

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
 96 makes fish easier to relocate for mark-recapture studies and simplifies the exchange between patches to only the dispersal during the larval phase. Patches, whether considered to be the reef patch or the anemone territory of the fish, are clearly discrete
 99 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
 102 make clownfish and other similarly territory-based reef fish useful model systems for studies of metapopulation dynamics and persistence (e.g. Buston and DAloia, 2013; Salles et al., 2015; Johnson et al., 2018).

105 **Field data collection**

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

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

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

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

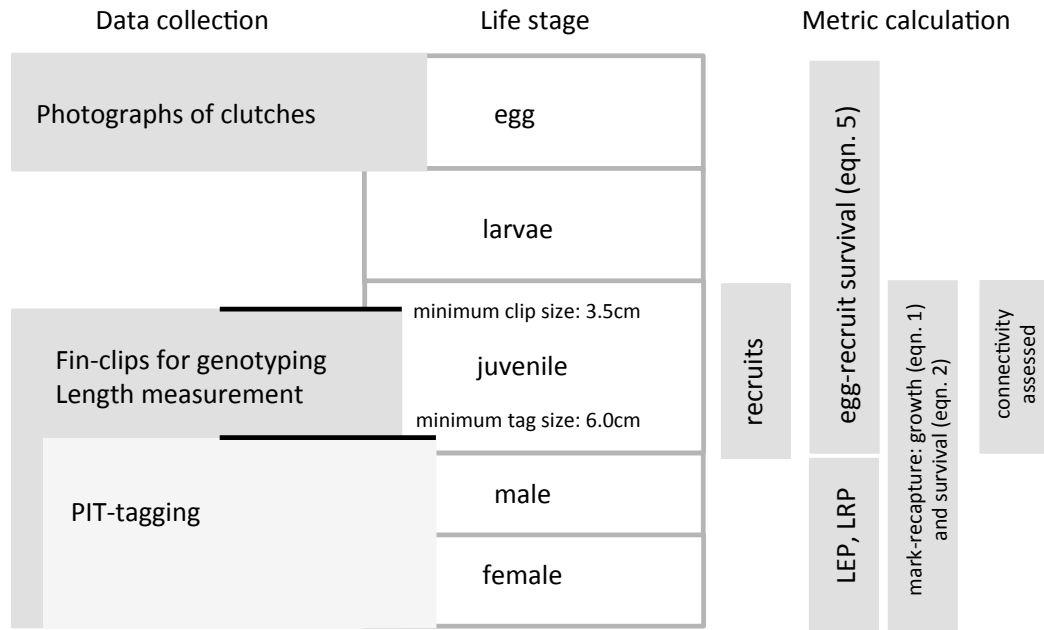


Figure 1: Here, we show the data collected for fish at each life stage (life stage boxes are not scaled by length of stage) and how the empirical data fit into the metric calculations.

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 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 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 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

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 $\beta_l = 2.388$, 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.

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 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 S_e from egg to recruit 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.1, A.2 for details on P_h and P_c estimates, respectively). Our estimated
 survival from egg to recruit is the number of tagged recruits divided by the number
 216 of tagged 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 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
 222 previous year; 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
 225 stage. In theory, it 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
 228 our estimate of egg-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

231 best estimate of the 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 larva 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; Hastings and Botsford, 2006). In our
 focal system, adults do not move among patches so we do not need to consider emmi-
 255 gration and only need to assess whether fish produce enough offspring that survive to
 recruitment to be able to replace themselves and where those offspring travel within
 the metapopulation. We consider three primary metrics to assess whether and how
 258 the population is persistent: 1) lifetime production of recruits, to assess whether the
 population has enough surviving offspring to achieve replacement 2) self-persistence,
 to assess whether any individual patches would be able to persist in isolation with-
 261 out any input from other patches, and 3) network persistence, to assess whether the
 metapopulation is persistent as a connected unit. We explain each metric below in
 detail.

264 Estimated abundance over time

[Add brief section here.]

Lifetime production of recruits

267 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)
270 by multiplying LEP by the estimated survival from egg to recruit S_e :

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

If $LRP \geq 1$, the population has the possibility for replacement; individuals produce
enough surviving offspring, before taking into account the probability of dispersal.

273 If $LRP < 1$, the individuals are not replacing themselves and the population cannot
persist without input from outside patches.

Self-persistence

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

to recruit to assess whether a particular patch i is self-persistent:

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

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

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

Realized connectivity matrix and network persistence

288 We find the probabilities of a recruit dispersing between each set of sites ($p_{i,j}$) by
 integrating the dispersal kernel (eqn. 7) over the distance between each set of sites.
 We then create a realized connectivity matrix C by multiplying the dispersal proba-
 291 bilities by the expected number of recruits an individual produces: $C_{i,j} = LRP \times p_{i,j}$
 (Burgess 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.

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

297 Incorporating uncertainty

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
 300 parameter from a distribution or range. In our results, we show the range of values of

each persistence metric as well as the value with our best estimate of each parameter.

For the dispersal kernel, we keep the shape parameter θ constant and pull the scale
 303 parameter k_d from a set capturing the 95% confidence intervals, which was produced
 during kernel estimation in Catalano et al. (in prep). To capture uncertainty in the
 size of a recruit $\text{size}_{\text{recruit}}$, and therefore the transition of mortality being captured by
 306 egg-recruit survival to being captured by LEP, we pull from a uniform distribution
 over the range of fish sizes (3.5 - 6.0 cm) considered as offspring in the parentage
 analyses (Catalano et al., in prep). We include uncertainty in the size of transition to
 309 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_∞ and
 K , we pull from the full set of estimates using different combinations of recapture
 312 pairs for fish recaptured more than twice. For uncertainty in adult survival, we
 pull from a normal distribution generated using the uncertainty estimated in the
 mark-recapture analysis for both the intercept b_ϕ and the size effect b_a .

315 To incorporate uncertainty in egg-recruit survival, we consider uncertainty in
 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
 318 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)
 321 and the probability of success on each trial is the assignment rate XX of offspring
 from the parentage analysis (Catalano et al., in prep). To represent uncertainty
 in the probability of capturing a fish, we pull values from a beta distribution with

324 parameters α_{P_e} and β_{P_e} , found using the mean and variance of capture probabilities
estimated from recapture dives across sites and sampling seasons (details in A.2).

