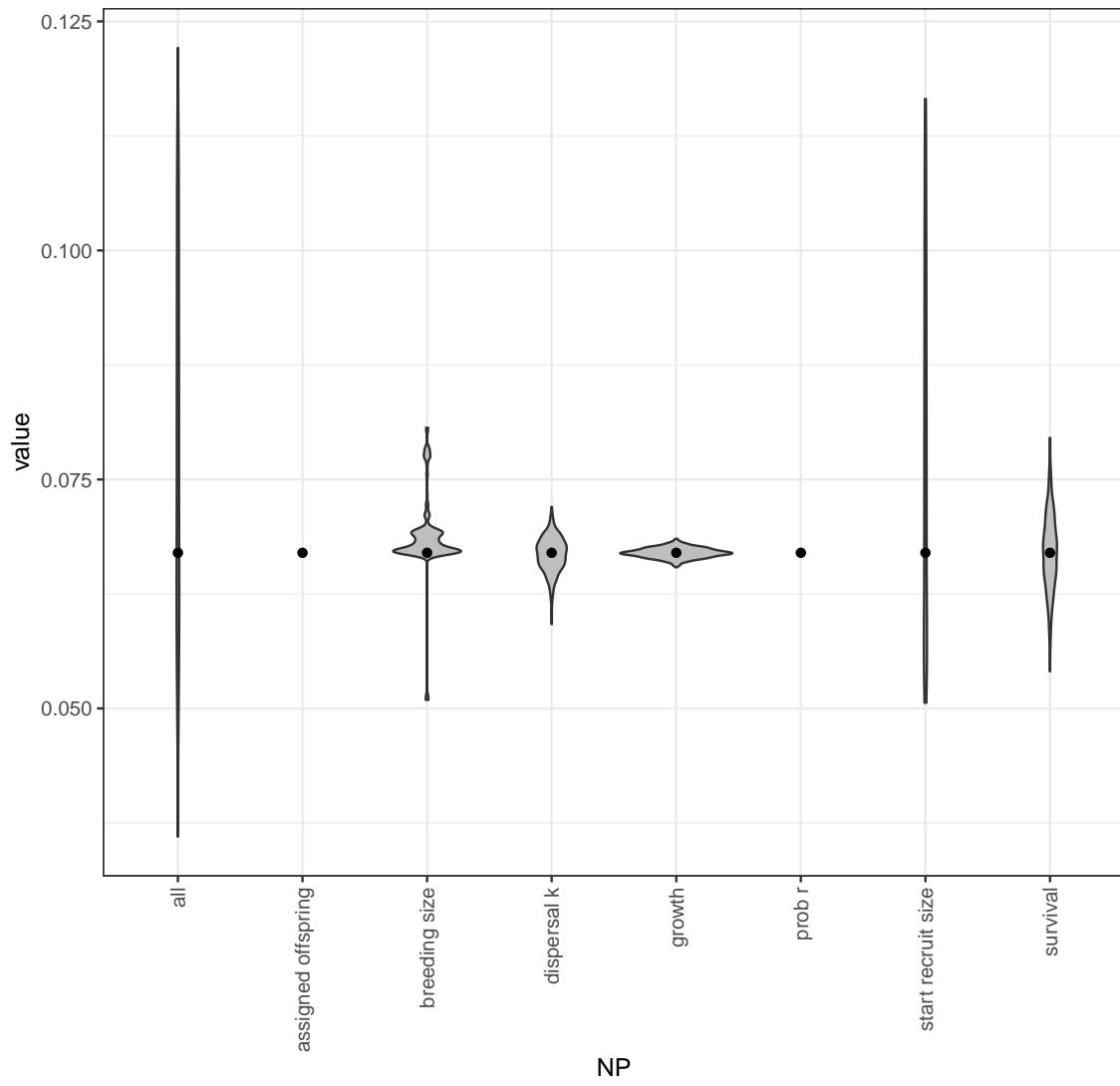


Figure B.10: The contribution of different sources of uncertainty in NP when we account for density-dependence in egg-recruit survival.

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