

# 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 individuals entering the population balances those lost to mortality or emigration,  
93

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).

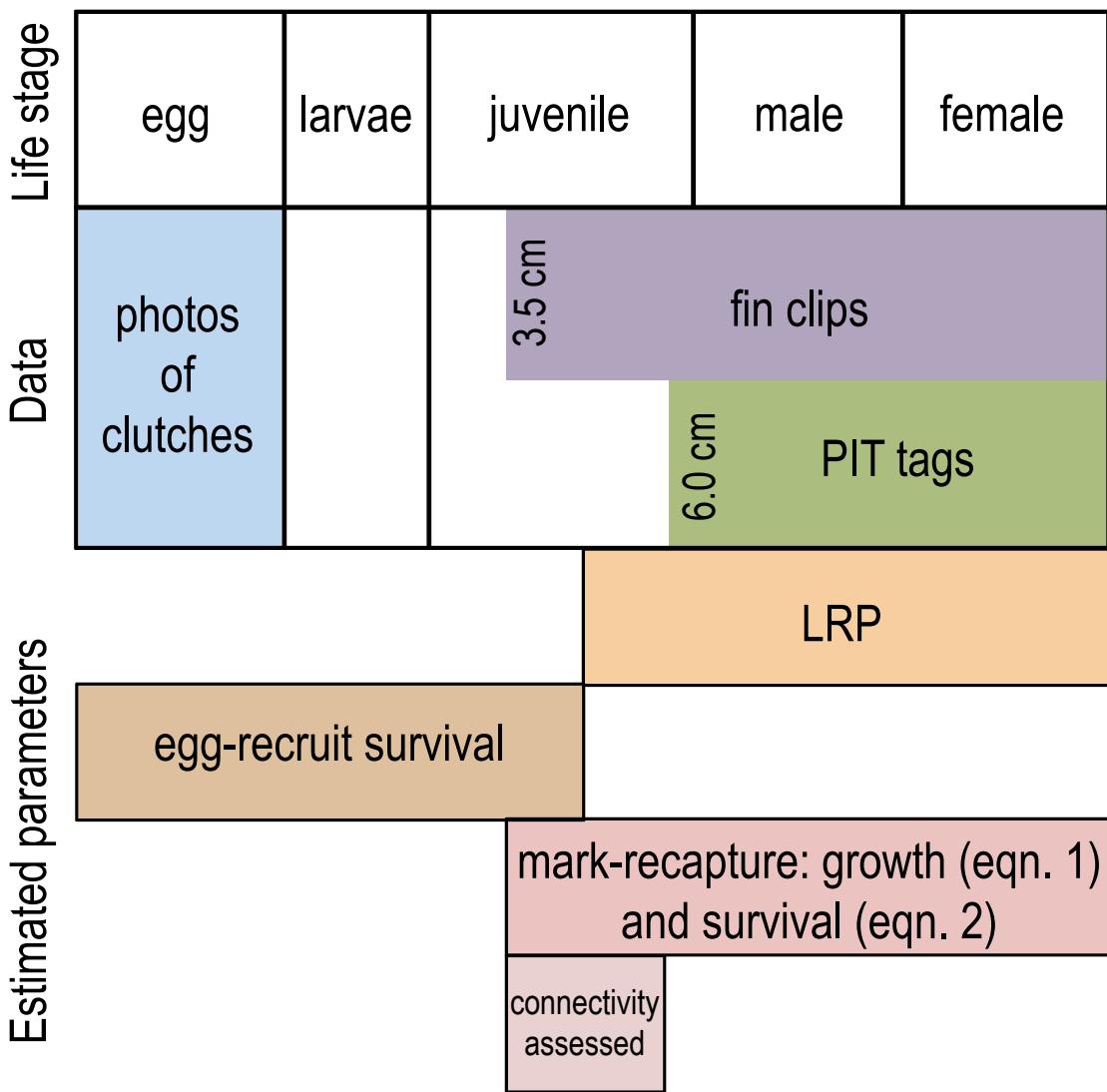


Figure 1: Here, we show the data collected for fish at each life stage (life stage boxes are not scaled by length of stage) and how the empirical data fit into our parameter and metric calculations.

## 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, 2003b; 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, 2003b), 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.

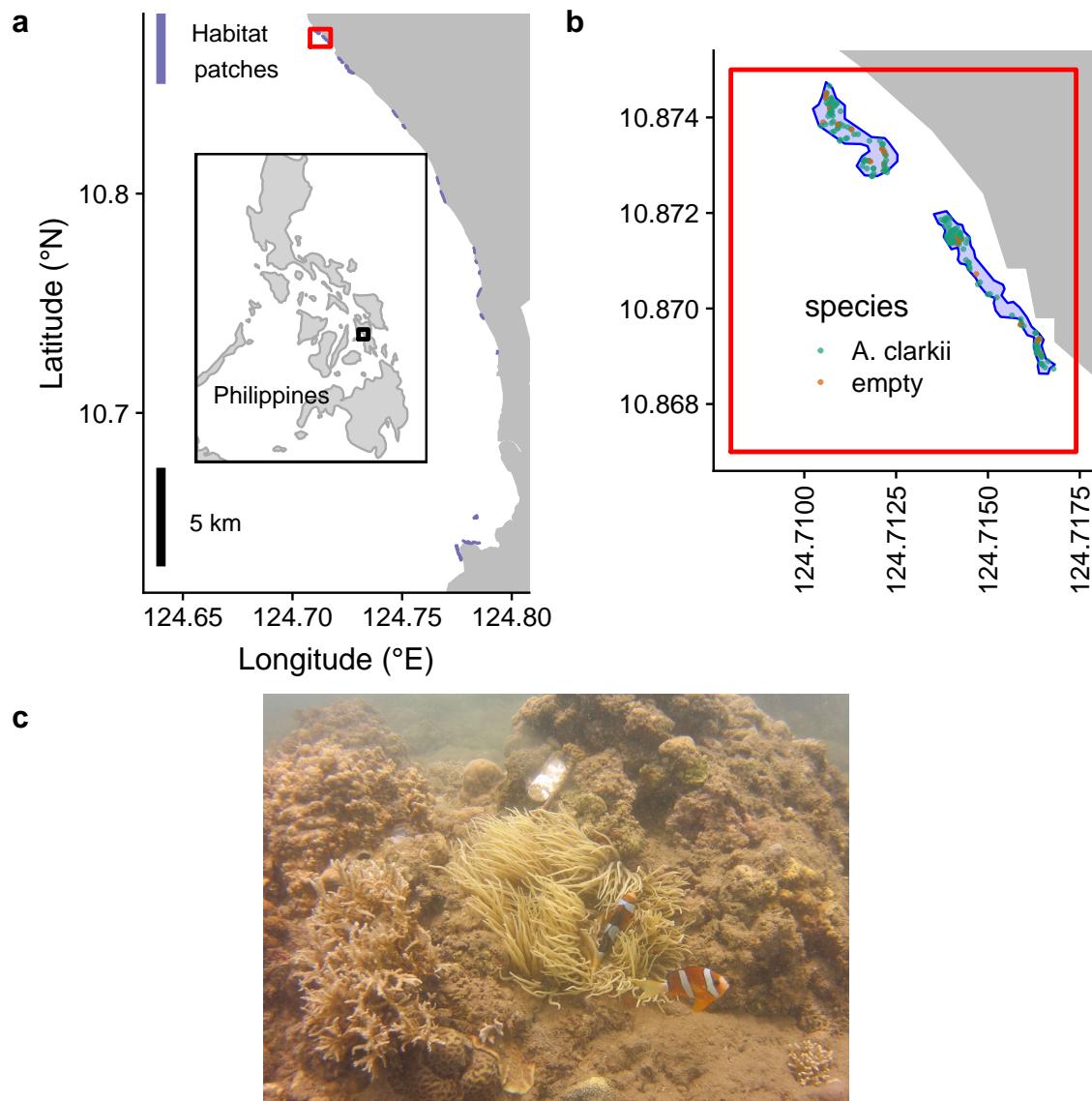


Figure 2: a) A map of the sites along the coast of Leyte in the Philippines. b) A zoomed-in map of Palanas and Wangag to show anemone arrangement for anemones occupied by *A. clarkii* (green) or unoccupied by clownfish (green). c) An example anemone occupied by *A. clarkii* in a typical habitat at the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

We use a method similar to that in Johnson et al. (2018), using parentage matches to estimate the number of surviving recruits produced by genotyped parents, to estimate survival from egg to recruit ( $S_e$ ). We estimate the number of eggs produced by genotyped parent fish by multiplying the number of genotyped parents ( $N_g = XXX$ ) by the expected lifetime egg production for a fish of parent size ( $\text{LEP}_p$ ), using LEP calculated for a fish of 6 cm, the minimum size to be considered a parent in the parentage analysis (Catalano et al., in prep). To get an estimate of the total number of recruits these parents might have produced, we scale the number of offspring we find that match to parents ( $R_m = XX$ , "tagged" recruits because they are able to be genetically matched back to their parents) by the proportion of our site habitat we sampled cumulatively across all sampling years ( $P_h = 0.34$ ) and the probability of capturing a fish if we sample its anemone ( $P_c$ ) (see A.1, A.2 for details on  $P_h$  and  $P_c$  estimates, respectively). Our sites do not encompass all of the area where an offspring might disperse and settle, so we also scale the estimated recruited offspring by the proportion of the total dispersal kernel area from each of our sites covered within our sampling region ( $P_d$ ) to account for offspring from our parents that might have settled outside our sampling areas (details in A.1). We then take this scaled number of estimated "tagged" recruits and divide it by the number of genetically tagged eggs produced by the genotyped parents to get an estimate of egg-recruit

survival:

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

### Accounting for density-dependence

Ideally we would assess persistence metrics when the population is at low abundance and not limited by density-dependence, so we attempt to account for the effects of density-dependence in the early life stages when it is likely strongest. Clownfish have strong social hierarchies and in other clownfish species, juveniles that have already settled on an anemone will prevent others from settling there as well (Buston, 2003a). Each anenome, therefore, can only house one settling clownfish, so having anemones already occupied by *A. clarkii* reduces the survival from egg to recruit if potential settlers get evicted by resident juveniles when they try to settle. We attempt to account for this density-dependent mortality by multiplying our estimate of settling recruits (the numerator of eqn. 8) by the proportional increase (DD) in unoccupied anemones at our sites if all of the *A. clarkii* anemones were unoccupied, where  $p_A$  is the proportion of anemones occupied by *A. clarkii* and  $p_U$  is the proportion of unoccupied anemones:  $\text{DD} = \frac{(p_U + p_A)}{p_U}$ . We present results both with and without this density-dependence modification.

## Estimated abundance over time

327 We also consider trends in abundance of breeding females at each site over time to  
328 compare to our replacement-based estimates of persistence. Similarly to as we do for  
329 offspring, we scale up the number of females caught at each site  $i$  in each sampling  
330 year  $t$  by the proportion of habitat sampled in that site and year  $P_{h_i,t}$  and by the  
331 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  
332 overall to assess whether the slope  $m$  over time indicates growth, decline, or stability  
333 in abundance:

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

## Incorporating uncertainty

336 To represent the uncertainty in our estimates of the parameters that go into calculating  
337 our persistence metrics, we calculate each metric 1000 times, pulling each  
338 parameter from a distribution or range. In our results, we show the range of values of  
339 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  
340 parameter  $k_d$  from a set capturing the 95% confidence intervals, which was produced  
341 during kernel estimation in Catalano et al. (in prep). To capture uncertainty in the  
342 size of a recruit  $\text{size}_{\text{recruit}}$ , and therefore the transition of mortality being captured by  
343 egg-recruit survival to being captured by LEP, we pull from a uniform distribution

<sup>345</sup> 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 <sup>351</sup> 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 <sup>354</sup> 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 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 <sup>357</sup> 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 <sup>360</sup> estimated from recapture dives across sites and sampling seasons (details in A.2). <sup>363</sup>

## Results

Our estimated abundance of females at each site over time is relatively constant [*add <sup>366</sup> some sort of actual analysis here*] (Fig. 3), suggesting that our sample populations

are stable over time.