Results

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

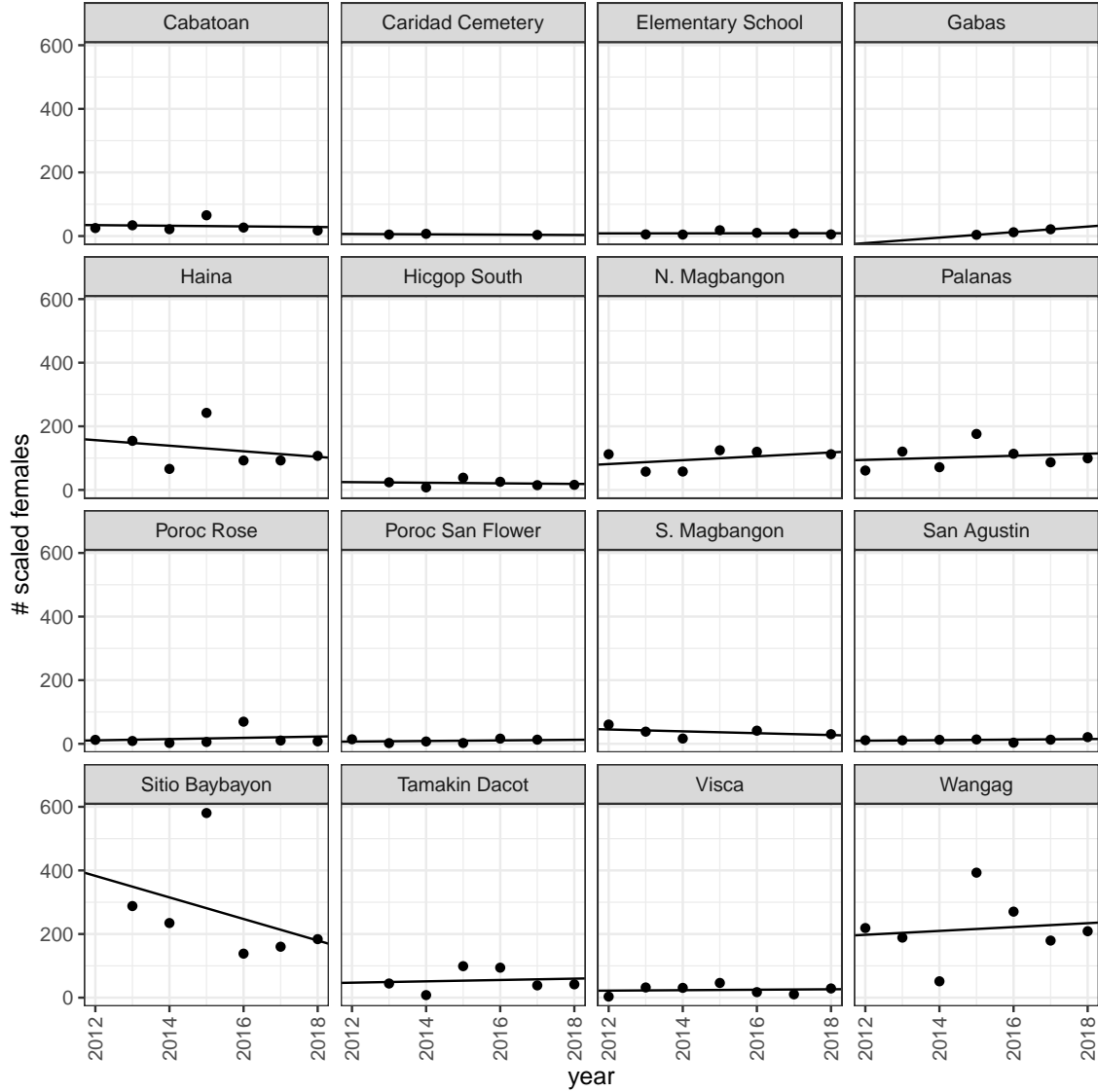


Figure 2: The estimated number of females at each site over the sampling years. The total number of females at each site was estimated by taking the number of females (fish > 5 cm with the yellow pointed tail indicating female) captured at each site in each year and scaling up by the proportion of habitat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

330 From the mark-recapture analysis of tagged and genotyped fish, we estimate mean
values of $L_\infty = 10.58\text{cm}$ (range of estimates 10.39 - 10.75 cm) and $K = 0.928$ (range
of estimates 0.854 - 1.025) for the von Bertalanffy growth curve parameters (Fig. 3b,
333 Table 1). For juvenile and adult (post-recruitment) survival on a log-odds scale, the
best-fit model has a coefficient $b_a = 0.74 \pm 0.060$ SE for the effect of size and an inter-
cept $b_\phi = -4.83 \pm 0.340$ SE. These results suggest that larger fish have higher annual
336 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
intercept $b_{pr} = 17.93 \pm 0.858$ SE, size effect $b_1 = -1.816 \pm 0.080$ SE, and effect of
339 diver distance from the anemone $b_2 = -0.171 \pm 0.021$ SE. The negative effect of both
size and distance suggest that divers are less likely to recapture larger fish and those
at anemones far from areas sampled, with the chance of recapturing an average-sized
342 fish falling below 5% if a diver stays farther than XX from its home anemone [add
the recapture probability plots, like the survival one in Fig. 3, to the appendix and
reference here.]

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

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

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 standard error	
b_a	size effect for adult survival	0.74	± 0.060 standard error	
b_{pr}	intercept for recapture probability from mark-recapture analysis	17.93	± 0.858 standard error	not used in persistence estimates
b_1	size effect for recapture	-1.816	± 0.080 standard error	not used in persistence estimates
b_2	distance effect for recapture	-0.171	± 0.021 standard error	not used in persistence estimates
size _{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:

