

Clownfish metapopulation persistence draft

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Introduction

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

1998). Many marine species exist in metapopulations, consisting of patch populations connected through dispersal where connectivity affects patch dynamics though individual patches are unlikely to go extinct (Kritzer and Sale, 2006). Assessing demographic parameters and levels of connectivity has been particularly challenging for marine species, where much of the mortality 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. In non-spatially structured populations, we use criteria such as the average number of recruiting offspring contributed by each individual 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 λ of an age-structured Leslie matrix) (Caswell, 2001; Burgess et al., 2014). To assess replacement, metrics must take into account the demographic processes across the whole life cycle, including how likely individuals are to survive to the next age or stage, their expected fecundity at each stage, and the survival of any offspring produced to recruitment.

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

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

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

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

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

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

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

Methods

Study system

We focus on a tropical metapopulation of yellowtail clownfish (*Ampiprion clarkii*) in the Philippines. Like many clownfish species, yellowtail clownfish have a mutualistic relationship with anemones, where small colonies of fish live (Buston, 2003; Fautin et al., 1992). Yellowtail clownfish are protandrous hermaphrodites and maintain a size-structured hierarchy; within an anemone, the largest fish is the breeding female, the next largest is the breeding male, and any smaller fish are non-breeding juveniles. The fish on an anemone maintain a strict social and size hierarchy (Buston, 2003), with fish moving up in rank to become breeders only after the larger fish have died 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). 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 lim-

ited movement as adults and clearly patchy habitat. Once fish have settled, they tend to stay within close proximity of their anemones [XX meters, CITATION]. This 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 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 DAloia, 2013; Salles et al., 2015; Johnson et al., 2018).

Field data collection

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

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

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

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

Genotyping and parentage analysis

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

Estimating inputs from empirical data

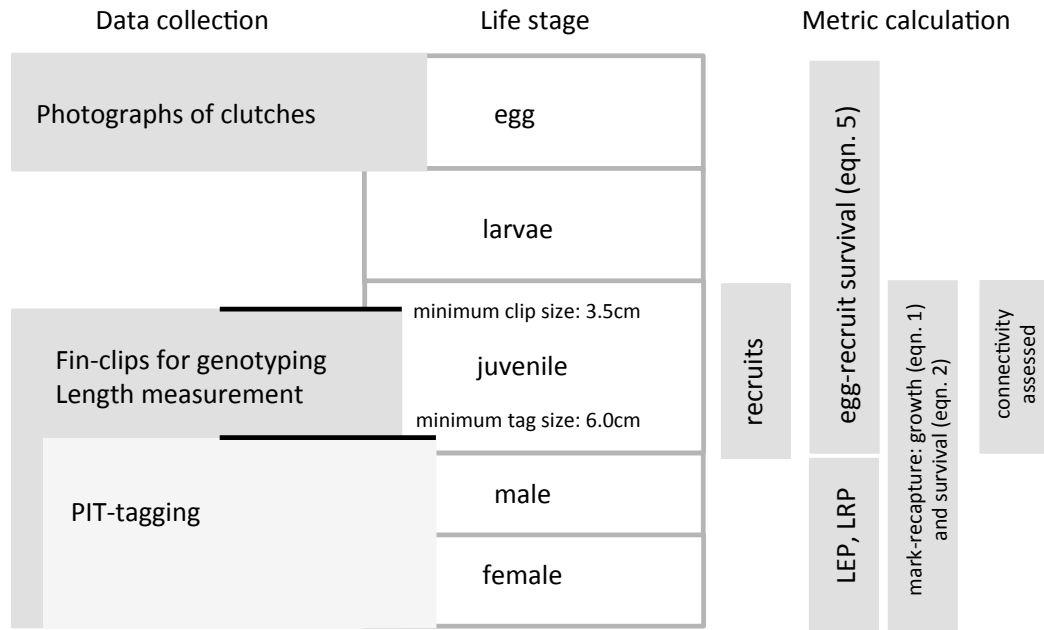


Figure 1: Here, we show the data collected for fish at each life stage (life stage boxes are not scaled by length of stage) and how the empirical data fit into the metric calculations.

Growth and survival: mark-recapture analyses

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

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

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

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

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

We use the full set of fish encountered multiple times to estimate annual sur-
vival ϕ and probability of recapture p_r using the mark-recapture program MARK
150 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 A1). For fish that
153 are not recaptured in particular year, we estimate their size using our growth model

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

The best-fit model using model selection with AICc has an effect b_a of fish size on
162 survival, and additive effects b_1 and b_2 of fish size and shortest distance to anemone on the probability of recapture:

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

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

Fecundity

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

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

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

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

177 **Lifetime egg production**

We use an integral projection model (IPM) (e.g. Rees et al., 2014) to estimate the
total number of eggs produced by one individual (lifetime egg production: LEP),
180 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
183 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
186 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.

189 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 func-
tions described above to project forward for 100 time steps. This gives us the size

192 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;
195 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-
198 dependent fecundity function described above (eqn. 4) to get the total number of
eggs produced at each time step. To get the total number of of eggs one individual is
likely to produce in its lifetime, we then sum across all time steps in the individual's
201 potential life.

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

Survival from egg to recruit

We estimate survival from egg to recruit S_e using the number of recruited offspring
204 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
the number of eggs produced by genotyped parent fish by multiplying the number of
207 genotyped parents ($N_g = 913$) by the expected lifetime egg production of a parent
fish LEP_p , using LEP calculated starting with an individual of 6 cm. We make the
assumption that all recruited offspring originating from the genotyped parents end
210 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 ($R_m = 90$)

by the proportion of our site habitat we sample cumulatively across all sampling
 213 years $P_h = 0.34$ and the probability of capturing a fish if we sample an anemone P_c
 (see A, A for details on P_c and P_h estimates, respectively). Our estimated survival
 from egg to recruit is the number of tagged recruits divided by the number of tagged
 216 eggs produced:

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

Defining recruit and census stage

When assessing persistence, it is important to consider mortality and reproduction
 219 that occurs across the entire life cycle to determine whether an individual is replacing
 itself with an individual that reaches its same life stage (Burgess et al., 2014). We
 define recruit to be a juvenile individual that has settled on the reef the previous year;
 222 lifetime egg production 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. In theory, it
 225 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-
 228 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

231 size of a recruit ($\text{size}_{\text{recruit}}$) and test sensitivity to different sizes within the range of
 sizes that the recruit stage covers (Table 1).

Probability of dispersal

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

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

We use a Laplacian dispersal kernel with shape parameters $\theta = 1$ and scale parameter
 240 $k_d = -1.84$ (Fig. 3a, estimated in (Catalano et al., in prep)).

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

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

Persistence metrics

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

Estimated abundance over time

264 [*Add brief section here.*]

Lifetime production of recruits

To assess whether individuals at our focal patches produce enough offspring that
 267 survive to become recruits themselves, we find the estimated number of recruits an

individual recruit will produce over its lifetime (lifetime recruit production: LRP) by multiplying LEP by the estimated survival from egg to recruit S_e :

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

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

Self-persistence

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

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

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

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
285 et al., 2014).