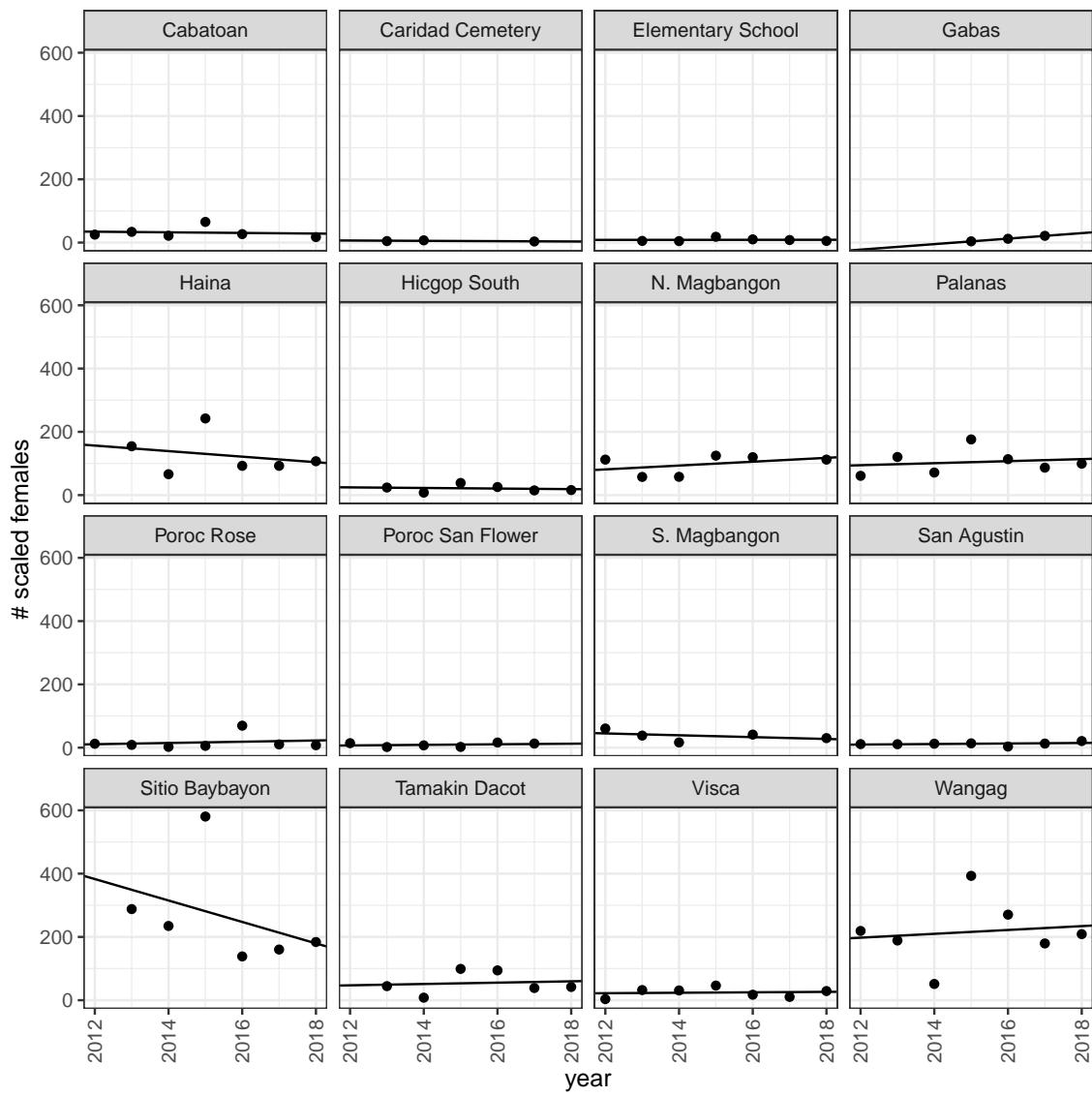


Figure 3: The estimated number of females at each site over the sampling years. The total number of females at each site was estimated by taking the number of females (fish  $> 5$  cm with the yellow pointed tail indicating female) captured at each site in each year and scaling up by the proportion of 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  
369 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  
372 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  
375 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  
378 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  
381 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  
384 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  
387 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:

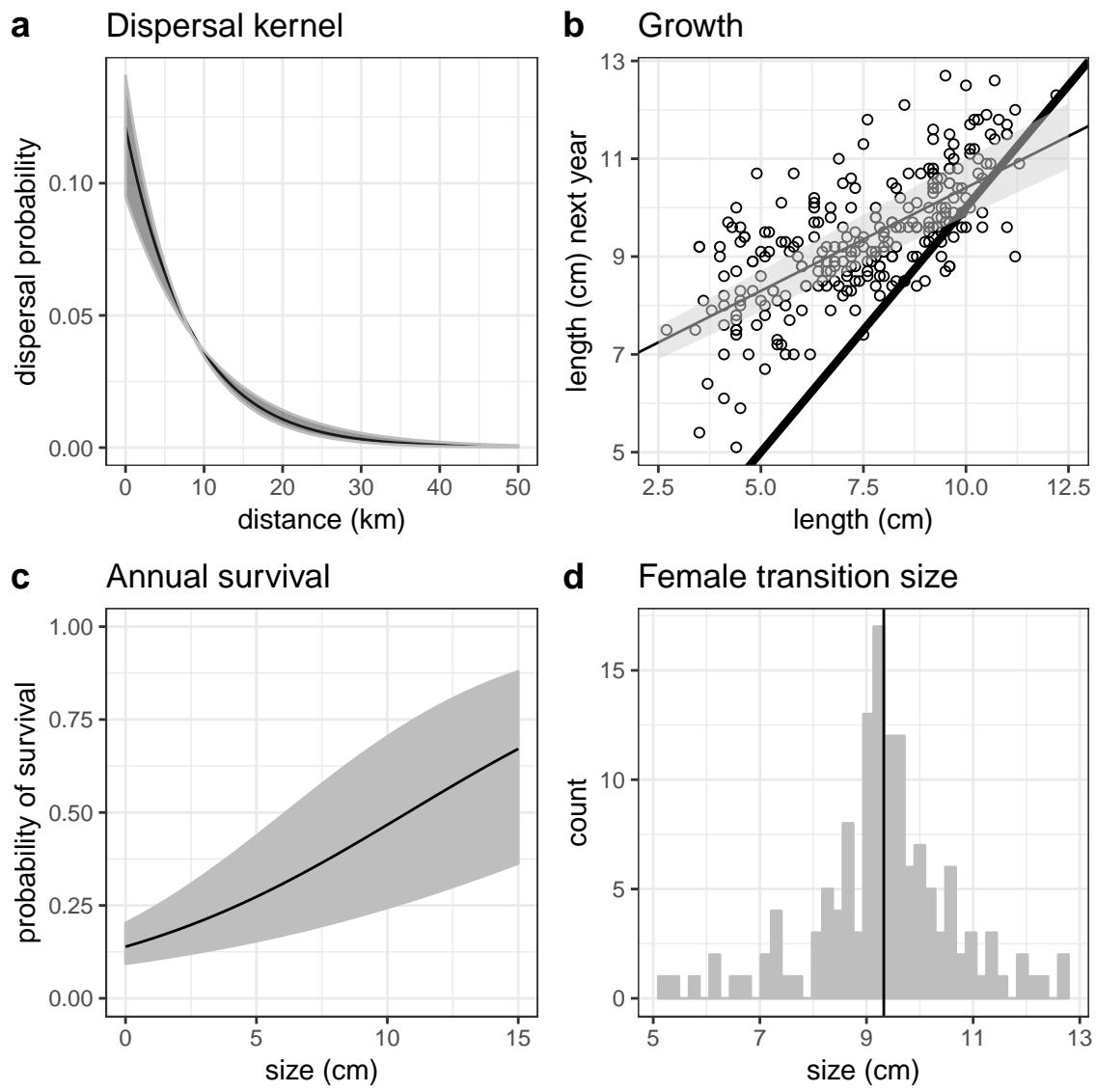


Figure 4: Best estimates (solid black line) and range included for uncertainty (gray) for dispersal (a), growth (b), post-recruit survival (c), and size at female transition (d) parameters.

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

<sup>390</sup> of LEP for 10876, ranging from XX to XX when we consider uncertainty in the inputs  
<sup>391</sup> (Fig. 5a). The size at recruitment - the census point between egg-recruit survival  
<sup>392</sup> and LEP - has the most effect on the value of LEP (Fig. B.4), with higher values of  
<sup>393</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>394</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>395</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>402</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>404</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.

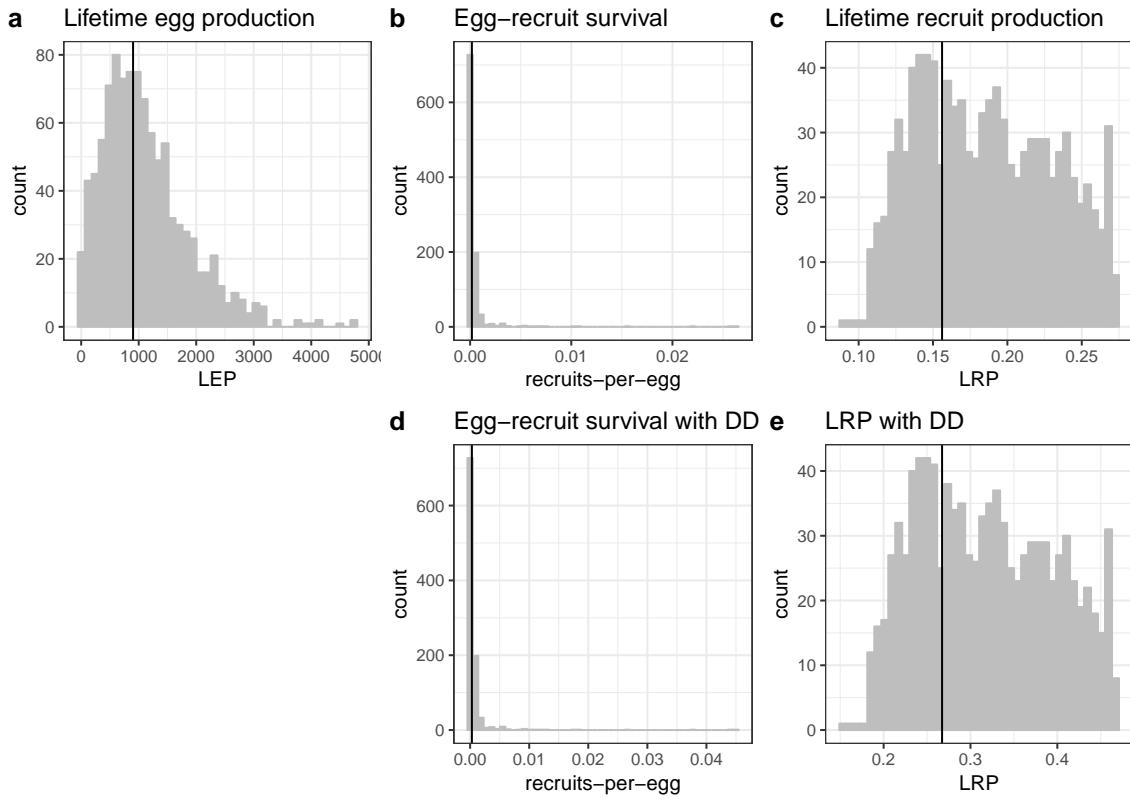


Figure 5: Estimates of a) LEP, b) egg-recruit survival, and c) LRP, showing the best estimate (black solid line) and range of estimates considering uncertainty in the inputs.