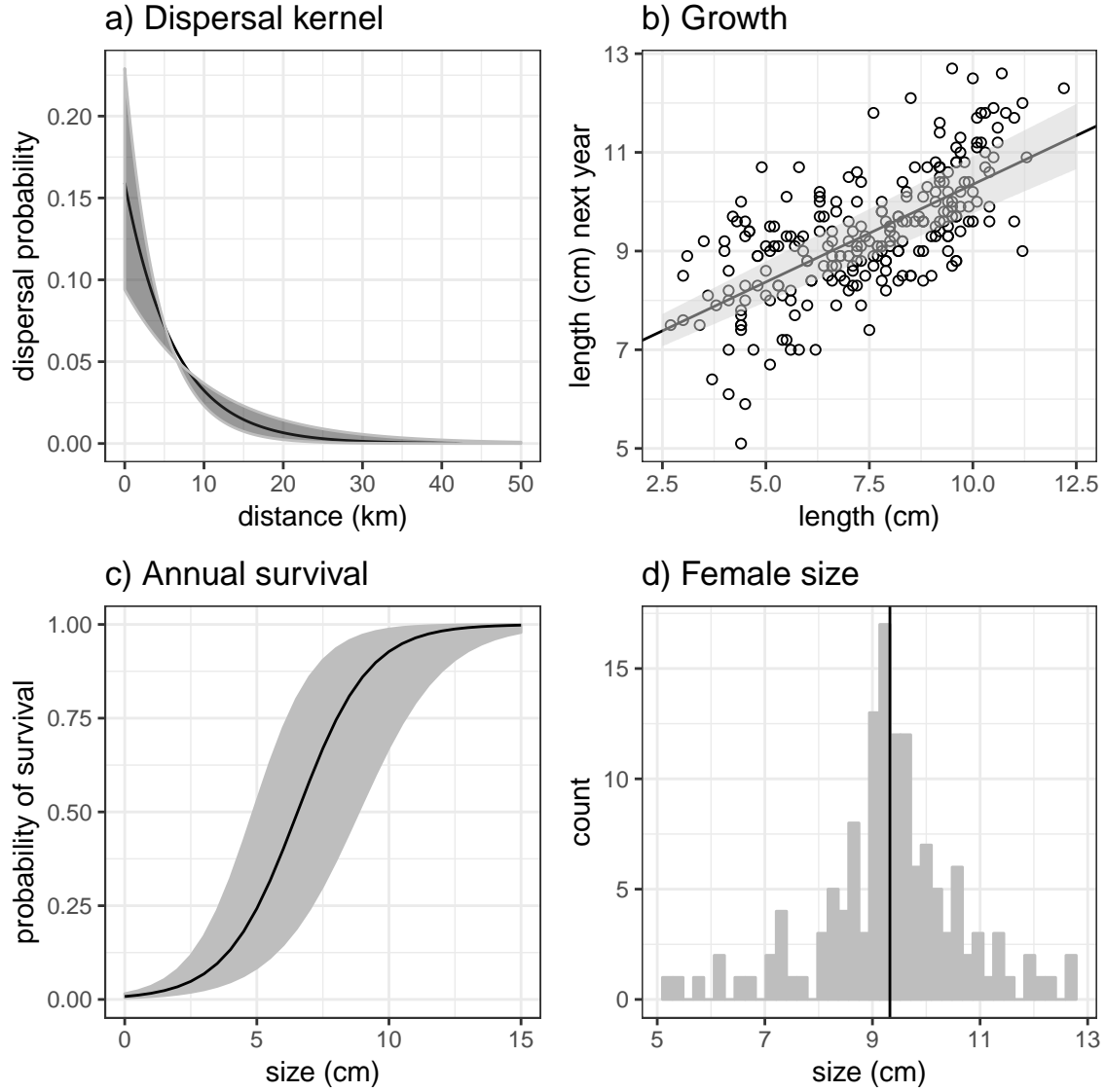


Figure 3: Best estimates (solid black line) and range included for uncertainty (gray) for dispersal (a), growth (b), post-recruit survival (c), and size at female transition (d) parameters.

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

of LEP for 10876, ranging from XX to XX when we consider uncertainty in the inputs (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 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 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 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.

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 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.

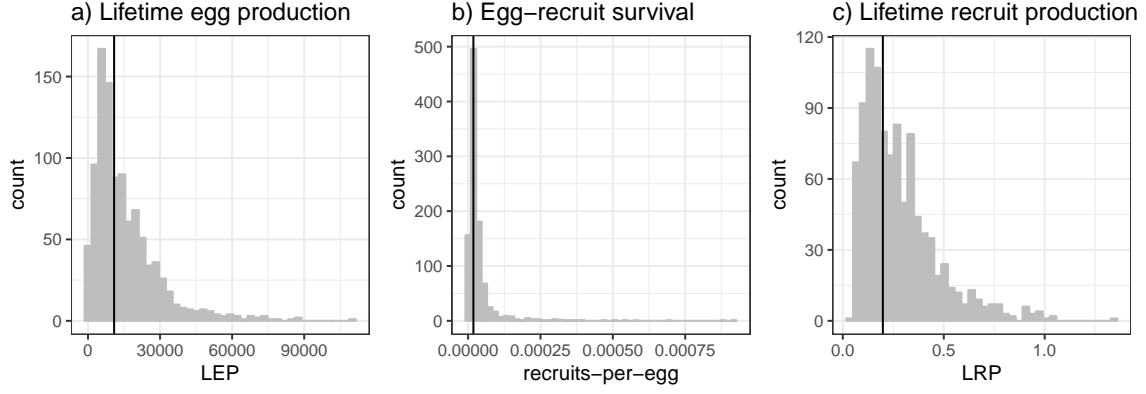


Figure 4: Estimates of a) LEP, b) egg-recruit survival, and c) LRP, showing the best estimate (black solid line) and range of estimates considering uncertainty in the inputs.

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
 372 replacement and only a fraction of that recruitment stays at the natal site, this makes sense. We see the highest values of self-persistence at Haina ($SP = 0.024$) and Wangag ($SP = 0.010$), our two widest sites.