Realized connectivity matrix and network persistence

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

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

Incorporating uncertainty

297 To represent the uncertainty in our estimates of the parameters that go into cal-
culating 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
300 each persistence metric as well as the value with our best estimate of each parameter.

For the dispersal kernel, we keep the shape parameter θ constant and pull the scale
parameter k_d from a set capturing the 95% confidence intervals, which was produced
303 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
306 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
309 their first recapture as a female. For the von Bertalanffy growth parameters L_∞ 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
312 pull from a normal distribution generated using the standard error estimated in the mark-recapture analysis for both the intercept b_ϕ and the size effect b_a .

To incorporate uncertainty in egg-recruit survival, we consider uncertainty in both
315 the number of offspring assigned to parents during the parentage analysis and the probability of capturing a fish P_c , which affects how the captured assigned offspring are scaled up to account for fish uncaught. For the number of assigned offspring,
318 we generate a set of values of number of assigned offspring using a random binomial, where the number of trials is the number of genotyped offspring (XX) and the probability of success on each trial is the assignment rate XX of offspring from the
321 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 α_{P_c} and β_{P_c} , found using the mean and variance of capture probabilities estimated
324 from recapture dives across sites and sampling seasons (details in A).

Results

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

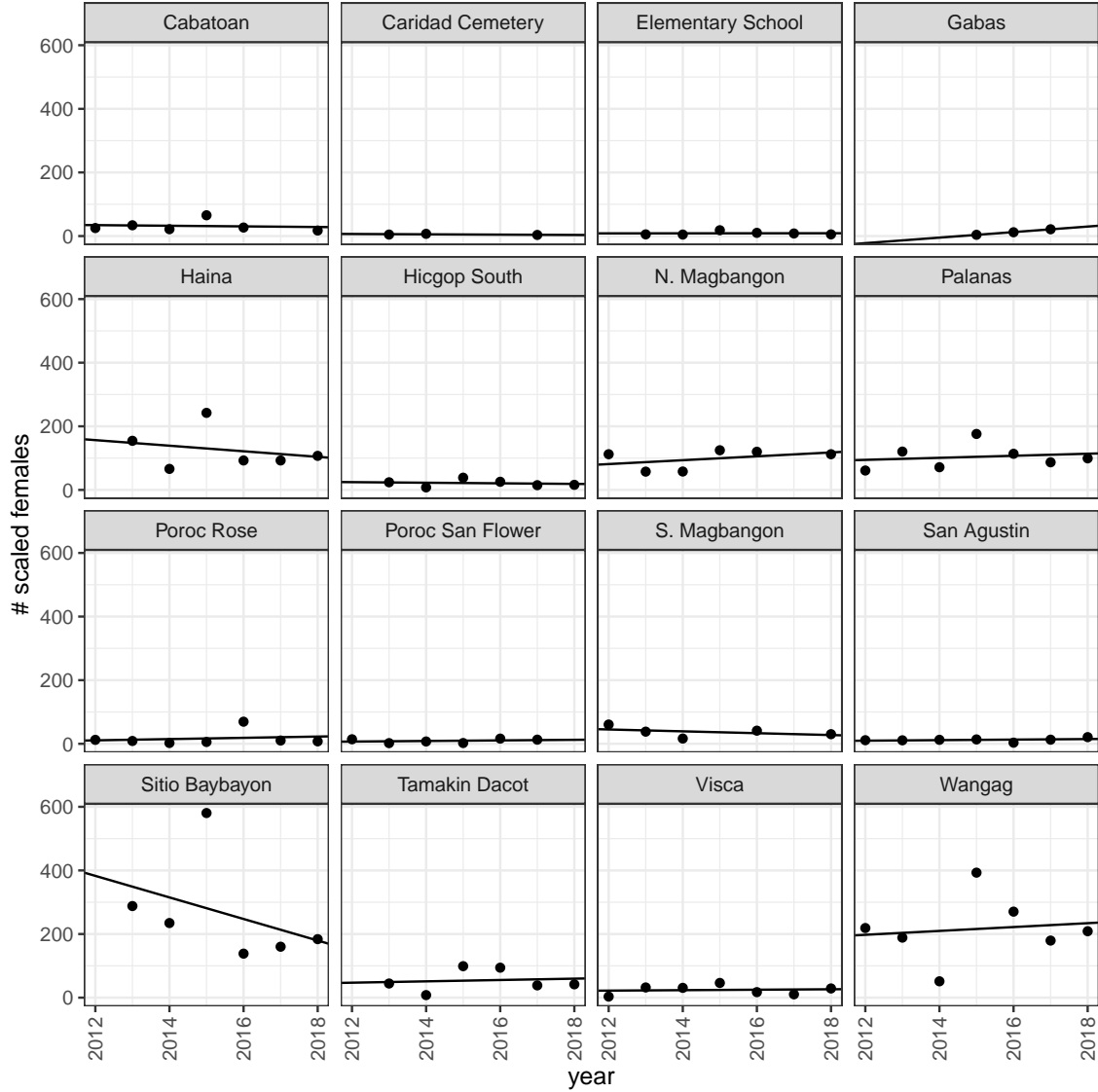


Figure 2: The estimated number of females at each site over the sampling years. The total number of females at each site was estimated by taking the number of females (fish ≥ 5 cm with the yellow pointed tail indicating female) captured at each site in each year and scaling up by the proportion of habitat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

From the mark-recapture analysis of tagged and genotyped fish, we estimate mean
 330 values of $L_\infty = 10.58\text{cm}$ (range of estimates 10.39 - 10.75 cm) and $K = 0.928$ (range
 of estimates 0.854 - 1.025) for the von Bertalanffy growth curve parameters (Fig. 3b,
 Table 1). For juvenile and adult (post-recruitment) survival on a log-odds scale, the
 333 best-fit model has a coefficient $b_a = 0.74 \pm 0.060$ SE for the effect of size and an
 intercept $b_\phi = -4.83 \pm 0.340$ SE. These results suggest that larger fish have higher
 annual survival, which is similar to survival estimates in other clownfish species
 336 (check Buston paper). The accompanying best-fit model for recapture probability
 has intercept $b_{pr} = 17.93 \pm 0.858$ SE, size effect $b_1 = -1.816 \pm 0.080$ SE, and effect of
 diver distance from the anemone $b_2 = -0.171 \pm 0.021$ SE. The negative effect of both
 339 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
 342 the recapture probability plots, like the survival one in Fig. 3, to the appendix and
 reference here.]