408 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  
 411 makes sense. We see the highest values of self-persistence at Haina ( $SP = 0.024$ ) and  
 Wangag ( $SP = 0.010$ ), our two widest sites.

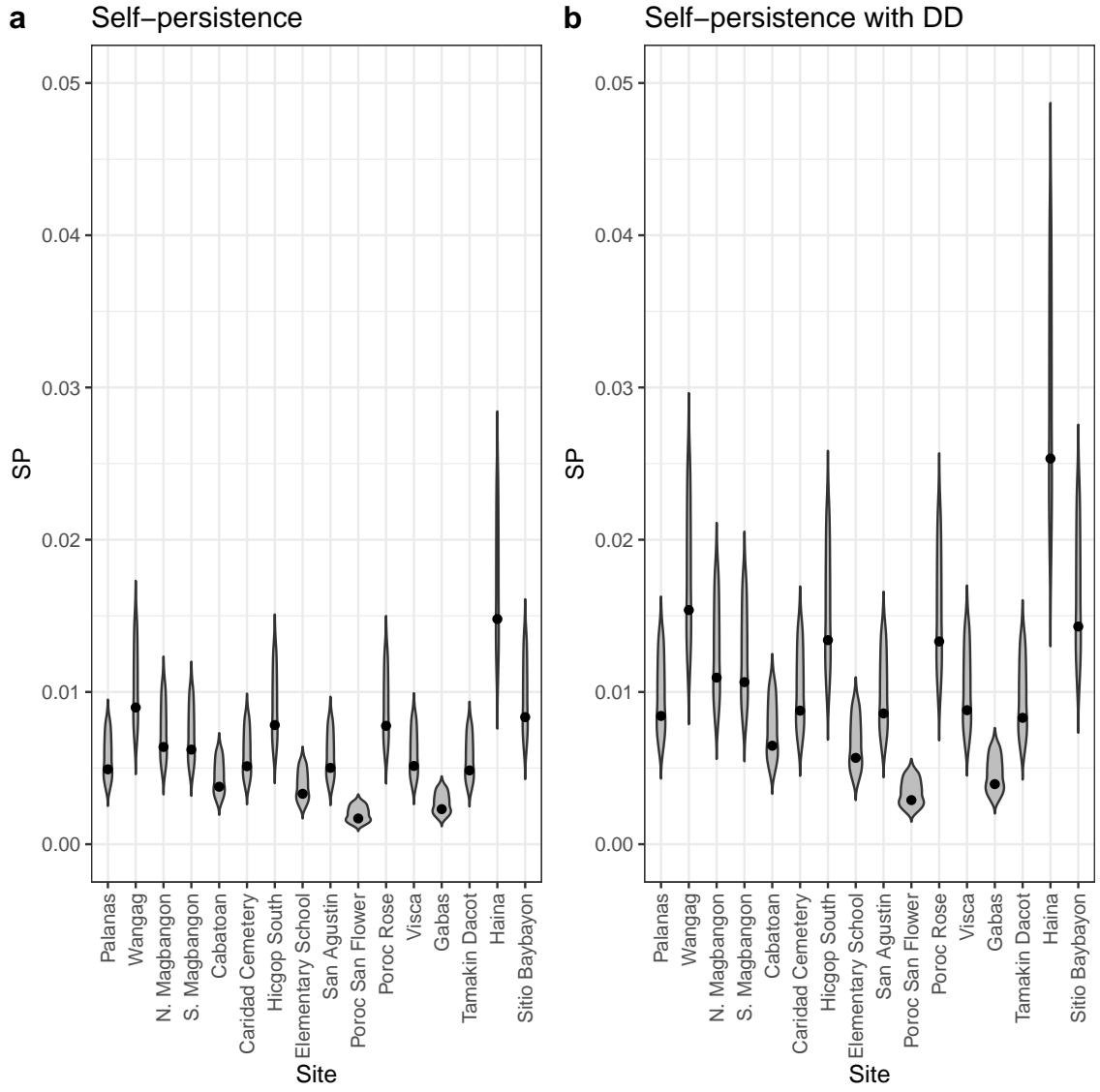


Figure 6: Values of self-persistence at each site, showing the best estimate (black point) and range of estimates considering uncertainty in the input parameters. No site reaches a value of  $SP > 1$ , necessary to be self-persistent.

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

<sup>414</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.

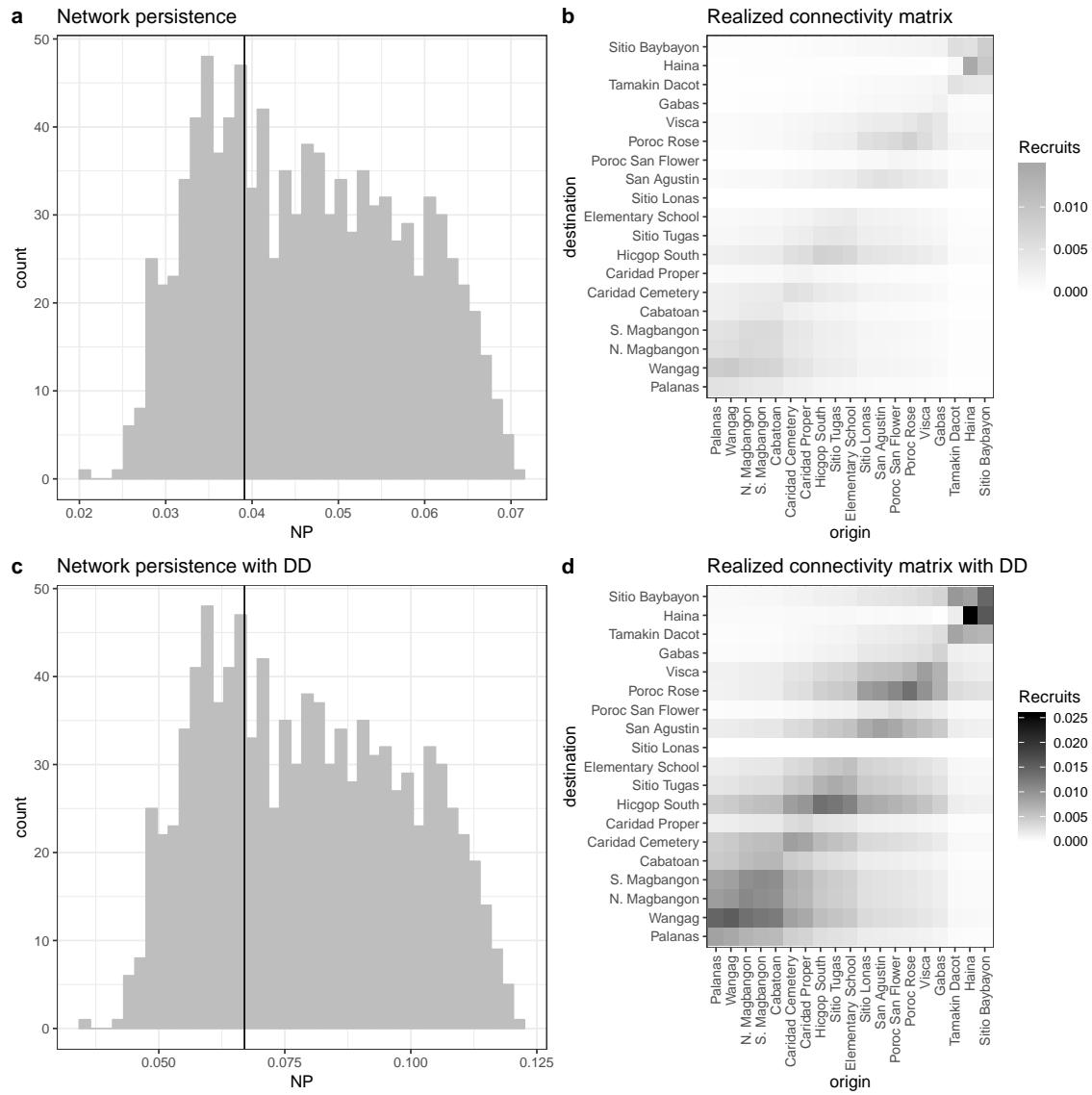


Figure 7: a) Network persistence values, showing the best estimate (black solid line) and range of estimates considering uncertainty. b) The realized connectivity matrix  $C$ , with sites arranged from north (Palanas) to south (Sitio Baybayon).

417 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  
420 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  
423 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  
426 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  
429 egg-recruit survival), to  $\lambda_c = 1$  and network persistence.

## Discussion

We do not see evidence for persistence in our metric estimates, neither self-persistence  
432 where an individual site could persist alone nor network persistence accounting for 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  
435 input of recruits from outside sites to persist. The portion of coastline we sampled is likely a sink portion of a larger metapopulation.

For our sites to be able to persist as a network on their own, the number of  
438 surviving recruits produced by an average recruit -  $LRP$  - would need to be higher. With our estimated connectivity among the sites,  $LRP$  would need to be at least XXX

to see network persistence among our sites, about XXX times higher than our best  
441 estimate and XXX times higher than the top of our range of uncertainty. To achieve  
that value of LRP, either production of eggs would need to increase to an LEP of XX  
or egg-recruit survival would need to be at least XX. Our estimate of LEP is XXX  
444 compared to estimates for similar fish (e.g. CITATIONS) and our estimate of egg-  
recruit survival is XXX compared to other estimates (e.g. CITATIONS), making a  
rise of XX for either XX. Since LRP is less than one for our sites - the average recruit  
447 only replaces itself with XX of a surviving recruit of the same stage - no amount  
of increased retention or connectivity, even retaining all of the recruits produced  
from our sites, would lead to network persistence. Similarly, if other surrounding  
450 patch populations had a similar LRP, increasing the area of the network to include  
them would also not achieve network persistence. If nearby sites have higher egg  
production or survival to recruit, however, it might not take much of an increase in  
453 area considered to create a persistence network. Nearby sites such as Quatros Islaes  
and XX have higher quality habitat and could be contributing recruits to our sites.

We were surprised that our estimates of persistence are so far from the threshold  
456 for network persistence for our sites because previous estimates of the mean dispersal  
distance of *A. clarkii* (10 km Pinsky et al., 2010) and those from our 2012-2018  
samples (Catalano et al., in prep, range from XX - XX km for individual-year kernels,  
459 XX for all-years kernel, which is used in this analysis) are well within the 30 km span  
of our sites. Our below-replacement estimate for LRP, however, suggests that lack  
of persistence in these sites is not due to excessive dispersal out of the area but due  
462 to low production and survival of offspring. The reef health and habitat quality in

our sites in generally low, due anthropogenic effects such as pollution and silt from a nearby gravel mining operations and habitat disturbance due to storms. Our sites  
465 are in an area that was hit by Typhoon XX, the strongest typhoon ever to make landfall, early in our sampling period, which destroyed much of the reef habitat in some of our northern sampling areas. WRAP-UP, CONCLUDING SENTENCE OR  
468 TWO!

3) Uncertainty in our estimates and why we need to consider it

- Try to consider uncertainty in a variety of our inputs, hard to estimate in the  
471 field
- Important to do this b/c not going to get a point estimate
- Think more about what the point of this paragraph is

474 4) How do we reconcile this with the finding that mean dispersal distance is within the reach of our sites but they don't persist as a contained metapopulation?

- They can both be true at the same time - maybe fish from our sites don't  
477 disperse very far but others in sites nearby have access to different currents, etc. send recruits farther and into our sites.
- It's a linear coastline but within a big bay - could have some interesting connectivity patterns via currents/eddies/etc. (reference how far the drifters went?)  
480 Are there some citations on this?