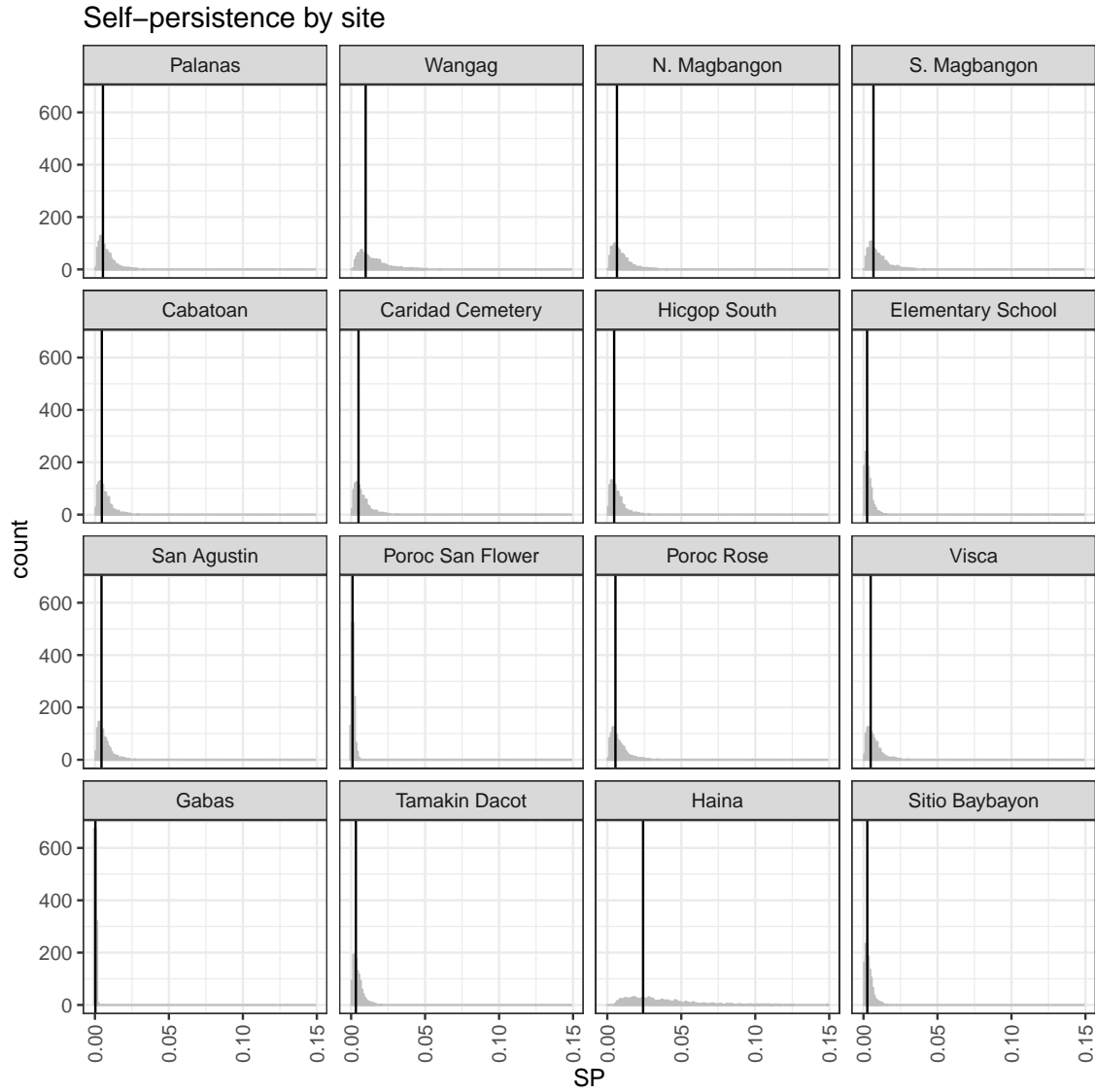


Figure 5: Values of self-persistence at each site, showing the best estimate (black line) and range of estimates considering uncertainty in the input paramters. No site reaches a value of $SP > 1$, necessary to be self-persistent.

375

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

the realized connectivity matrix λ_c 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.

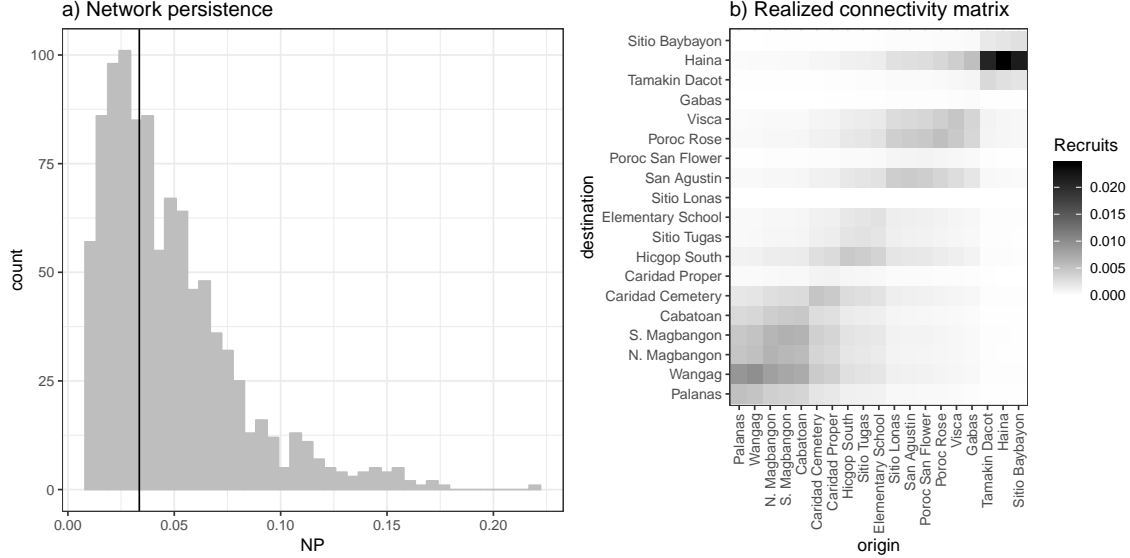


Figure 6: a) Network persistence values, showing the best estimate (black solid line) and range of estimates considering uncertainty. b) The realized connectivity matrix C , with sites arranged from north (Palanas) to south (Sitio Baybayon).

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 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. 7a). When we add in the connectivity, we see a higher value

of λ_c 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 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 estimated value of egg-recruit survival), to $\lambda_c = 1$ and network persistence.

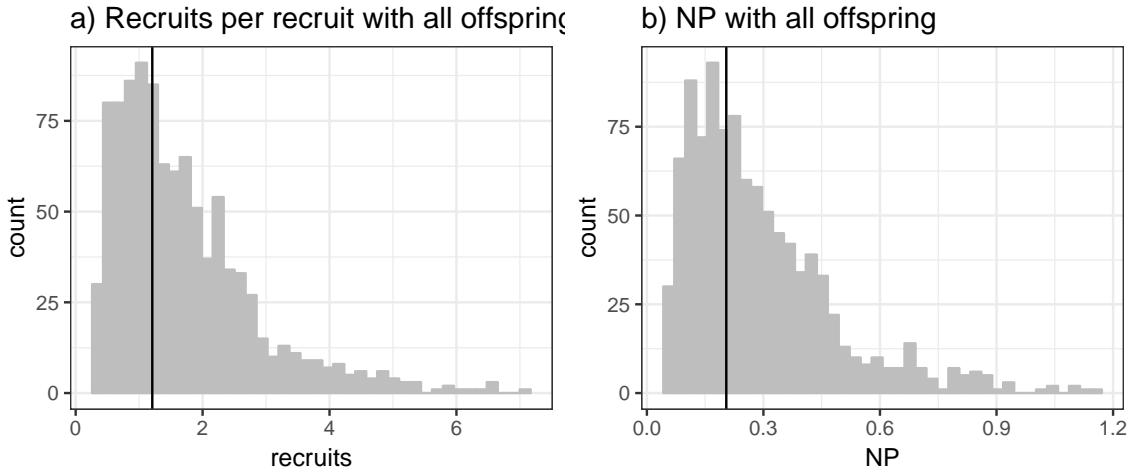


Figure 7: a) Recruits per recruit when we consider all arriving recruits to have originated from our sites. b) Range of values of NP considering all arriving recruits to be offspring from our sites, with the best estimate in a black solid line.