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

[*Not sure where to put this - kind of a methods/results hybrid, or if it should
 exist, but seems like it might be helpful - not fully filled out yet. Need to clarify
 348 somewhere what kind 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)
θ	shape parameter in dispersal kernel	0.5	NA	estimated using methods in Bode et al. (2018) in Catalano et al. (in prep)
L_∞	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_ϕ	intercept for adult survival	-4.83	± 0.340 stan- dard error	
b_a	size effect for adult survival	0.74	± 0.060 stan- dard error	
b_{pr}	intercept for recapture prob- ability from mark-recapture analysis	17.93	± 0.858 stan- dard error	not used in persis- tence estimates
b_1	size effect for re- capture	-1.816	± 0.080 stan- dard error	not used in persis- tence estimates
b_2	distance effect for recapture	-0.171	± 0.021 stan- dard error	not used in persis- tence estimates
size _{recruit}	size (cm) of re- cruited offspring	mean of size of off- spring in parentage analysis = 4.4 cm	3.5 - 6.0 cm	
S_e	egg-recruit sur- vival			
b_e	coefficient for eyed eggs	-0.608		Yawdoszyn et al. (in prep)

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

Table 1:

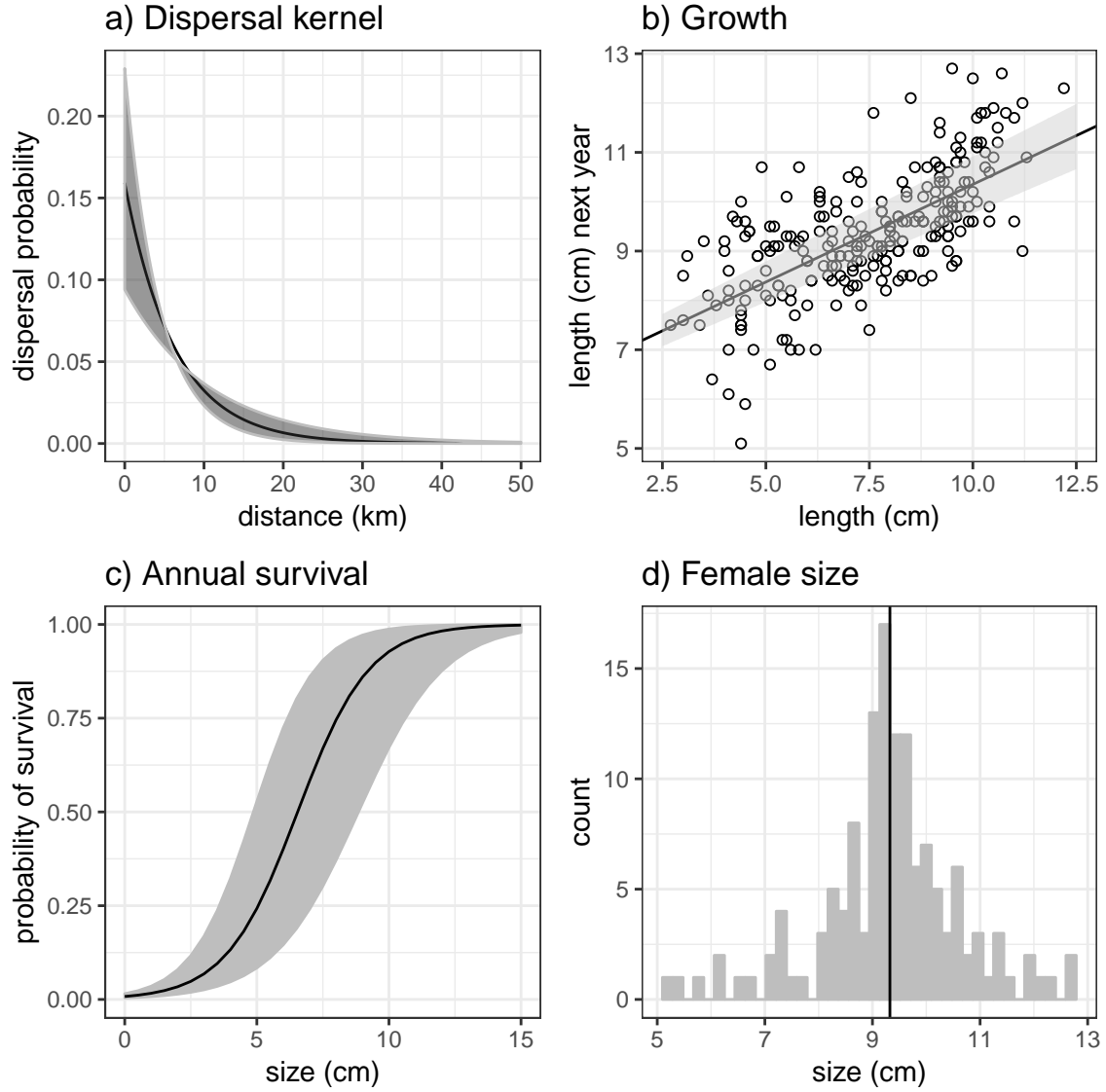


Figure 3: Best estimates (solid black line) and range included for uncertainty (gray) for dispersal (a), growth (b), post-recruit survival (c), and size at female transition (d) parameters.

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

351 of LEP for 10876, ranging from XX to XX when we consider uncertainty in the inputs
 (Fig. 4a). The size at recruitment - the census point between egg-recruit survival
 and LEP - has the most effect on the value of LEP (Fig. B.3), with higher values of
 354 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
 357 when we include uncertainty in the number of offspring assigned to parents and
 the probability of catching a fish (Fig. 4b). Uncertainty in the size of transition
 to breeding female L_f has the largest effect on egg-recruit survival (Fig. B.5); we
 360 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.

363 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
 366 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.

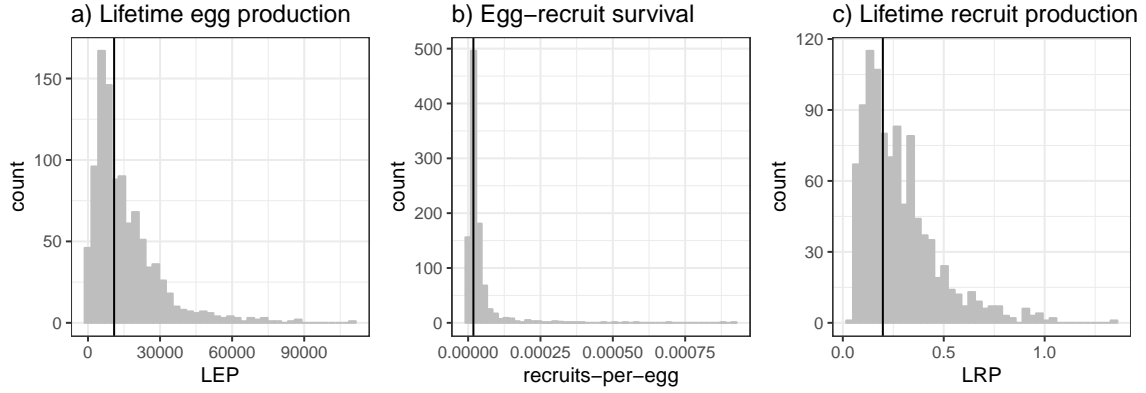


Figure 4: Estimates of a) LEP, b) egg-recruit survival, and c) LRP, showing the best estimate (black solid line) and range of estimates considering uncertainty in the inputs.