5) Caveats paragraph

- 483     ● Density-dependence - likely plays a larger role throughout the life cycle, not just  
at early life - particularly important in this species (and others with strong  
social hierarchies)
- 486     ● Site-specific demographic rates - coming in the future as get more of a handle on  
predator densities and such. Not have enough data from some of the sites and  
some of the params (fecundity) to get site-specific rates, though those have  
been interesting/important in other systems. If our larger sites had higher  
production/survival, might see persistence.

489     6) Wrap-up paragraph

- 492     ● How does this contribute to our understanding of metapopulation persistence?  
Where do we go from here?

We do not see evidence for persistence in our metric estimates, either self-persistence  
495 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  
498 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  
501 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

504 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.

- 507
- 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  
in an area range that spans the estimated spread? (This point might change,  
depending on mean dispersal distance from the new kernels)

- 510
- Sensitivity - how would our parameters need to change to see persistence?  
513 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. Contextualize this with what other studies have found for these parameters, how  
516 reasonable it would be to get better estimates in the field.

Persistence criteria, such as those detailed in Hastings and Botsford (2006) and  
519 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  
522 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*,  
525 density-dependence is likely most important in early life stages, as for many fish

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

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

543 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 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  
549 enough?

- 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  
552 about resolving them, whether we would expect to see them.
- Contextualize our parameter estimates with those from other studies (esp. survival, growth, fecundity).

555 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  
558 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.

# Appendix

## A Method details

### A.1 Proportion of habitat sampled

567 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  
570 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  
573 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  
576 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  
579 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,  
582 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.

585      Add details about how sometimes it is  $\neq 1$  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.

## Proportion of dispersal kernel area sampled

588 [Add in description of calculation and equation]

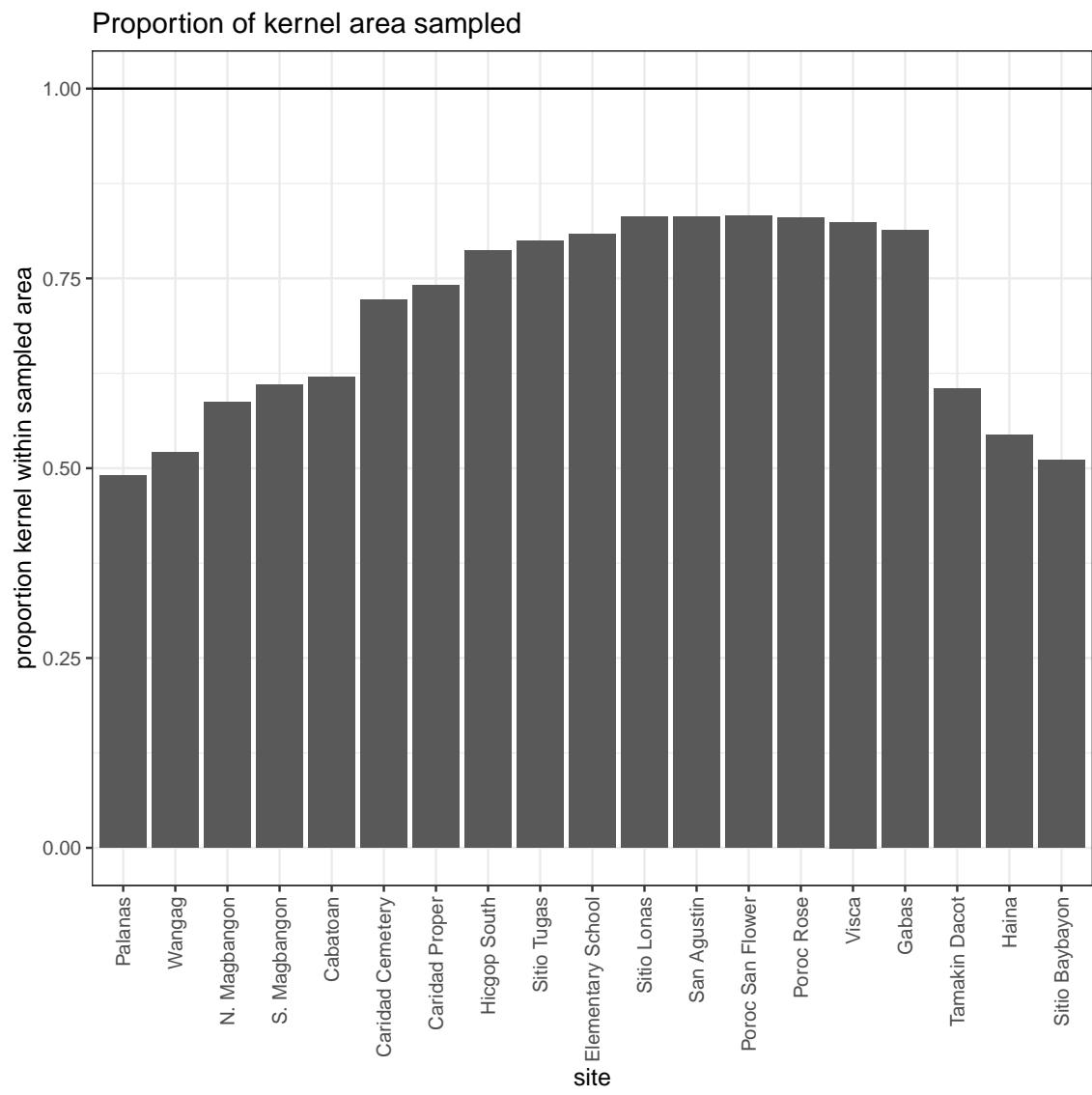


Figure A.1: Proportion of the dispersal kernel area from the center of each site covered by our sampling.

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

We use mark-recapture data from recapture dives done within a sampling season to  
591 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  
594 dives and the recapture dives because they are so close in time and that fish do not  
change their behavior or response 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.  
597 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  
600  $P_c$  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  
603 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  
606 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  
609 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  $\beta_{P_c} = 1.13$ .
- 612 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.
- 615 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

618 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 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 A2:

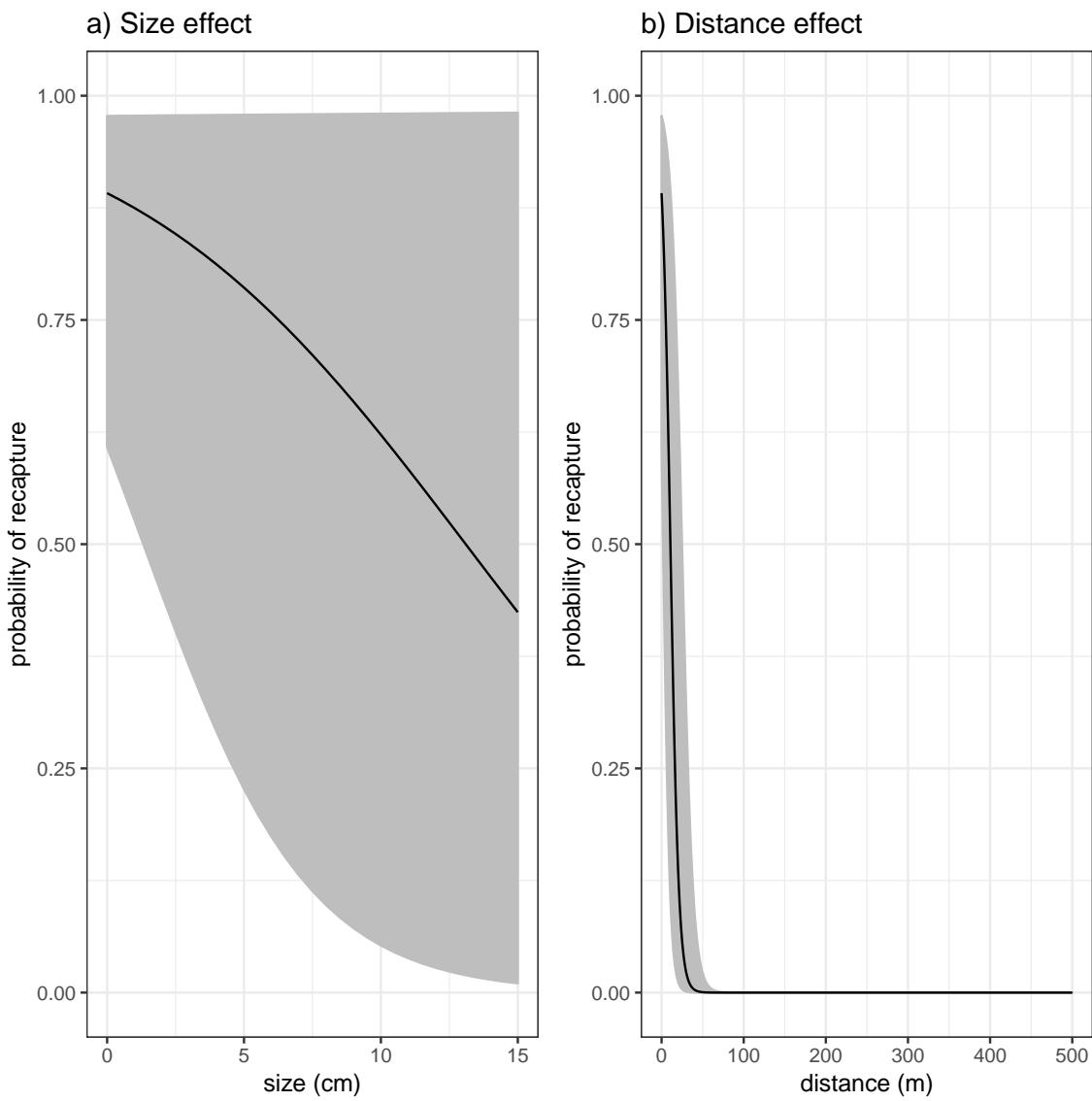


Figure A.2: Effects of a) fish size and b) minimum distance between divers and the anemone where the fish was first caught on the probability the fish will be recaptured, estimated along with survival in a mark-recapture analysis. Size has a slightly negative effect on the probability of recapture - 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

621 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,  
624 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  
our sites  $P_h$  and the probability of capturing a fish  $P_c$ , as our estimate of recruited  
627 tagged offspring. We see XXX, which means YYY.