Discussion

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

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
399 but relies on outside immigration to persist.

• 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,
402 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)

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),
408 what we see for persistence when estimate recruits/recruits instead. Context-
tualize this with what other studies have found for these parameters, how
reasonable it would be to get better estimates in the field.

411 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
414 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
417 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
420 about resolving them, whether we would expect to see them.

- Contextualize our parameter estimates with those from other studies (esp. survival, growth, fecundity).

423 Broadening back out:

- What does this mean for moving forward in understanding metapopulation persistence more broadly? Stability in abundance doesn't mean the population
426 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
429 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.

432 Appendix

A Method details

A.1 Proportion of habitat sampled

435 [*Need to add in the details here*]

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

We use mark-recapture data from recapture dives done within a sampling season to
438 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
441 dives and the recapture dives because they are so close in time and that fish do not
change their behavior or reponse to divers, so therefore assume that the probability
of recapturing a fish is the same as the probability of capturing a fish on a sample dive.
444 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
447 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
450 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
453 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 μ_{P_c} and variance V_{P_c} of the set of 14 values to find
456 the appropriate α_{P_c} and β_{P_c} parameters, where

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

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

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 $\beta_{P_c} = 1.13$.
459 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.
462 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

⁴⁶⁵ 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 A1:

B Uncertainty details

B.1 Sensitivity to parameters

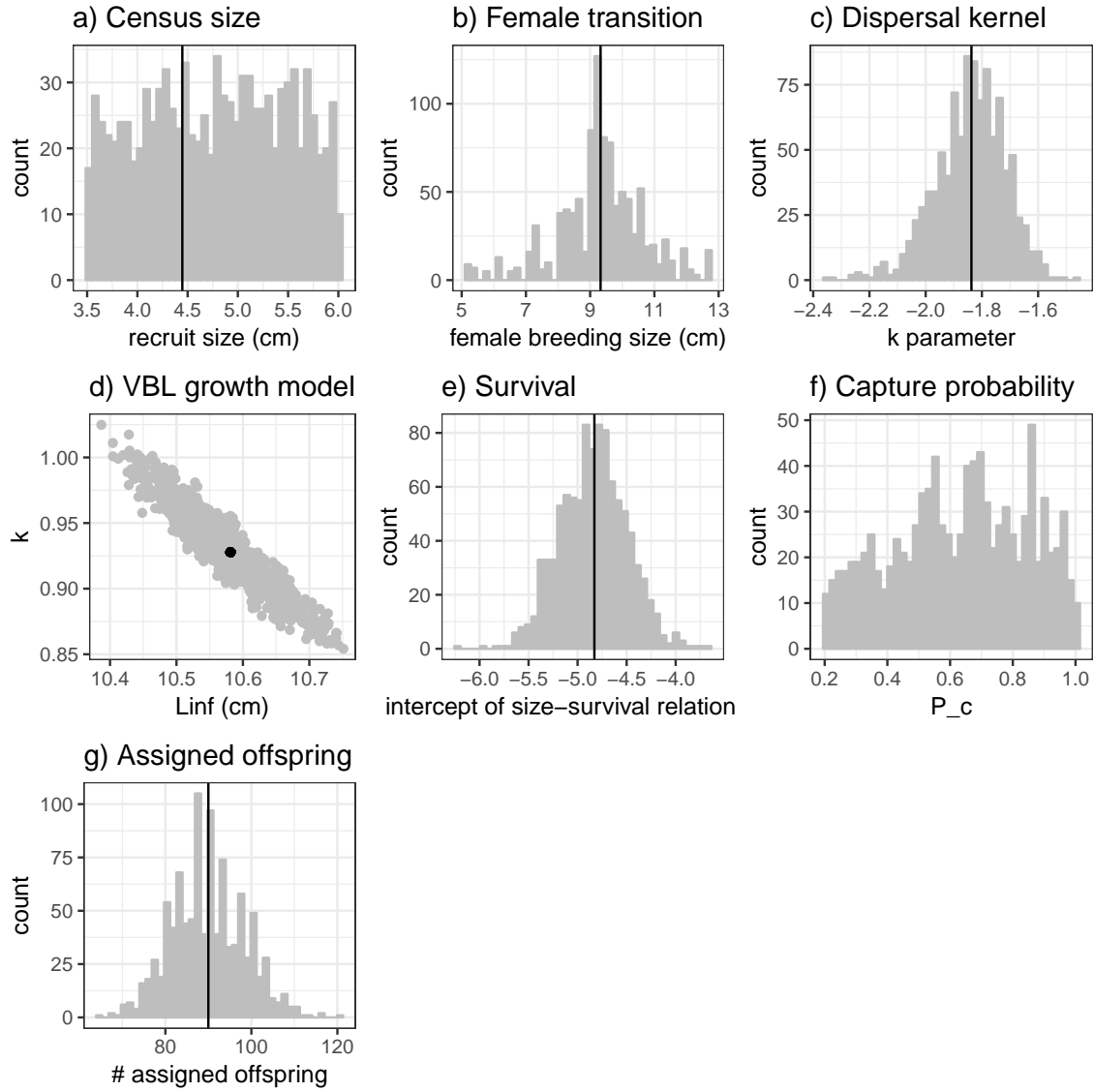


Figure B.1: Range of parameter inputs for uncertainty runs with all uncertainty included: a) $\text{size}_{\text{recruit}}$, the census size at which fish are considered to have recruited after egg-recruit survival occurs; b) L_f , the size at which fish transition from male to female and their reproductive 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;