369 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
 372 makes sense. We see the highest values of self-persistence at Haina ($SP = 0.024$) and
 Wangag ($SP = 0.010$), our two widest sites.

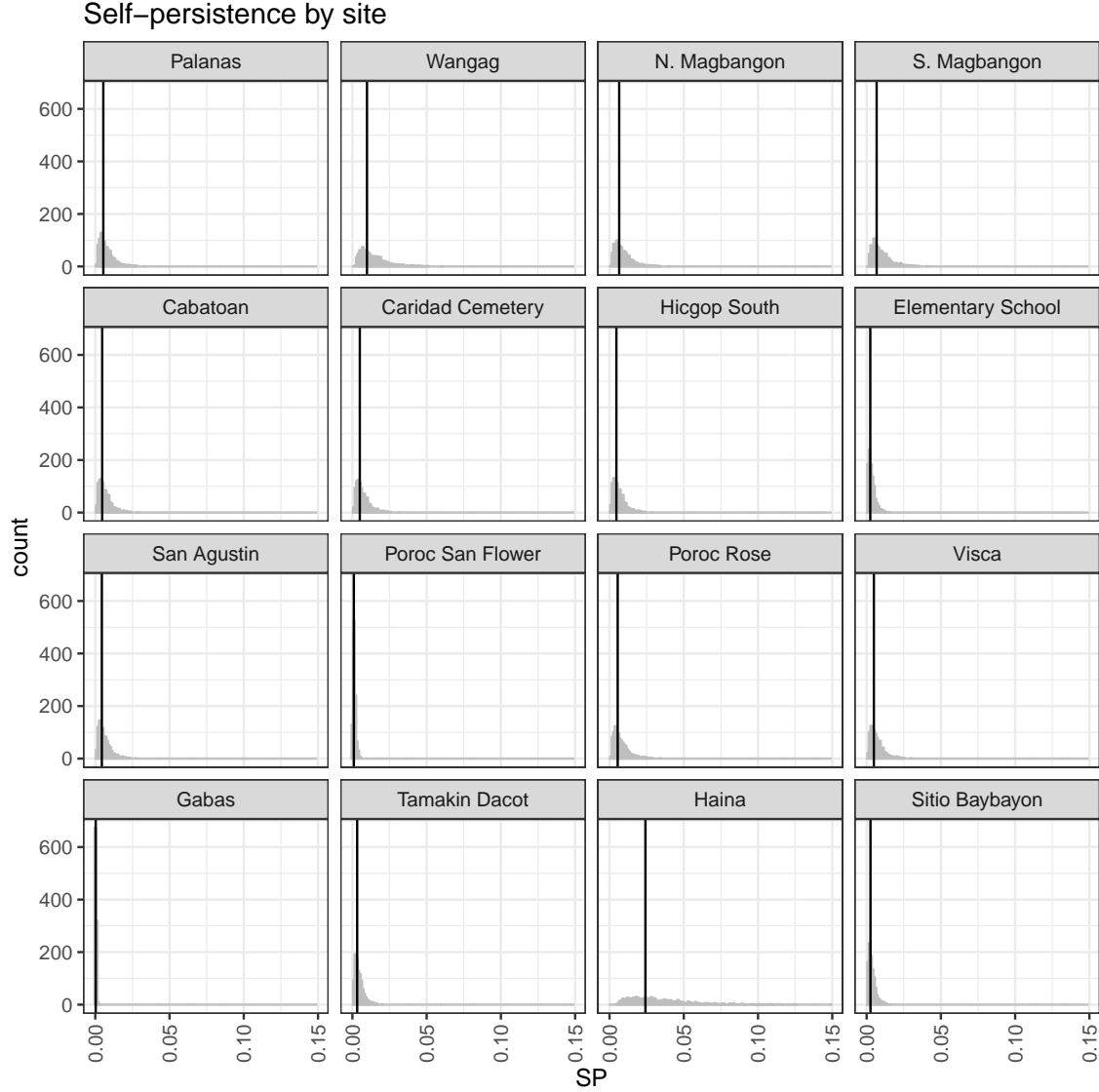


Figure 5: Values of self-persistence at each site, showing the best estimate (black line) and range of estimates considering uncertainty in the input paramters. No site reaches a value of $SP > 1$, necessary to be self-persistent.

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

the realized connectivity matrix is 0.034, well below the value of 1 that indicates network persistence (Fig. 6a). We see that most of the connectivity occurs among the sites in the northern part of our sample area, from Palanas to Caridad Cemetery.

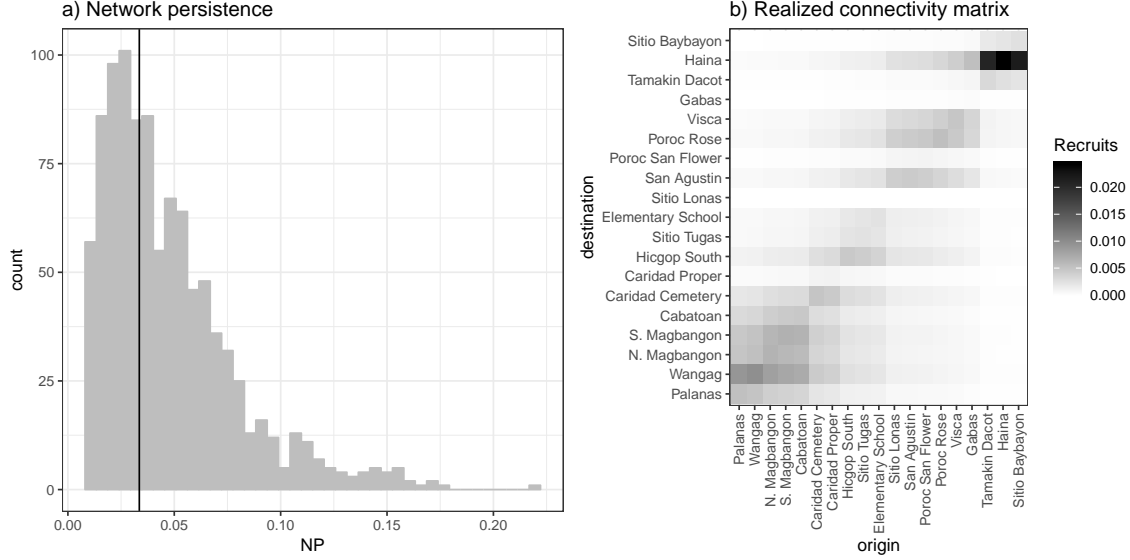


Figure 6: a) Network persistence values, showing the best estimate (black solid line) and range of estimates considering uncertainty. b) The realized connectivity matrix C , with sites arranged from north (Palanas) to south (Sitio Baybayon).

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 closed and say 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. 7a). When we add in the connectivity, we see a

384 higher value of network persistence in our best estimate ($NP = 0.20$) but still not high
 enough to indicate network persistence (Fig. 7b). We see more of the distribution
 of estimates above 1, however, suggesting that network persistence is within our
 387 range of uncertainty 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
 390 estimated value of egg-recruit survival).