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

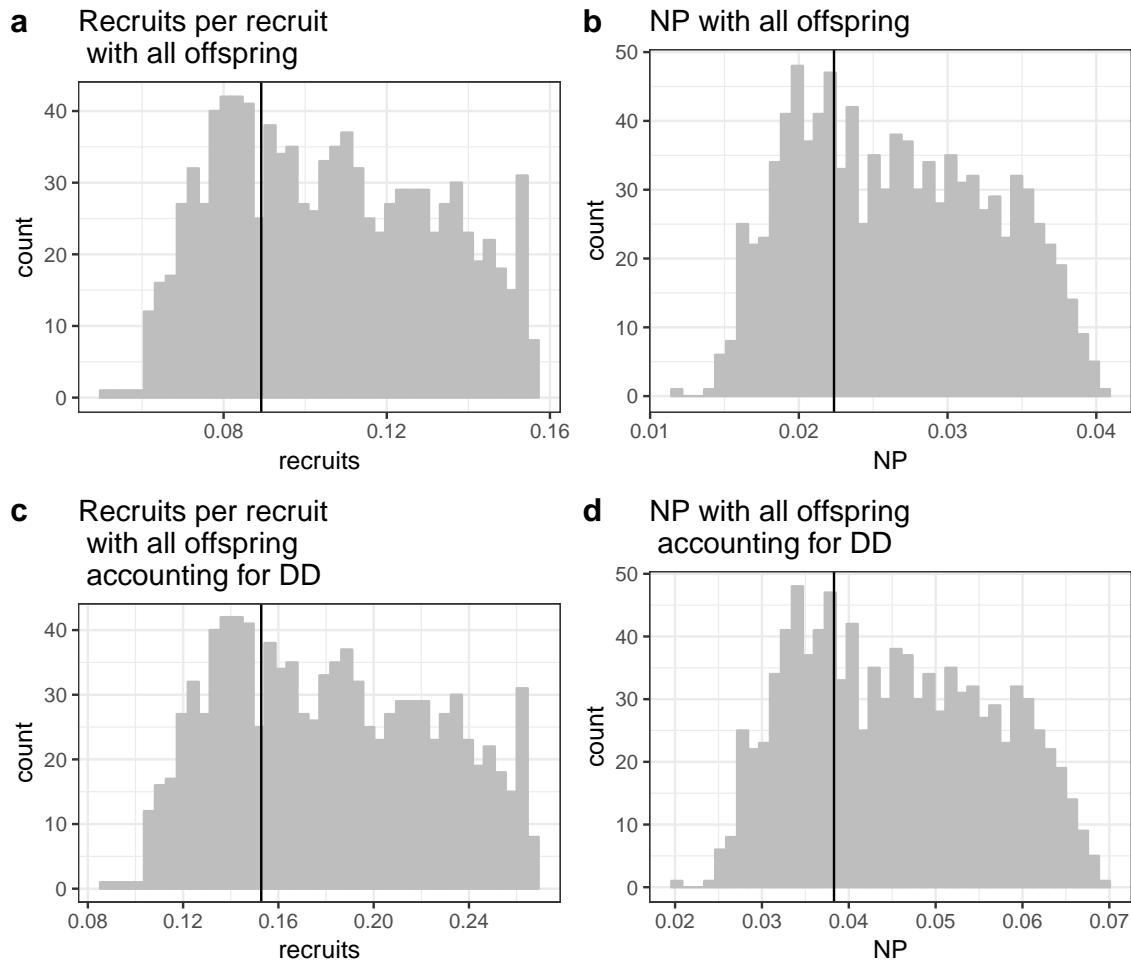


Figure B.1: a) Recruits per recruit when we consider all arriving recruits to have originated from our sites. b) Range of values of NP considering all arriving recruits to be offspring from our sites, with the best estimate in a black solid line.

630 **B.2 Sensitivity to parameters**

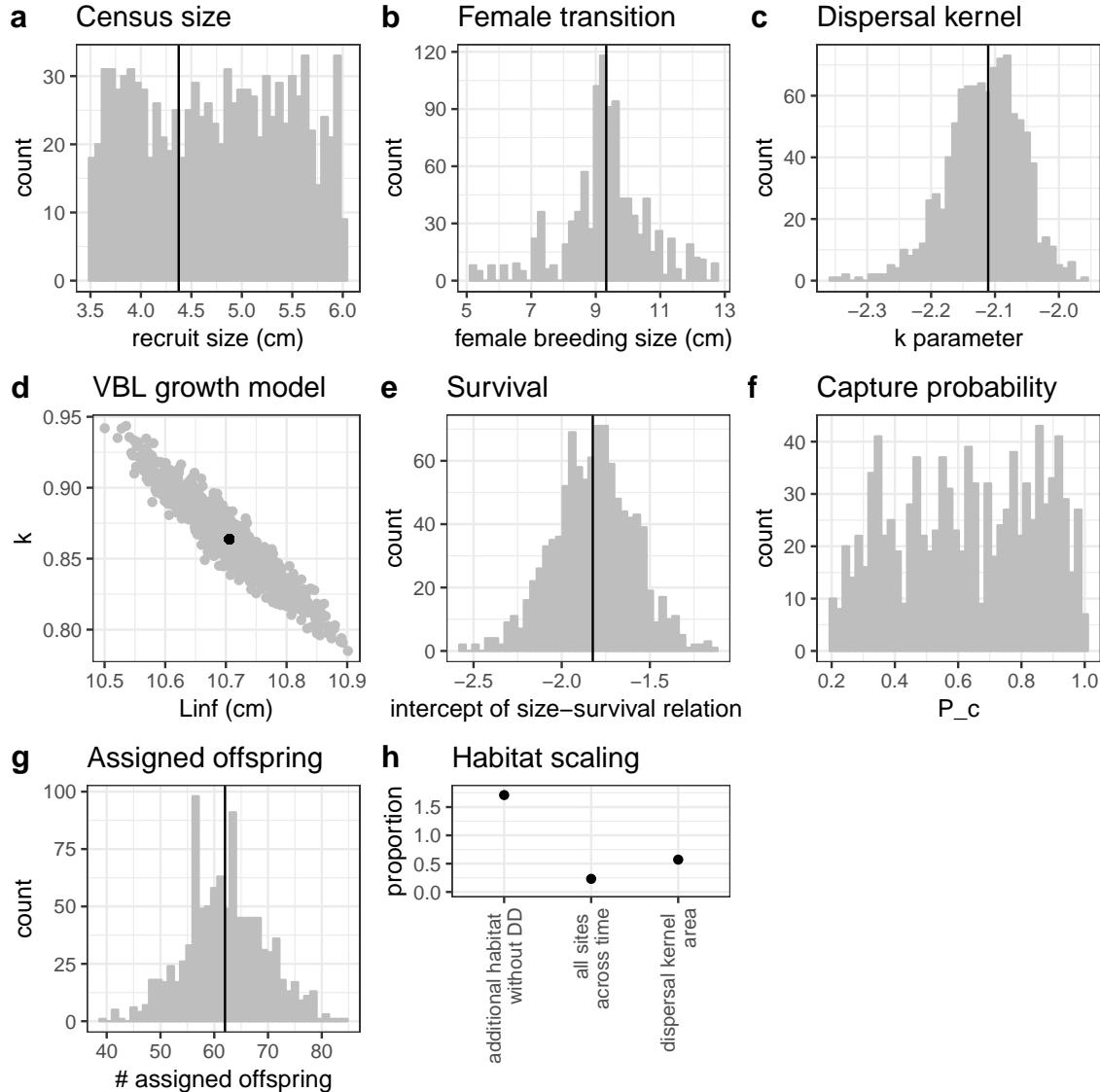


Figure B.2: Range of parameter inputs for uncertainty runs with all uncertainty included: a)  $\text{size}_{\text{recruit}}$ , the census size at which fish are considered to have recruited after egg-recruit survival occurs; b)  $L_f$ , the size at which fish transition from male to female and their reproductive output<sup>53</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.

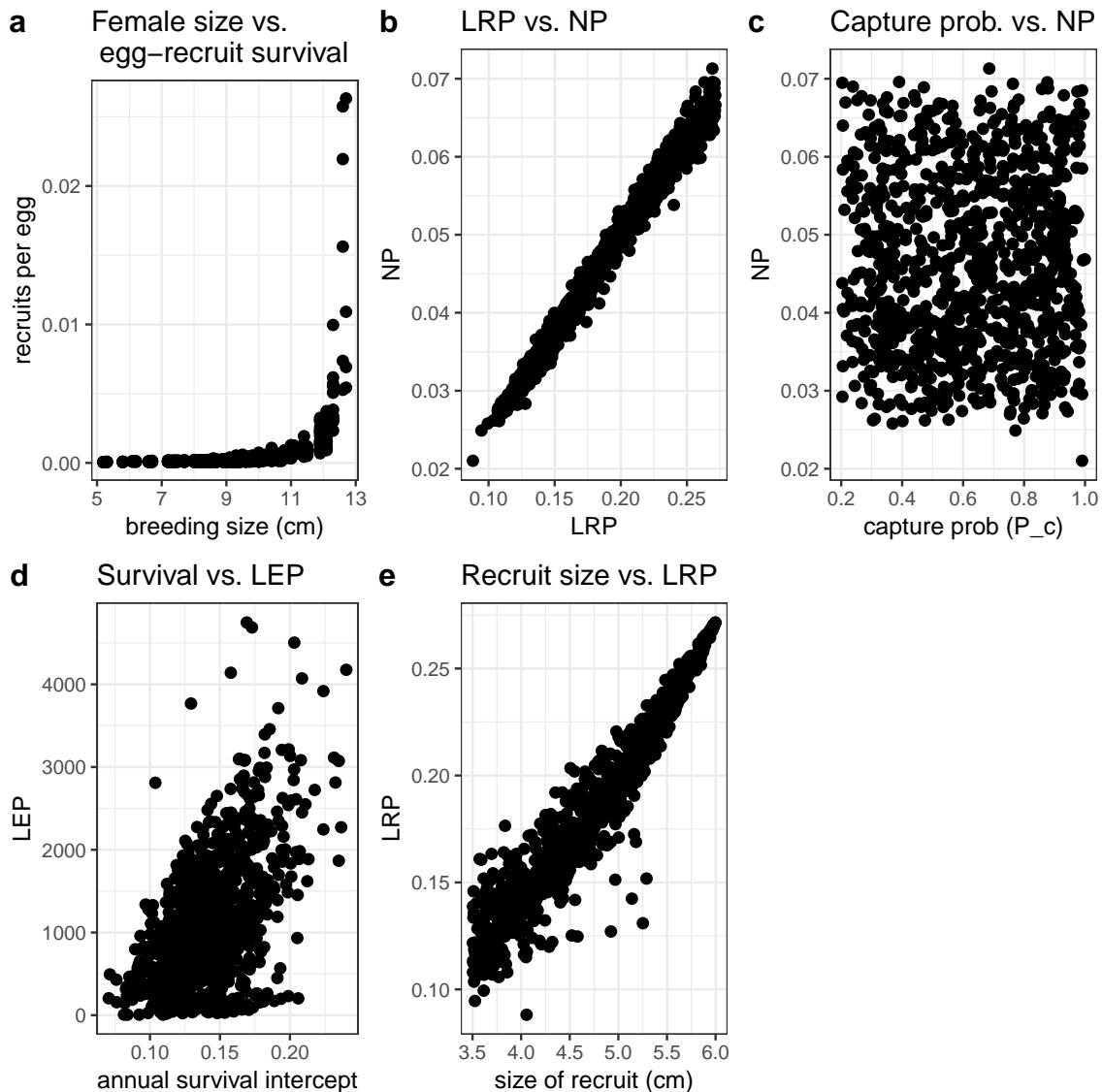


Figure B.3: Relationships among parameters and metrics. a) We only count reproductive effort by fish in the female stage so the higher the transition size to breeding female, the fewer eggs parents are considered to produce, which increases the estimated egg-recruit survival. b) LRP strongly affects 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)

- 633 Annual survival post-recruitment provides 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  
636 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