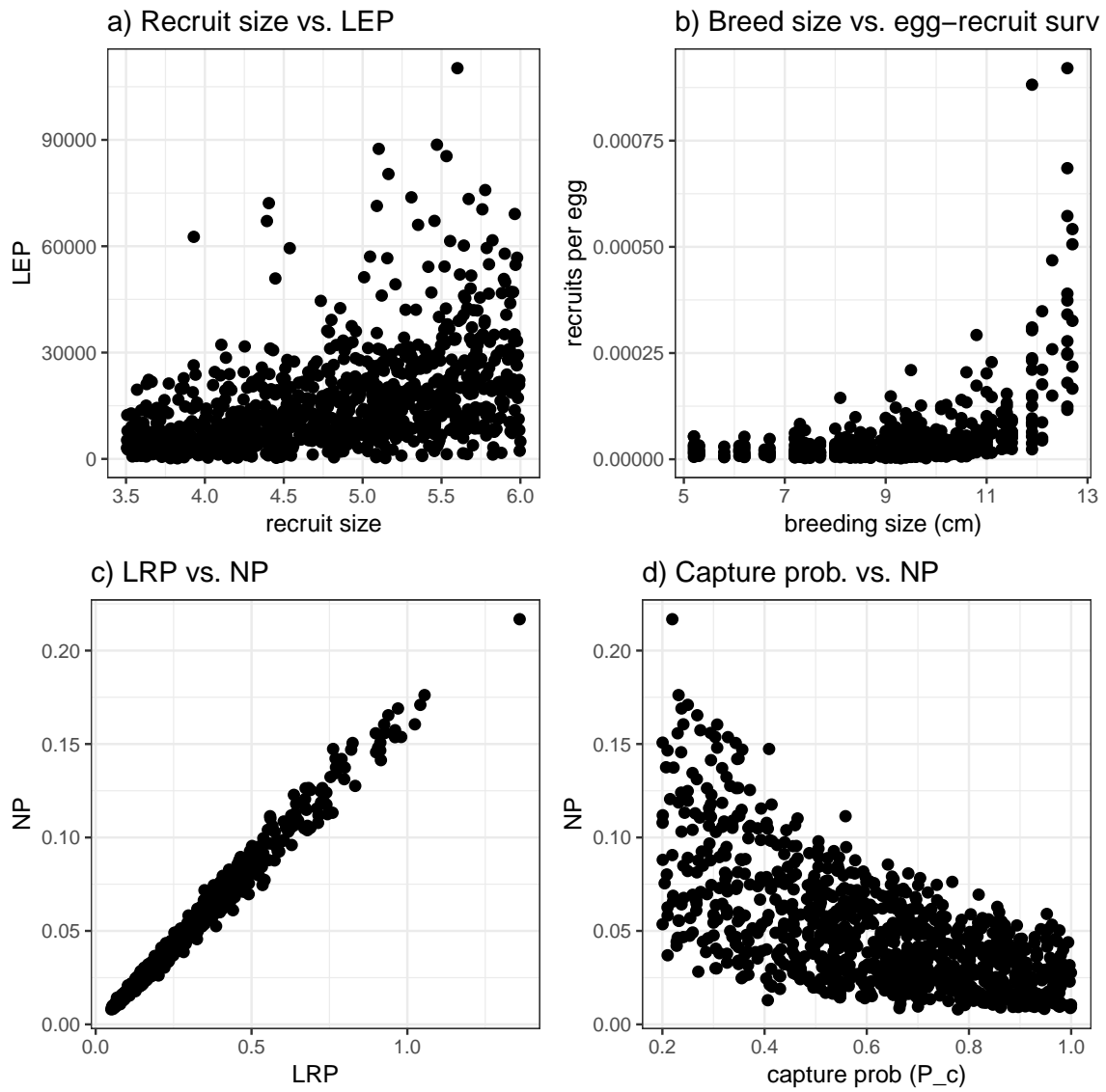


Figure B.2: Relationships among parameters and metrics.