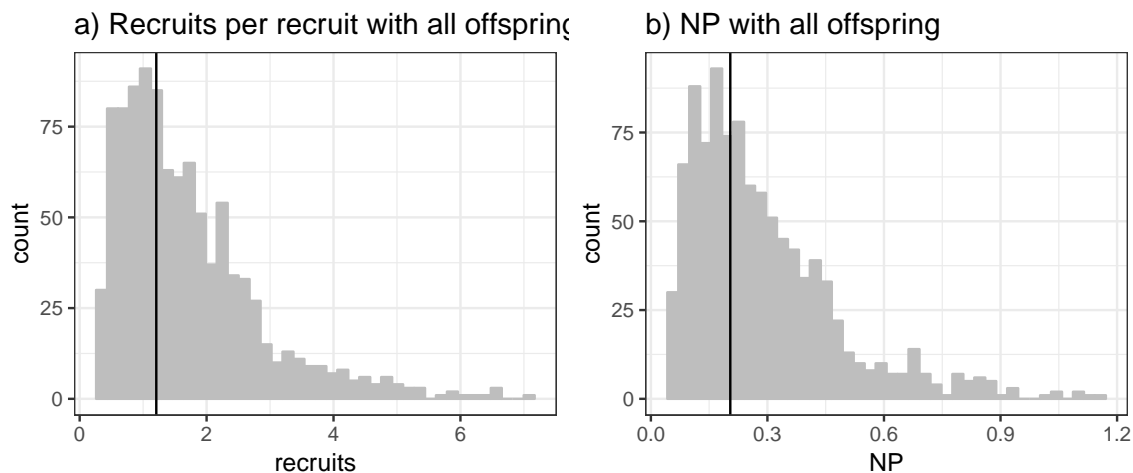


Figure 7: a) Recruits per recruit when we consider all arriving recruits to have originated from our sites. b) Range of values of NP considering all arriving recruits to be offspring from our sites, with the best estimate in a black solid line.

Discussion

Big picture: What do our results mean for persistence in this system and our understanding of metapopulations generally?
 393

- 396 • So we don't see persistence in our metrics, either self-persistence or network persistence but our abundances don't seem to be changing. Suggests that this is just a portion of a larger metapopulation, rather than a self-contained metapopulation. Maybe it is a sink? Persistent in terms of constant abundance but relies on outside immigration to persist.
- 399 • 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

402 in an area range that spans the estimated spread? (This point might change, depending on mean dispersal distance from the new kernels)
- 405 • Sensitivity - how would our parameters need to change to see persistence? 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

408 reasonable it would be to get better estimates in the field.

More detailed discussion of our estimates, limitations, ways to move forward:

- 411 • 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

414 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?

- 417 • 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.
- 420 • Contextualize our parameter estimates with those from other studies (esp. survival, growth, egg-recruit survival).

Broadening back out:

- 423 • 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
426 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
429 some local retention, maybe broader connectivity is still the story in terms of receiving enough recruitment to persist.

Appendix

432 **A Method details**

Proportion of habitat sampled

[Need to add in the details here]

435 **Probability of capturing a fish, from recapture dives**

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

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

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

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

456 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 $\beta_{P_c} = 1.13$.
We sample 1000 values from the beta distribution, then truncate the sample to only
459 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.
We then sample with replacement from the truncated set to get a vector of values
462 the length of the number of runs.

Full set of MARK models

We consider the following set of models in MARK:

Model	Model description	AICc	dAICc
	survival size, recapture size+distance	3348.861	0
	survival size, recapture distance	3359.998	-11.1371
	survival constant, recapture 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 A1:

B Uncertainty details

B.1 Sensitivity to parameters

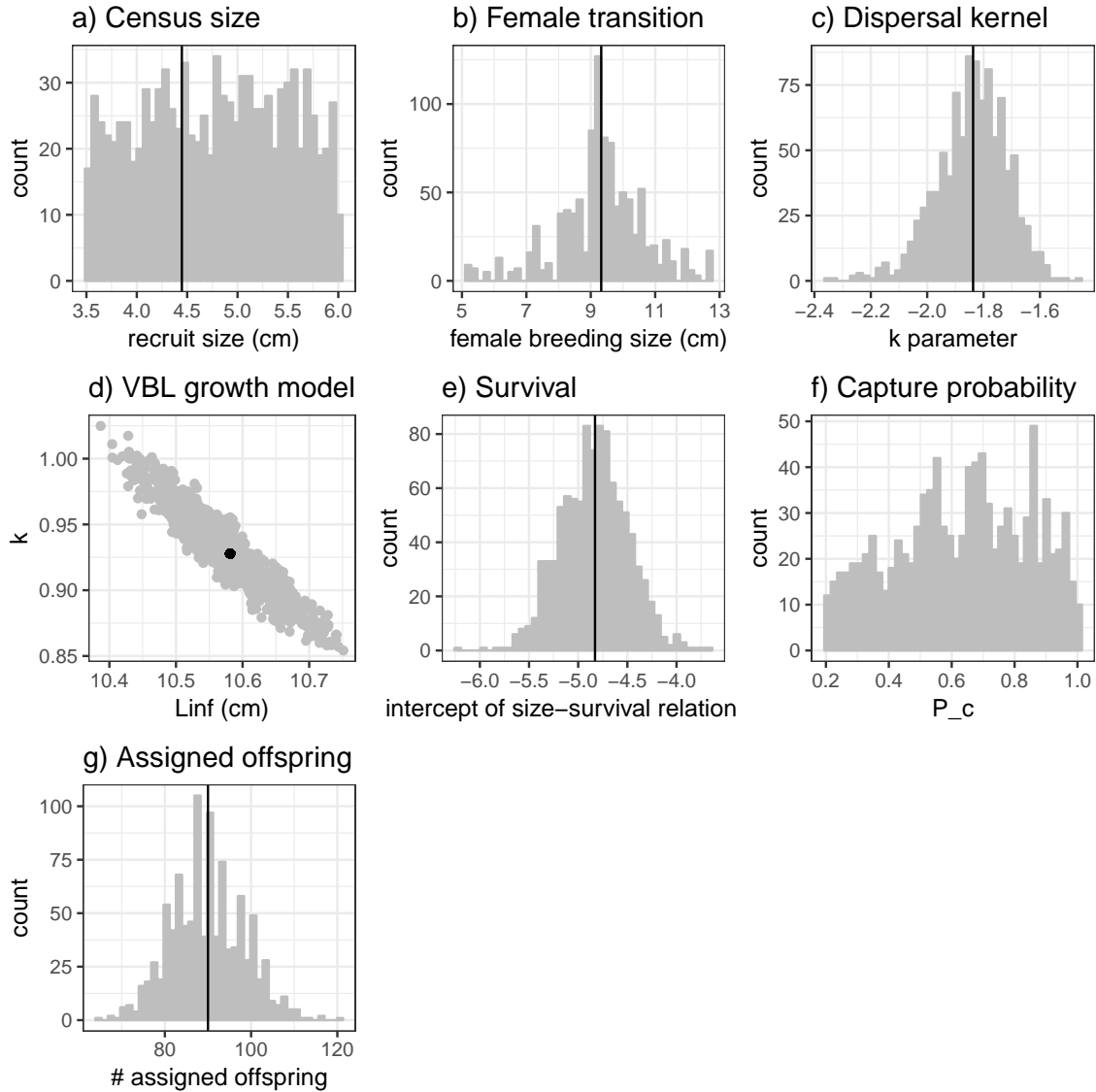


Figure B.1: Range of parameter inputs for uncertainty runs with all uncertainty included: a) $\text{size}_{\text{recruit}}$, the census size at which fish are considered to have recruited after egg-recruit survival occurs; b) L_f , the size at which fish transition from male to female and their reproductive output is included in the estimate of lifetime egg production (LEP); c) k_d , the scale parameter in the dispersal kernel; d) the parameters L_∞ and K of the von Bertalanffy growth model; e) the intercept b_ϕ of the adult size dependent survival relationship; f) P_c , the probability of capturing a fish;

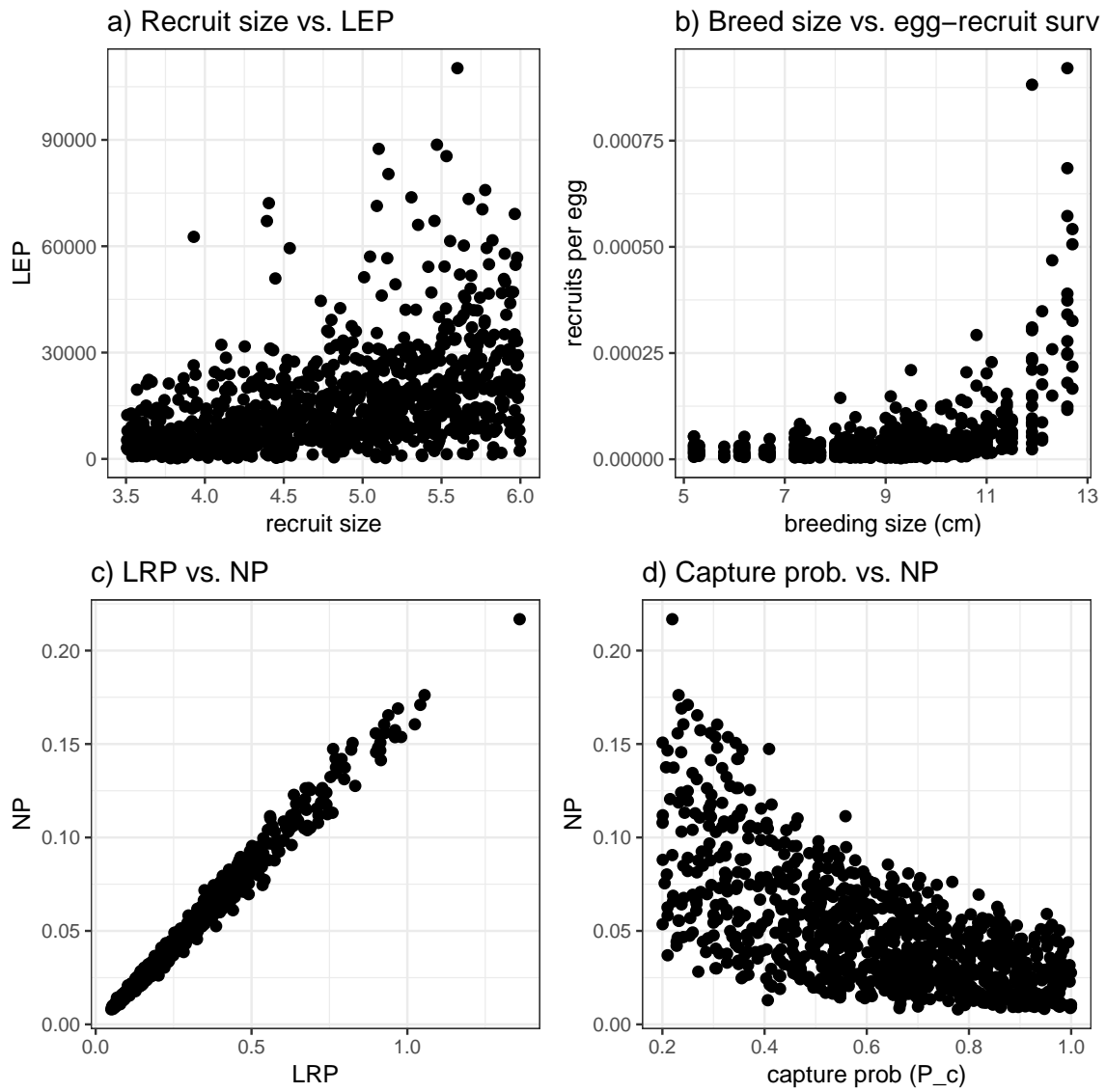


Figure B.2: Relationships among parameters and metrics.