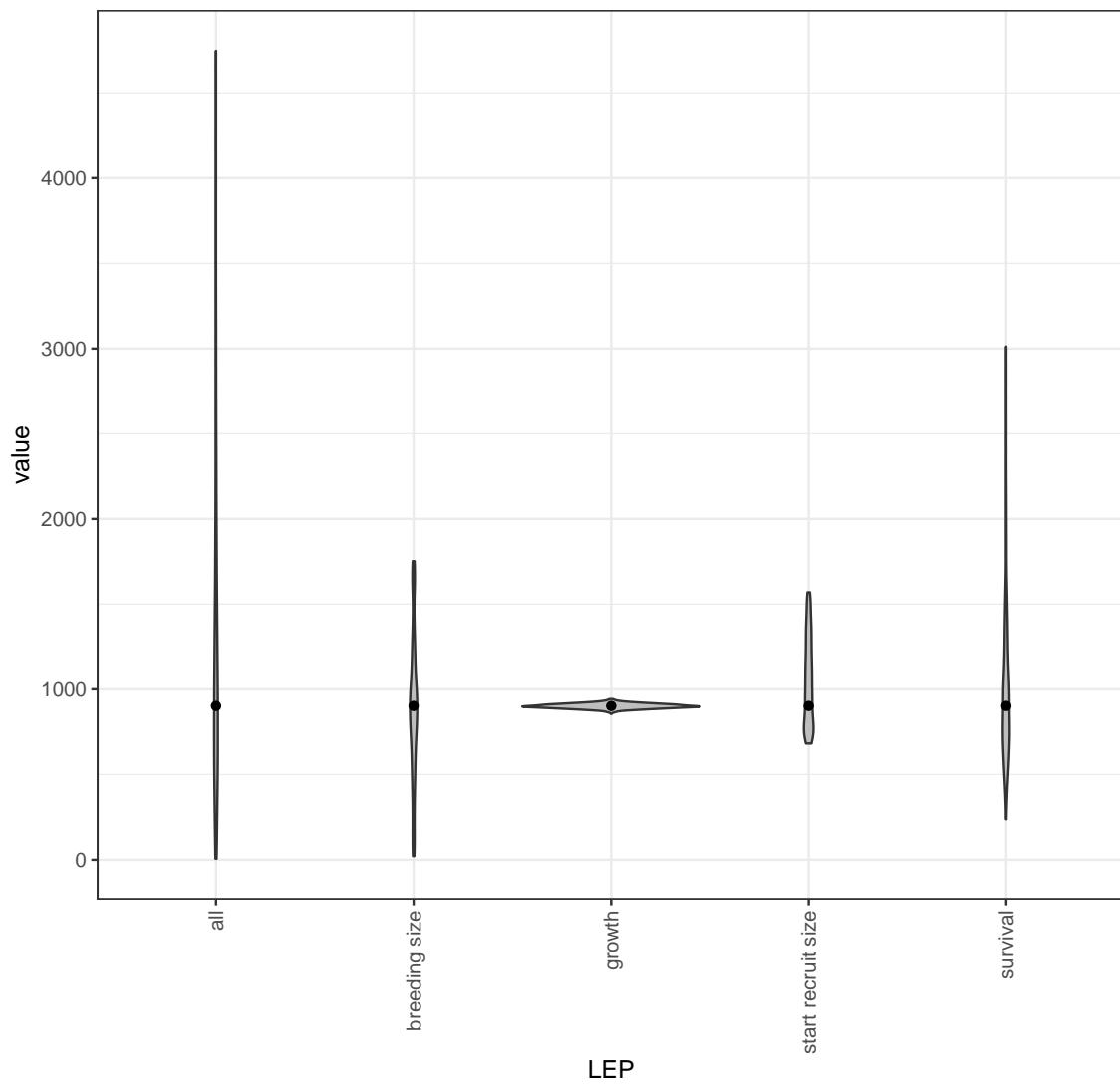


Figure B.4: The contribution of different sources of uncertainty in LEP.

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

639 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  
642 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

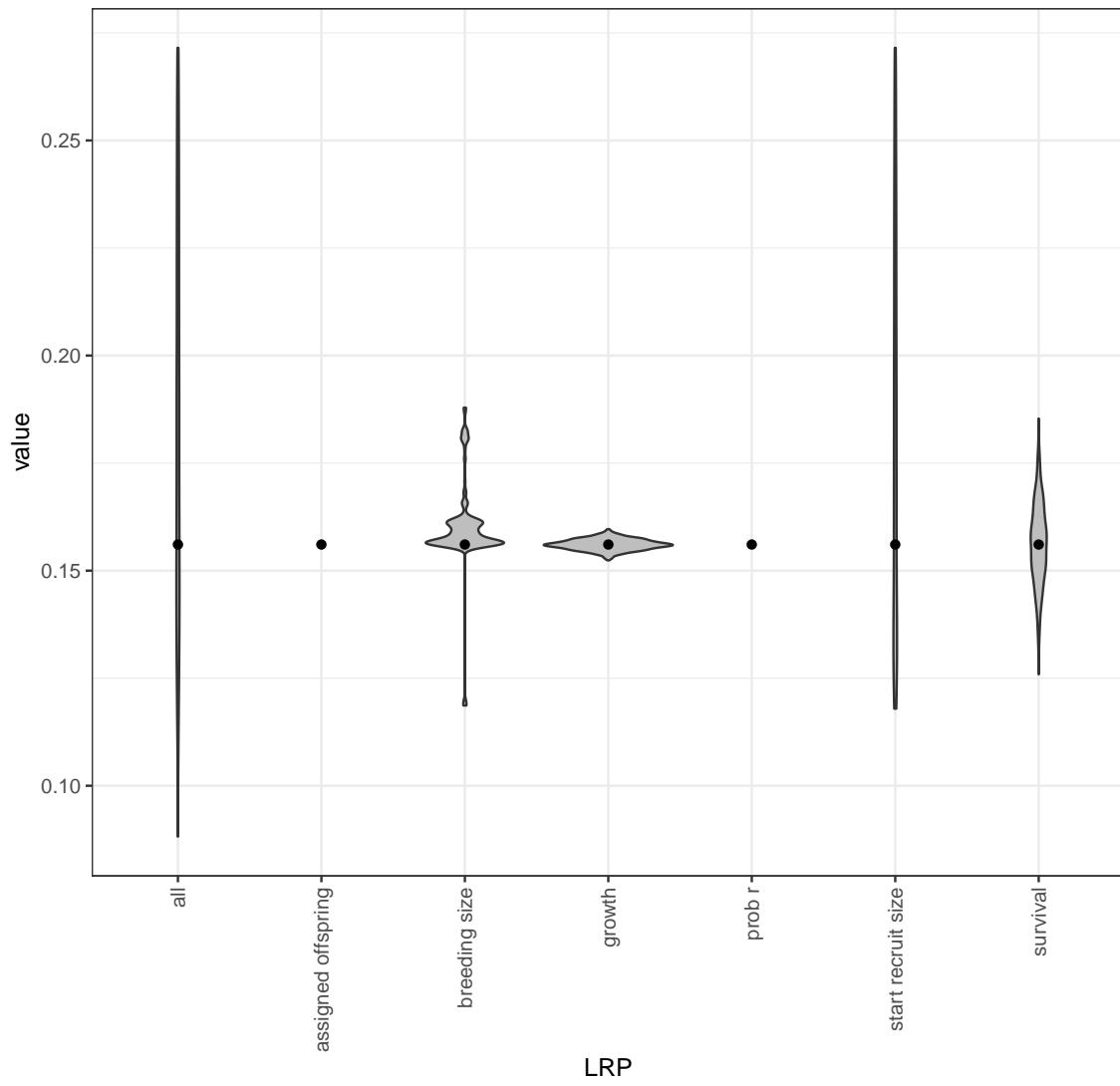


Figure B.5: The contribution of different sources of uncertainty in LRP.

### Uncertainty in LRP accounting for DD

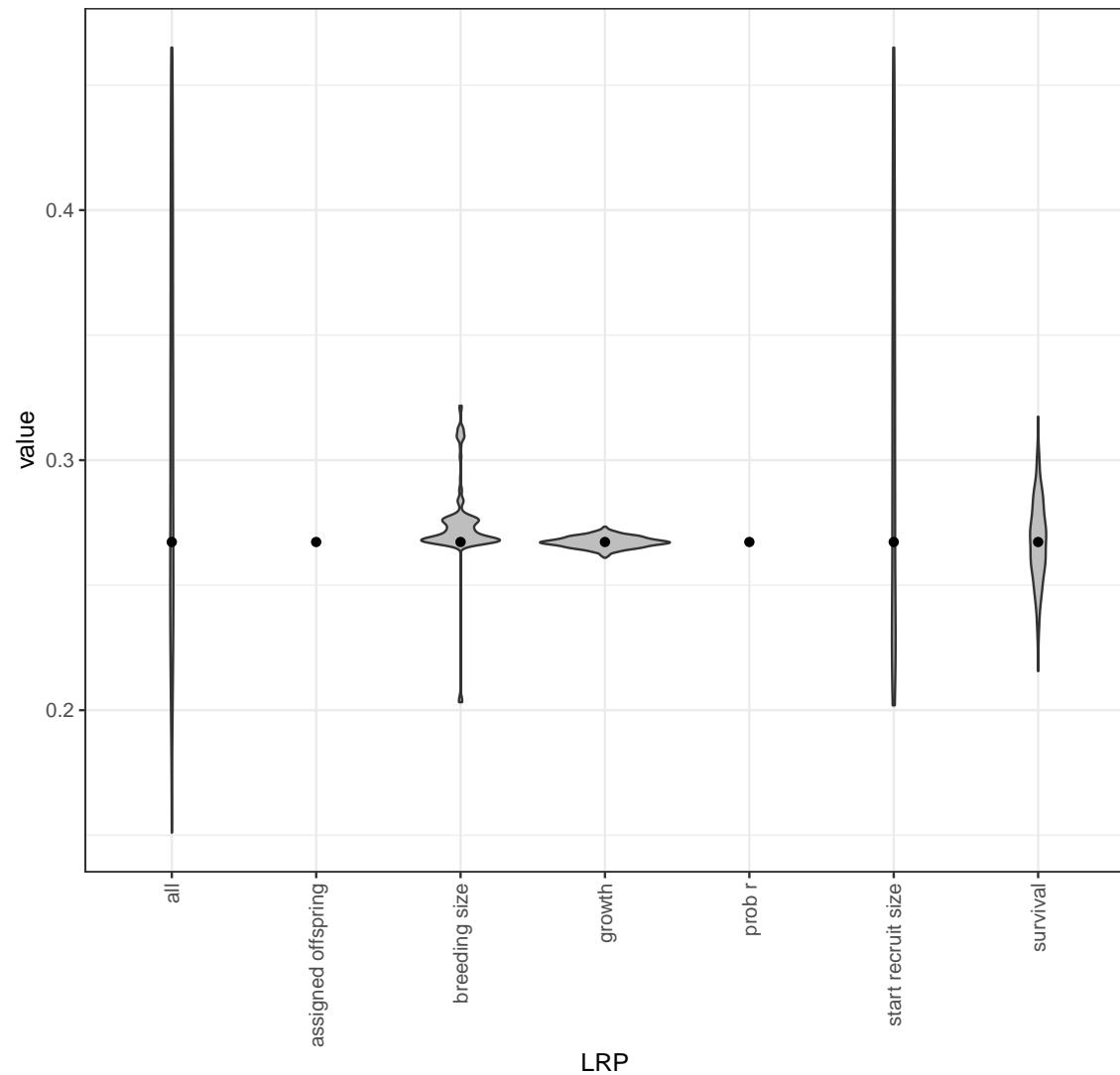


Figure B.6: The contribution of different sources of uncertainty in LRP, when we account for density-dependence in egg-recruit survival.