B.2 Effects of different types of uncertainty on metrics

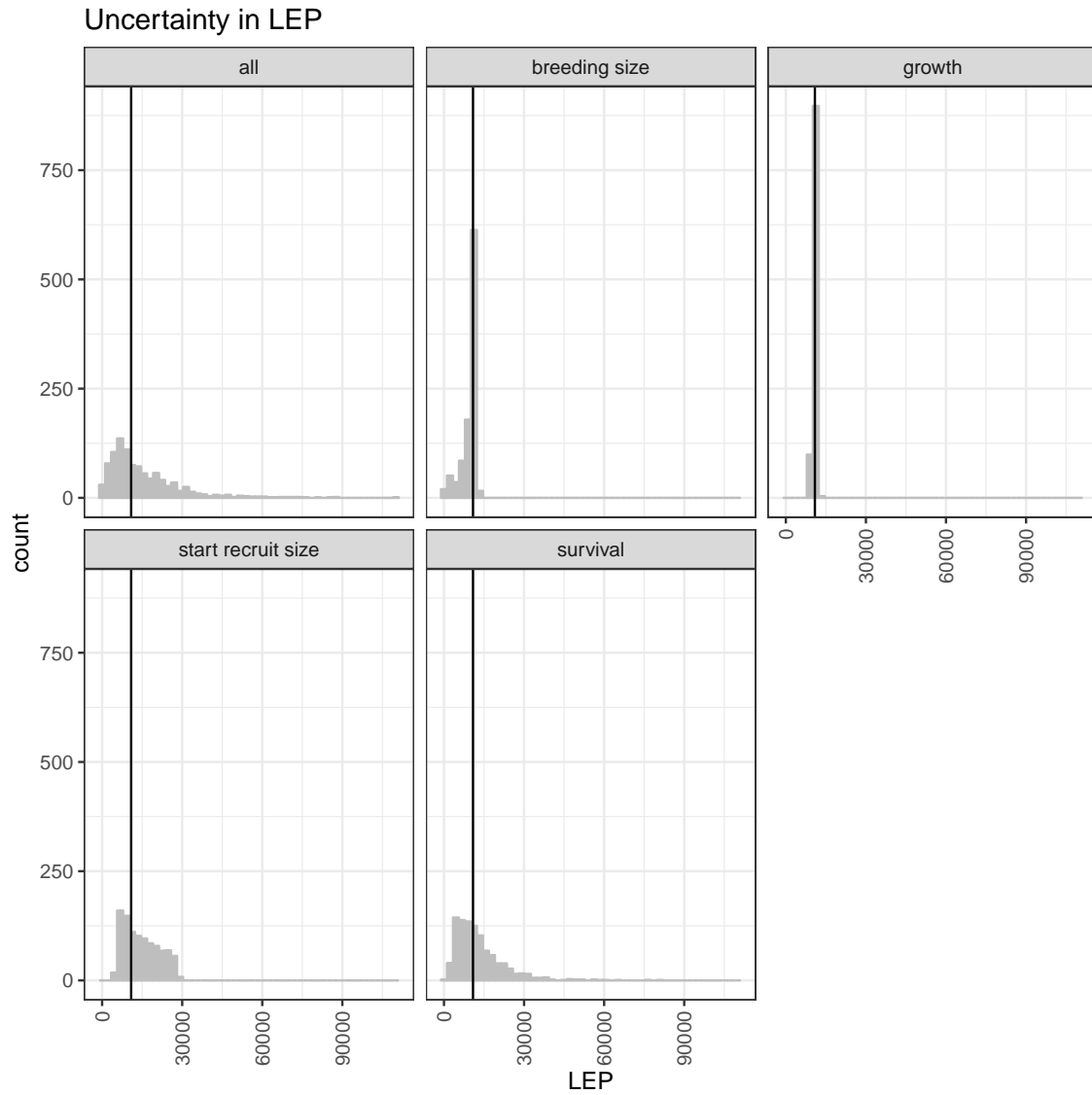


Figure B.3: The contribution of different sources of uncertainty in LEP.

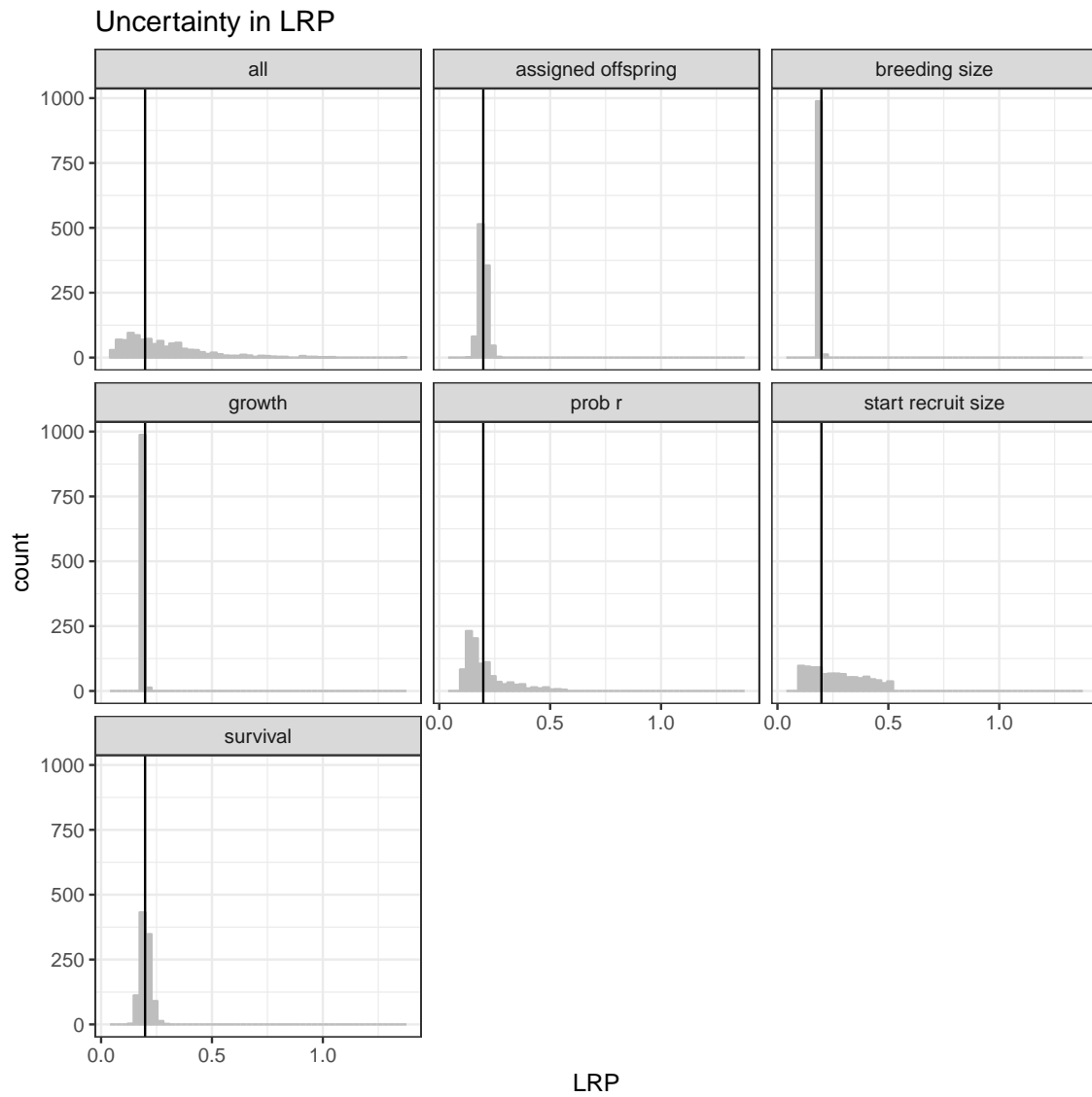


Figure B.4: The contribution of different sources of uncertainty in LRP.