B.2 Effects of different types of uncertainty on metrics

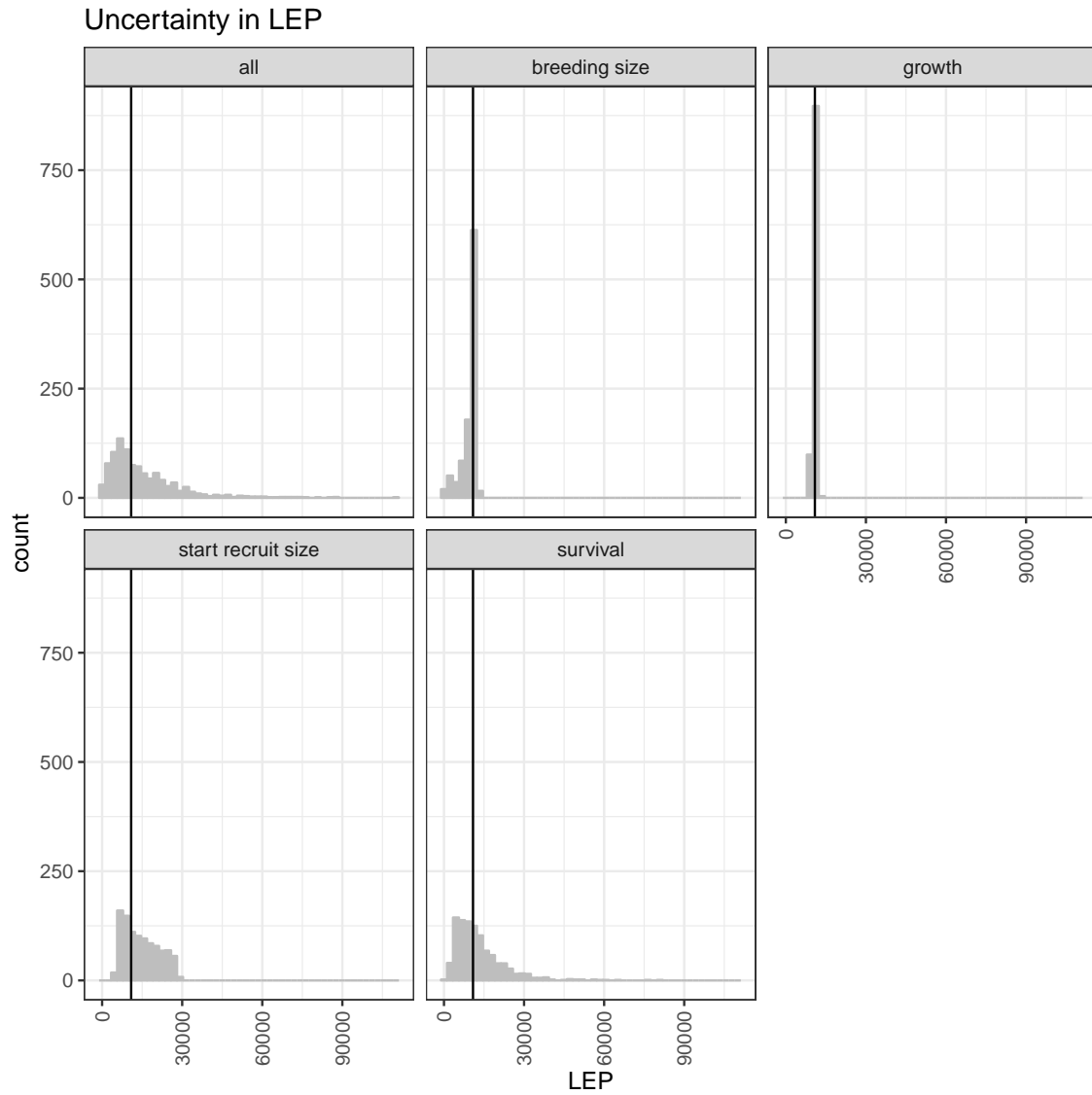


Figure B.3: The contribution of different sources of uncertainty in LEP.

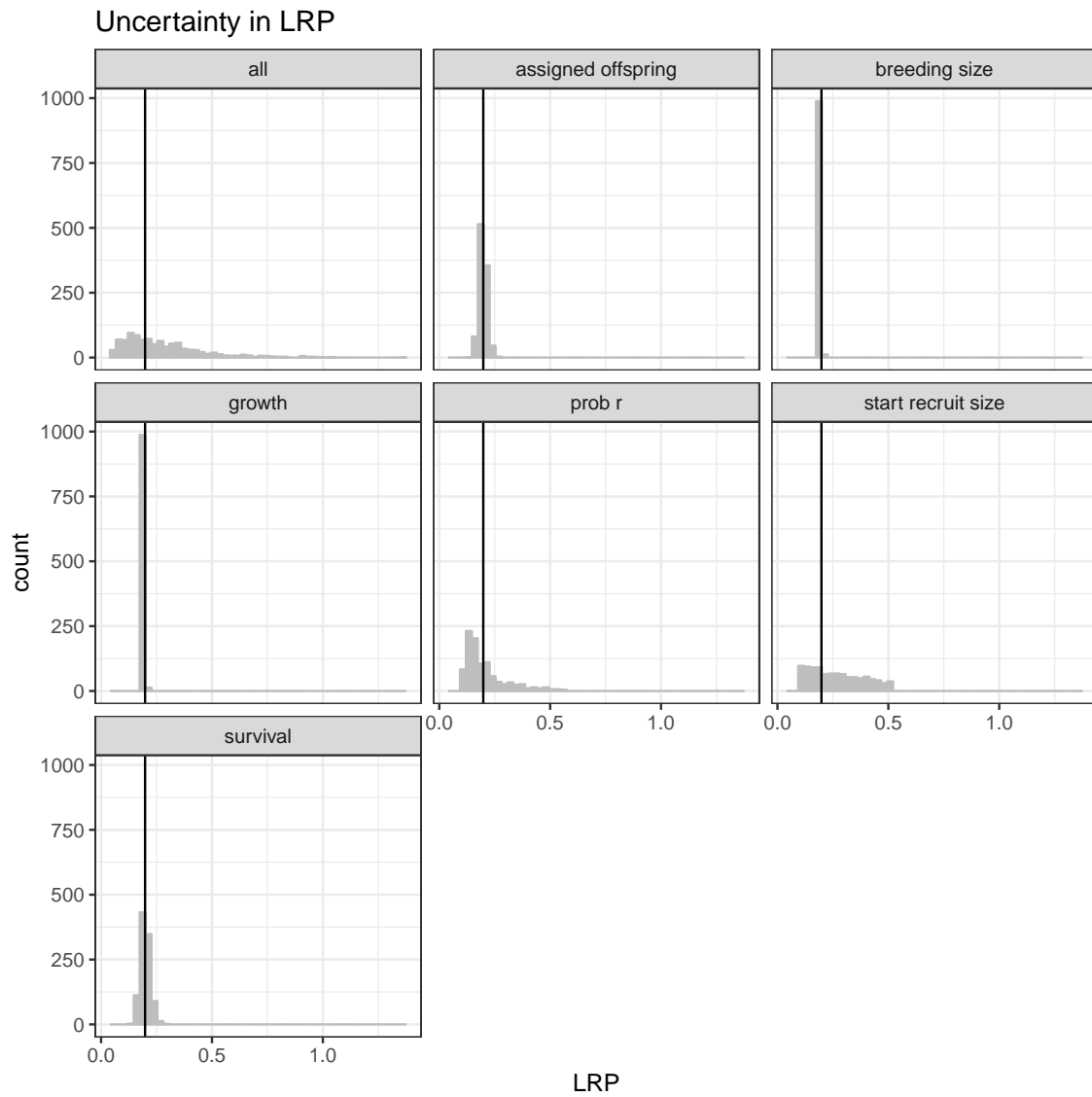


Figure B.4: The contribution of different sources of uncertainty in LRP.