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

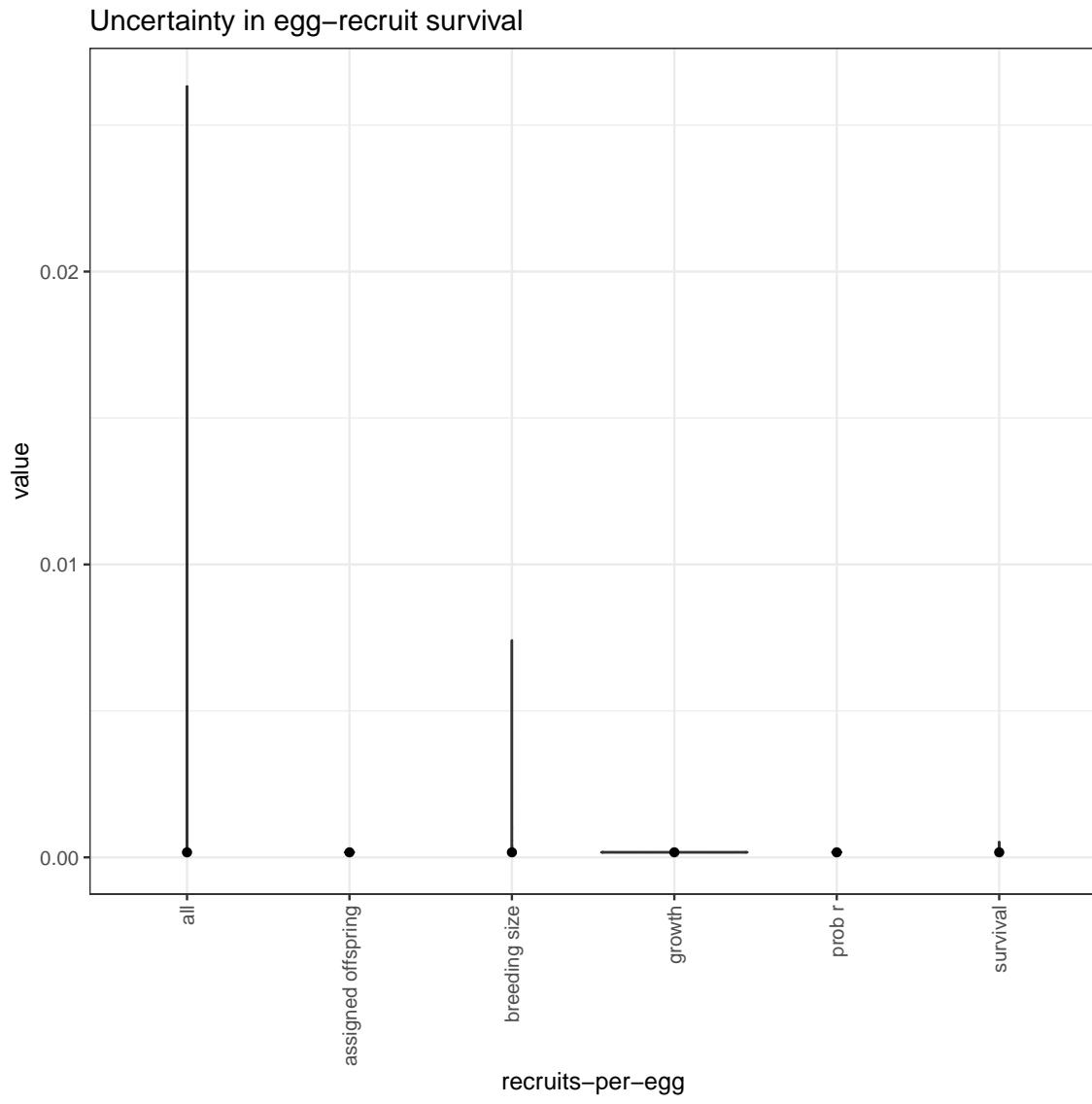


Figure B.7: The contribution of different sources of uncertainty in egg-recruit survival.

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

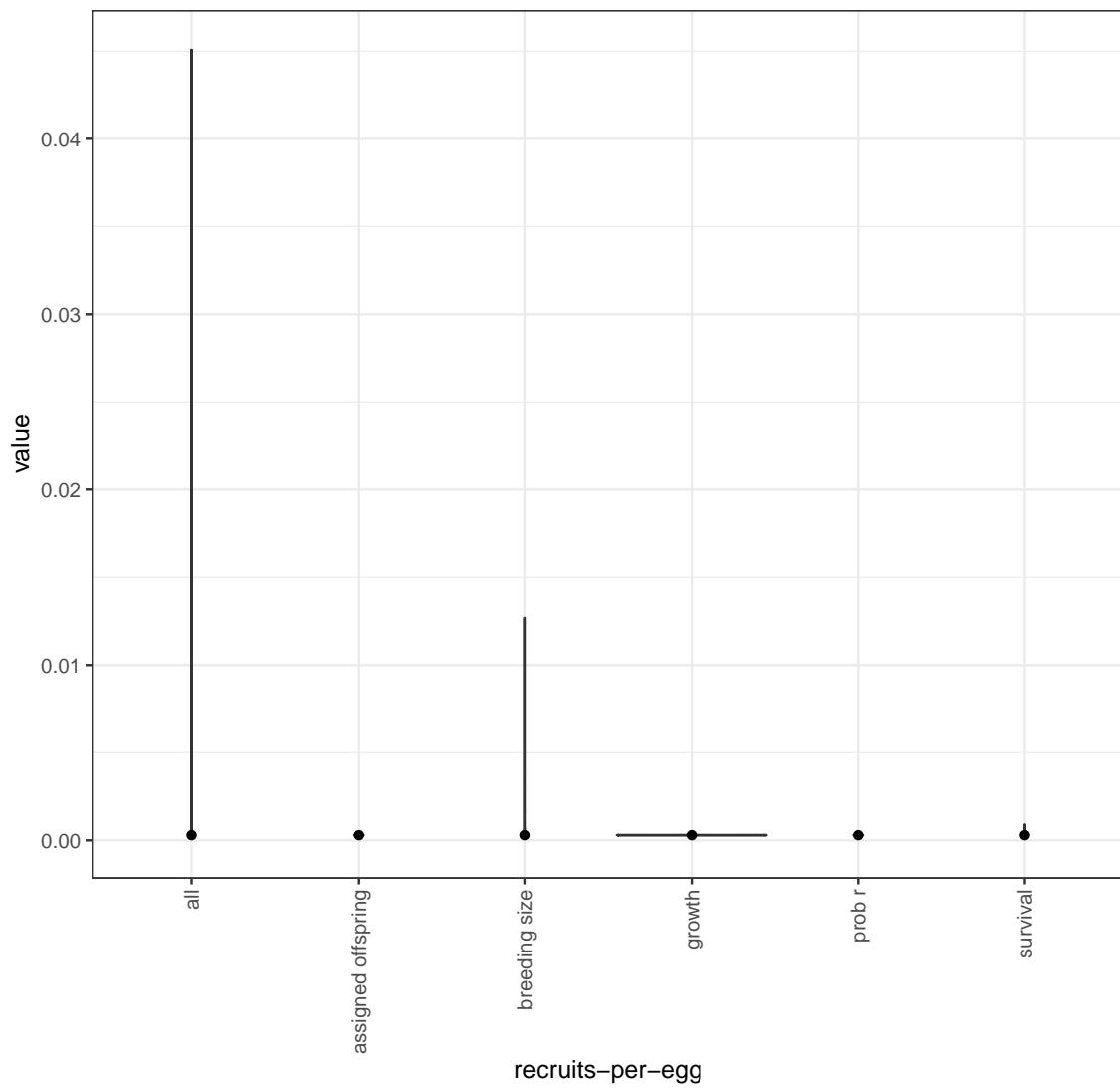


Figure B.8: The contribution of different sources of uncertainty in egg-recruit survival when we account for density-dependence in egg-recruit survival.

<sup>645</sup> B.3.0.4 Network persistence (NP)

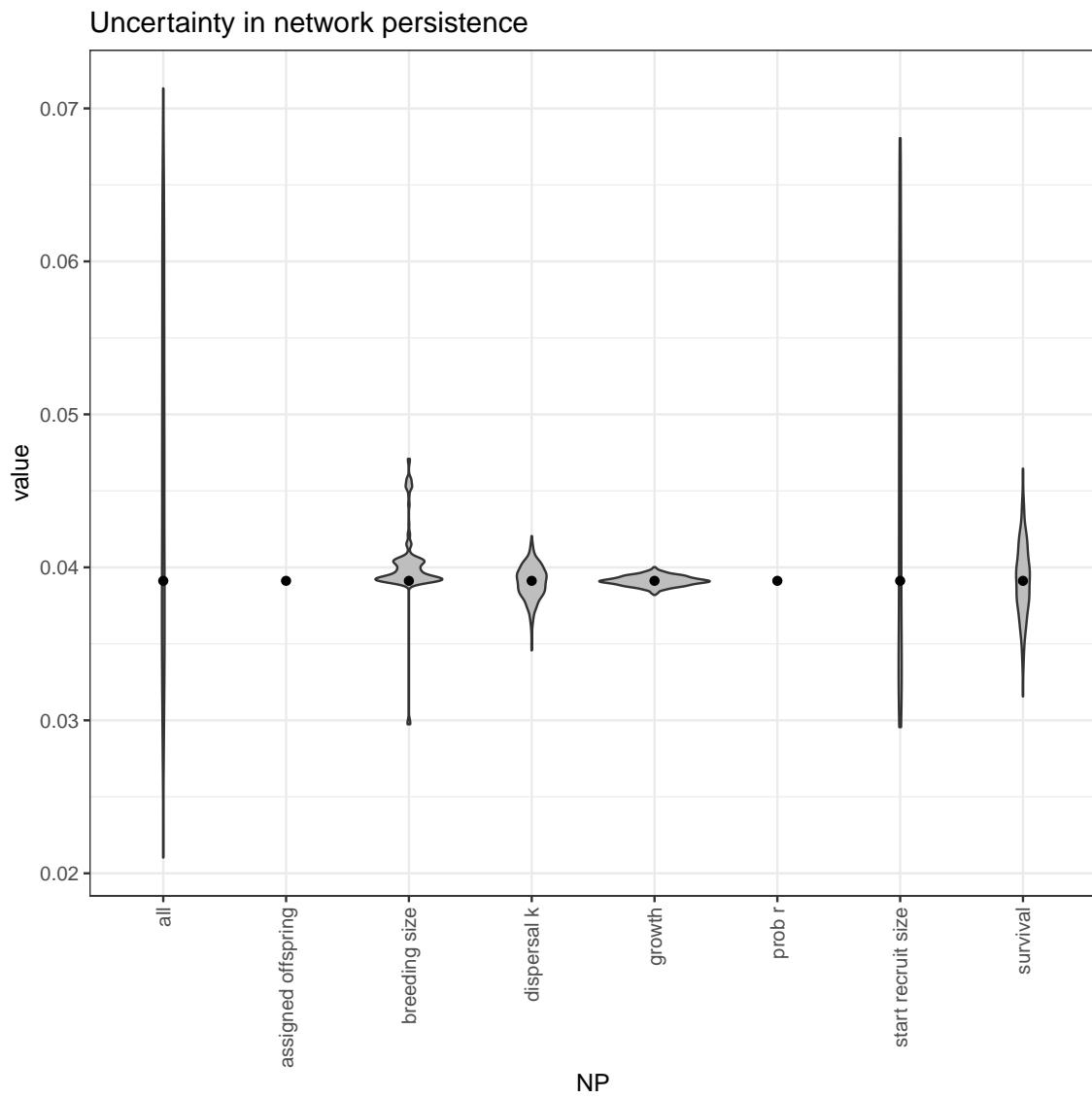


Figure B.9: The contribution of different sources of uncertainty in NP.