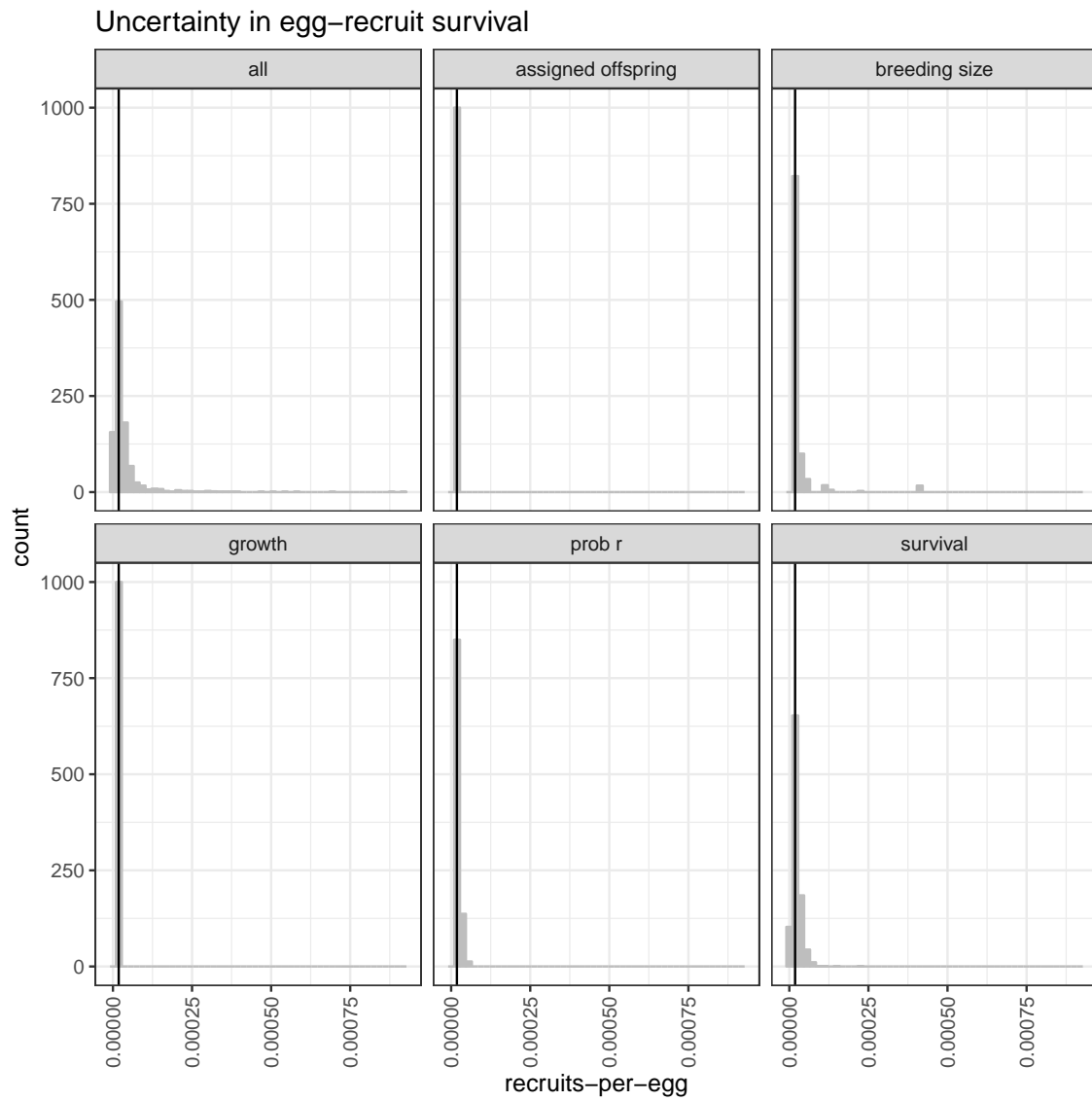


Figure B.5: The contribution of different sources of uncertainty in egg–recruit survival.

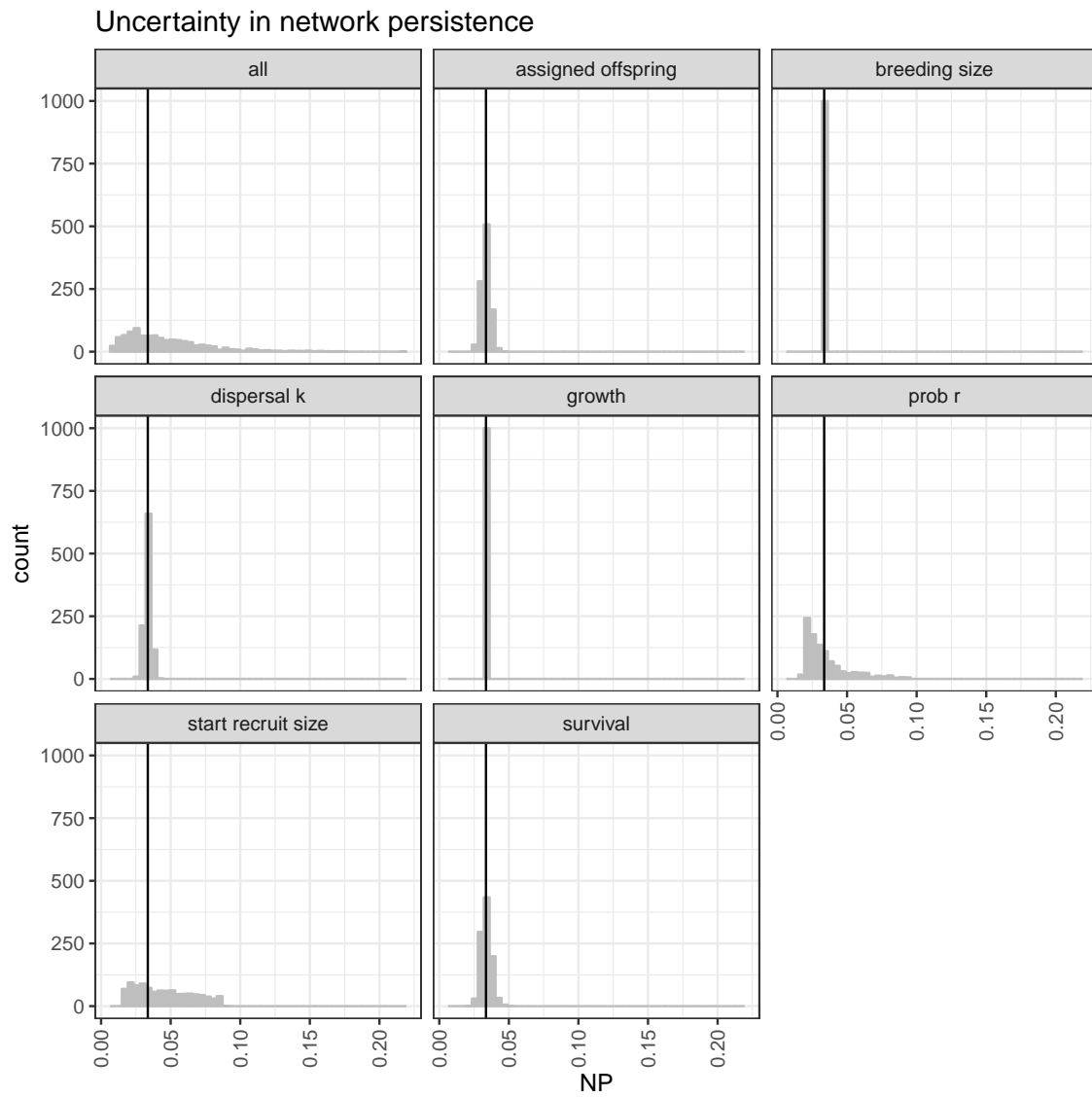


Figure B.6: The contribution of different sources of uncertainty in NP.

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