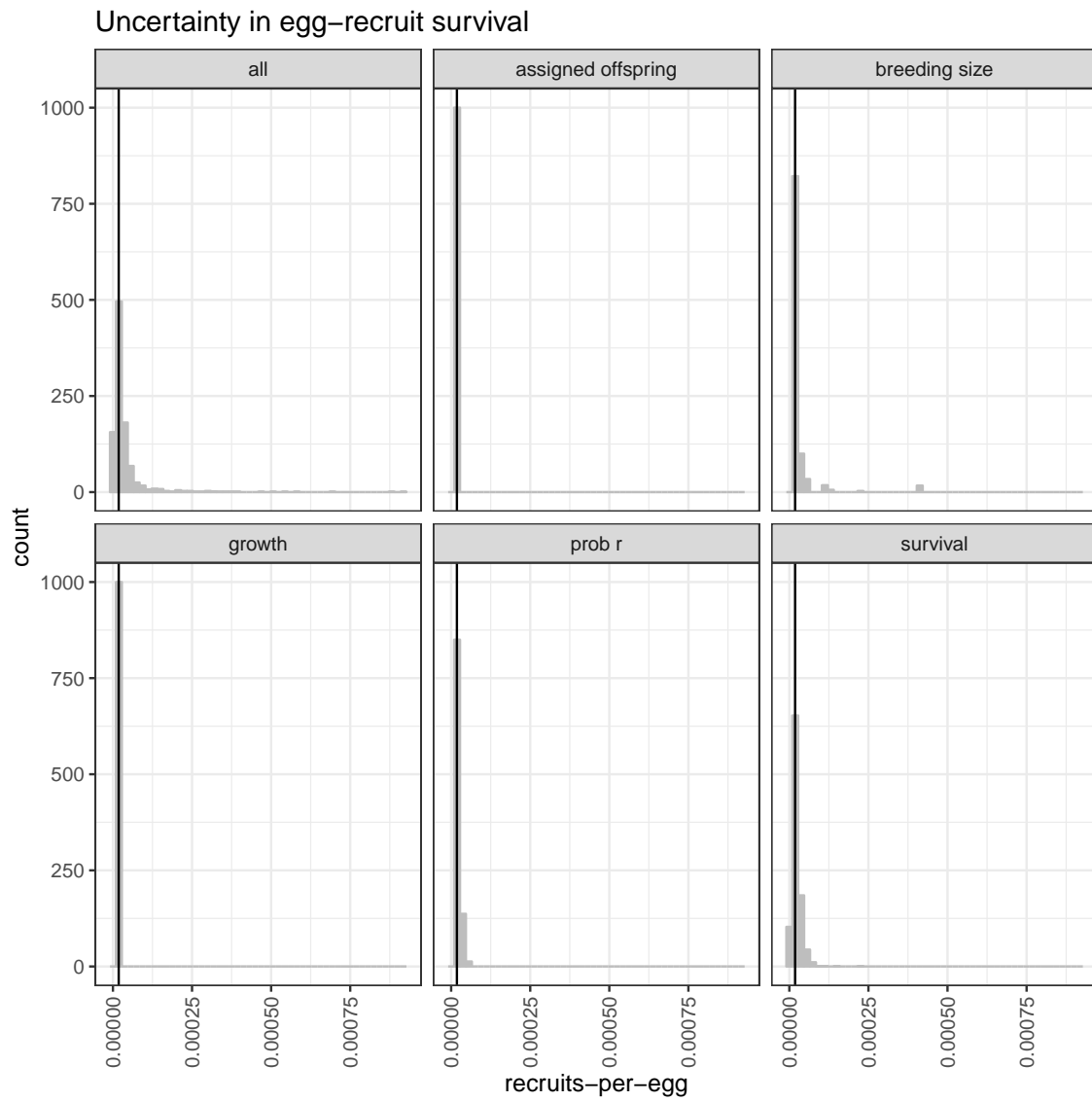


Figure B.5: The contribution of different sources of uncertainty in egg–recruit survival.

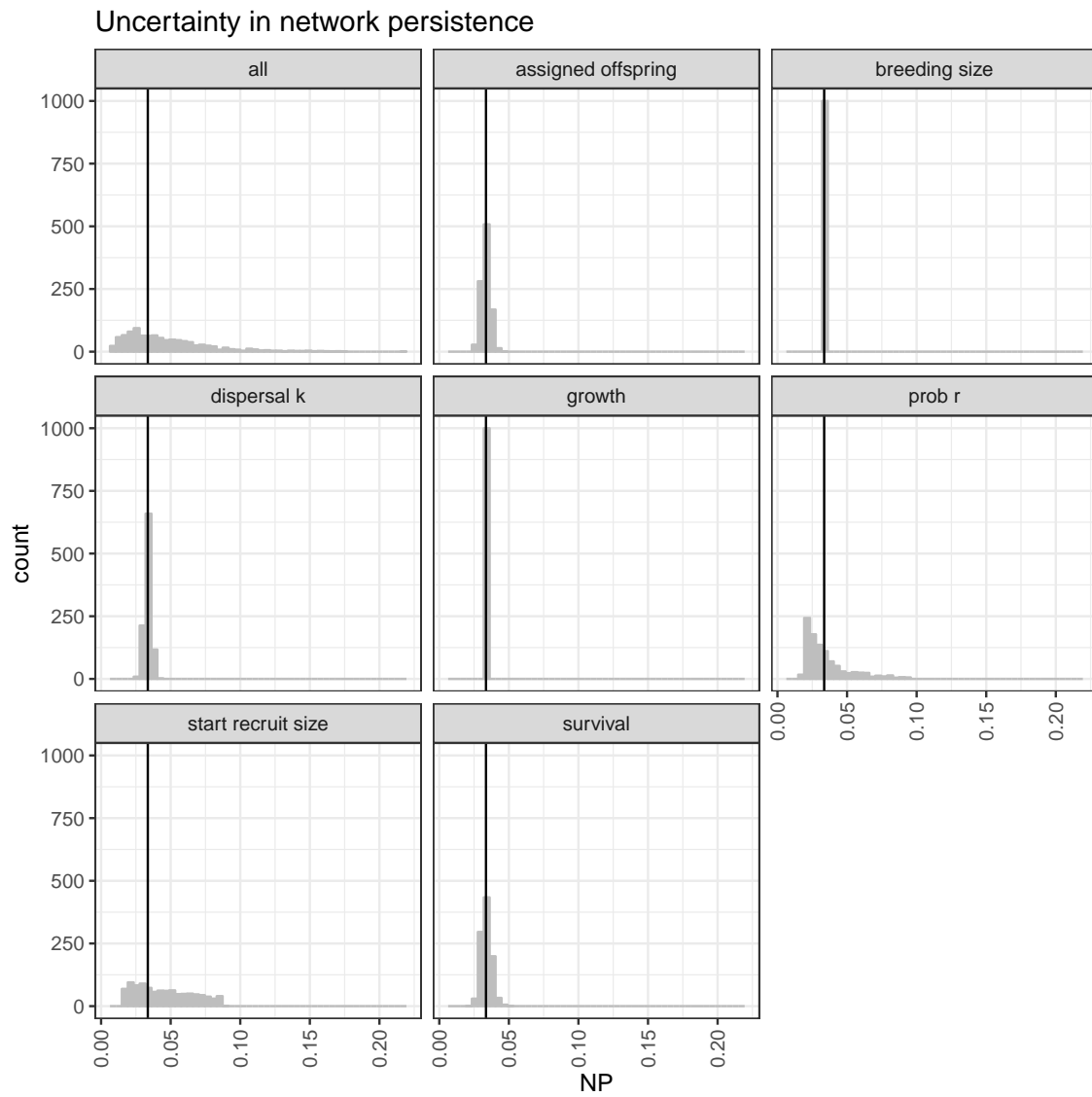


Figure B.6: The contribution of different sources of uncertainty in NP.

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