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

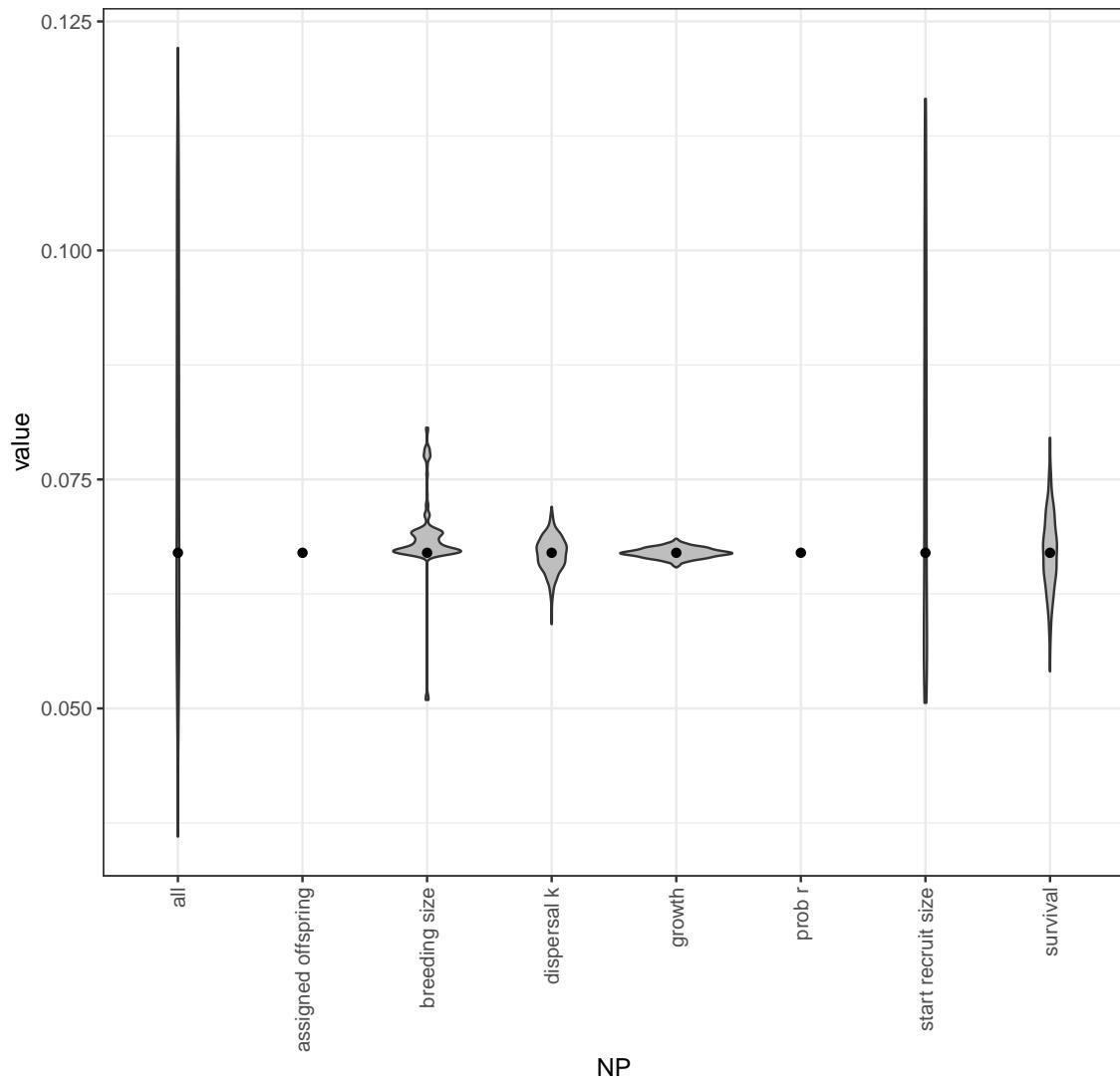


Figure B.10: The contribution of different sources of uncertainty in NP when we account for density-dependence in egg-recruit survival.

## References

- Glenn R Almany, Serge Planes, Simon R Thorrold, Michael L Berumen, Michael  
648 Bode, Pablo Saenz-Agudelo, Mary C Bonin, Ashley J Frisch, Hugo B Harrison,  
Vanessa Messmer, et al. Larval fish dispersal in a coral-reef seascape. *Nature  
Ecology & Evolution*, 1:0148, 2017.
- Michael Bode, David H Williamson, Hugo B Harrison, Nick Outram, and Geoffrey P  
651 Jones. Estimating dispersal kernels using genetic parentage data. *Methods in  
Ecology and Evolution*, 9(3):490–501, 2018.
- Louis W. Botsford, Alan Hastings, and Steven D. Gaines. Dependence of sustainability  
654 on the configuration of marine reserves and larval dispersal distance. *Ecology  
Letters*, 4:144–150, 2001.
- Scott C Burgess, Kerry J Nickols, Chris D Griesemer, Lewis AK Barnett, Alli-  
657 son G Dedrick, Erin V Satterthwaite, Lauren Yamane, Steven G Morgan, J Wilson  
White, and Louis W Botsford. Beyond connectivity: how empirical methods can  
660 quantify population persistence to improve marine protected-area design. *Ecological  
Applications*, 24(2):257–270, 2014.
- Peter Buston. Forcible eviction and prevention of recruitment in the clown anemone-  
663 fish. *Behavioral Ecology*, 14(4):576–582, 2003a.
- Peter Buston. Social hierarchies: size and growth modification in clownfish. *Nature*,  
424(6945):145–146, 2003b.

666 Peter M Buston and Cassidy C DAloia. Marine ecology: reaping the benefits of local  
dispersal. *Current Biology*, 23(9):R351–R353, 2013.

Peter M Buston, Geoffrey P Jones, Serge Planes, and Simon R Thorrold. Probability  
669 of successful larval dispersal declines fivefold over 1 km in a coral reef fish. *Proceedings of the Royal Society of London B: Biological Sciences*, page rspb20112041,  
*2011*.

672 Hal Caswell. *Matrix population models: construction, analysis, and interpretation*.  
Sinauer Associates Inc., Sunderland, Massachusetts, 2nd edition, 2001.

Katrina A Catalano, Allison G Dedrick, Michelle Stuart, Jonathan Purtiz, Humberto  
675 Montes, Jr., and Malin Pinsky. Interannual variability of genetic connectivity in  
a coral reef fish *Amphiprion clarkii*. in prep.

Robert K. Cowen and Su Sponaugle. Larval Dispersal and Marine Population Con-  
678 nectivity. *Annual Review of Marine Science*, 1(1):443–466, January 2009. ISSN  
1941-1405, 1941-0611. doi: 10.1146/annurev.marine.010908.163757. URL <http://www.annualreviews.org/doi/abs/10.1146/annurev.marine.010908.163757>.

681 C. C. D’Aloia, S. M. Bogdanowicz, J. E. Majoris, R. G. Harrison, and P. M. Buston.  
Self-recruitment in a Caribbean reef fish: a method for approximating dispersal  
684 kernels accounting for seascape. *Molecular Ecology*, 22(9):2563–2572, May 2013.  
ISSN 09621083. doi: 10.1111/mec.12274. URL <http://doi.wiley.com/10.1111/mec.12274>.

- Augustus J. Fabens. Properties and fitting of the von bertalanffy growth curve.  
687      *Growth*, 29:265–289, 1965.
- Daphne Gail Fautin, Gerald R Allen, Gerald Robert Allen, Australia Naturalist,  
Gerald Robert Allen, and Australie Naturaliste. Field guide to anemonefishes and  
690      their host sea anemones. 1992.
- Sarah O Hameed, J Wilson White, Seth H Miller, Kerry J Nickols, and Steven G  
Morgan. Inverse approach to estimating larval dispersal reveals limited population  
693      connectivity along 700 km of wave-swept open coast. *Proceedings of the Royal  
Society B: Biological Sciences*, 283(1833):20160370, 2016.
- Ilkka Hanski. Metapopulation dynamics. *Nature*, 396(6706):41–49, 1998.
- 696      Deborah R Hart and Antonie S Chute. Estimating von bertalanffy growth parameters  
from growth increment data using a linear mixed-effects model, with an application  
to the sea scallop *placopecten magellanicus*. *ICES Journal of Marine Science*, 66  
699      (10):2165–2175, 2009.
- Alan Hastings and Louis W. Botsford. Persistence of spatial populations depends on  
returning home. *Proceedings of the National Academy of Sciences*, 103:6067–6072,  
702      2006.
- Jordan N. Holtswarth, Shem B. San Jose, Humberto R. Montes Jr., James W. Morley,  
and Malin. L Pinsky. The reproductive seasonality and fecundity of yellowtail  
705      clownfish (*amphiprion clarkii*) off the philippines. *Bulletin of Marine Science*, 93,  
2017.

Darren W Johnson, Mark R Christie, Timothy J Pusack, Christopher D Stallings,  
708 and Mark A Hixon. Integrating larval connectivity with local demography reveals  
regional dynamics of a marine metapopulation. *Ecology*, 99(6):1419–1429, 2018.

Jacob P Kritzer and Peter F Sale. *Marine metapopulations*. Elsevier Academic Press,  
711 2006.

J.L. Laake. RMark: An r interface for analysis of capture-recapture data with  
MARK. AFSC Processed Rep. 2013-01, Alaska Fish. Sci. Cent., NOAA,  
714 Natl. Mar. Fish. Serv., Seattle, WA, 2013. URL <http://www.afsc.noaa.gov/Publications/ProcRpt/PR2013-01.pdf>.

Haruki Ochi. Mating behavior and sex change of the anemonefish, amphiprion clarkii,  
717 in the temperate waters of southern japan. *Environmental Biology of Fishes*, 26  
(4):257–275, 1989.

Brant K Peterson, Jesse N Weber, Emily H Kay, Heidi S Fisher, and Hopi E Hoek-  
720 stra. Double digest radseq: an inexpensive method for de novo snp discovery and  
genotyping in model and non-model species. *PloS one*, 7(5):e37135, 2012.

Malin L Pinsky, Humberto R Montes Jr, and Stephen R Palumbi. Using isolation  
723 by distance and effective density to estimate dispersal scales in anemonefish. *Evolution*, 64(9):2688–2700, 2010.

Jonathan B Puritz, Christopher M Hollenbeck, and John R Gold. ddocent: a radseq,  
726 variant-calling pipeline designed for population genomics of non-model organisms.  
*PeerJ*, 2:e431, 2014.

- Mark Rees, Dylan Z Childs, and Stephen P Ellner. Building integral projection  
729 models: a user's guide. *Journal of Animal Ecology*, 83(3):528–545, 2014.
- J Roughgarden, S Gaines, and H Possingham. Recruitment dynamics in complex  
life cycles. *Science*, 241(4872):1460–1466, September 1988. ISSN 0036-8075, 1095-  
732 9203. doi: 10.1126/science.11538249. URL <http://www.sciencemag.org/cgi/doi/10.1126/science.11538249>.
- Ocane C. Salles, Jeffrey A. Maynard, Marc Joannides, Corentin M. Barbu, Pablo  
735 Saenz-Agudelo, Glenn R. Almany, Michael L. Berumen, Simon R. Thorrold, Ge-  
offrey P. Jones, and Serge Planes. Coral reef fish populations can persist without  
immigration. *Proceedings of the Royal Society B: Biological Sciences*, 282(1819):  
738 20151311, November 2015. ISSN 0962-8452, 1471-2954. doi: 10.1098/rspb.2015.  
1311. URL <http://rspb.royalsocietypublishing.org/lookup/doi/10.1098/rspb.2015.1311>.
- 741 Jinliang Wang. Sibship reconstruction from genetic data with typing errors. *Genetics*,  
166(4):1963–1979, 2004.
- Jinliang Wang. Computationally efficient sibship and parentage assignment from  
744 multilocus marker data. *Genetics*, 191(1):183–194, 2012.
- Jinliang Wang. Estimation of migration rates from marker-based parentage analysis.  
*Molecular ecology*, 23(13):3191–3213, 2014.
- 747 Jw White, Lw Botsford, A Hastings, and Jl Largier. Population persistence in ma-  
rine reserve networks: incorporating spatial heterogeneities in larval dispersal.

*Marine Ecology Progress Series*, 398:49–67, January 2010. ISSN 0171-8630, 1616-

750 1599. doi: 10.3354/meps08327. URL <http://www.int-res.com/abstracts/meps/v398/p49-67/>.

Adam Yawdoszyn. Fecundity in clownfish. in prep.