

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. Metapopulations exist along a continuum, with
6 the balance of extinction and colonization of local patches at one extreme and a balance of immigration and emigration at constantly-occupied local patches at the other (Kritzer and Sale, 2006). Terrestrial metapopulations often show extinction/colonization dynamics (e.g. Hanski, 1998), while local extinction of patches is relatively uncommon in marine metapopulations, where connectivity mostly drives the origin of recruits (Kritzer and Sale, 2006). Assessing levels of connectivity and
9 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
12 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
15 et al., 2010), however, has led to a large body of theory describing how marine
18 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
21 to the next age or stage, their expected fecundity at each stage, and the survival
24 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. Ma-

27 rine larvae were once thought to be well-mixed and dispersed far on ocean currents
(e.g. Roughgarden et al., 1988), suggesting widespread connectivity among patches.
Recent advances in estimating connectivity through natural tags and genetics, how-
ever, suggest that dispersal may be more limited (e.g. D'Aloia et al., 2013) (ADD
30 OTHER EXAMPLE CITATIONS), and local persistence of marine populations is
seeming more possible.

33 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 recruitment
36 to achieve replacement through multi-generational 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 pro-
duced at a patch is retained at the patch for the patch to persist. If one patch is
able to persist, the metapopulation as a whole is persistent. In the second (network
persistence), closed loops of connectivity among at least some of the patches - where
42 individuals from one patch settle at another and 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 challenging to estimate the parameters necessary
45 to understand how actual metapopulations persist, a large work of theory developed
in part to guide marine protected area design helps predict when each type of per-
sistence is likely to occur (i.e., large patches relative to the mean dispersal distance
48 are likely to be self-persistent, Botsford et al., 2001).

New ways of identifying individuals and determining their origins, such as otolith

microchemistry and genetic parentage analysis (e.g. Wang, 2004, 2014) are making
51 it increasingly possible to estimate both the demographic [ADD EXAMPLE CITA-
TIONS] and the connectivity (e.g. Hameed et al., 2016; Almany et al., 2017) param-
eters necessary to assess persistence in real metapopulations. We might expect that
54 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 im-
57 migration. 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
60 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.

63 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 a 30 km stretch
66 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-
tion. With seven years of sampling data, we are able to estimate persistence metrics
69 and replacement over the longer term, rather than just capturing a snapshot of the
population dynamics, and compare with abundance trends. Here, we use a long-
term data set from habitat patches on a continuous set of coastline to understand
72 persistence within a local network.

Methods

Persistence theory and metrics

- 75 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 λ of an age-structured Leslie matrix) (Caswell, 2001; Burgess et al., 2014).
- 78 81 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 84 individuals entering the population balances those lost to mortality or emigration, for a metapopulation to persist (Burgess et al., 2014; Hastings and Botsford, 2006).

We consider three primary metrics to assess whether and how the population 87 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 90 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

93 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)
96 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
100 S_e :

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

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

Self-persistence

A patch is able to persist in isolation (self-persistent) if individuals produce enough
105 offspring that disperse back to the natal patch and survive to recruitment (LRP) to
be able to replace themselves (LR): $LRP \times LR \geq 1$ (Burgess et al., 2014, modified
so that egg-to-recruit survival is included in the LEP term instead of the LR). Our
108 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
111 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:

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

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

Realized connectivity matrix and network persistence

117 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.
We then create a realized connectivity matrix C by multiplying the dispersal proba-
120 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.

123 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).

126 Defining recruit and census stage

When assessing persistence, it is important to consider mortality and reproduction
that occurs across the entire life cycle to determine whether an individual is replacing
129 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 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. 2). 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 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 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).

Study system

We focus on a tropical metapopulation of yellowtail clownfish (*Ampiprion clarkii*, Fig. 1c) 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
153 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).

156 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
159 makes fish easier to relocate for mark-recapture studies and simiplifies 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 dis-
crete and easily delineated, which makes determining the spatial structure of the
162 metapopulation clear. Additionally, clear patches make it easier to assess how much
of the site has been surveyed. These simplifying characterstics in habitat and fish
behavior make clownfish and other similarly territory-based reef fish useful model
165 systems for studies of metapopulation dynamics and persistence (e.g. Buston and
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
168 extend beyond single anemones (CITATION) and strong enough swimming skills
that movement between patch reefs is possible though unusual (CITATION), than
the smaller clownfish *A. percula* commonly used in previous metapopulation studies
171 (e.g. Buston et al., 2011; Salles et al., 2015).

Field data collection

¹⁷⁴ 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. 1a). The sites consist of
rocky patches of coral reef and are separated by sand flats (Fig. 1b). Previous work
¹⁷⁷ 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
¹⁸⁰ from nearby habitat with no substantial reef habitat for at least 20 km.

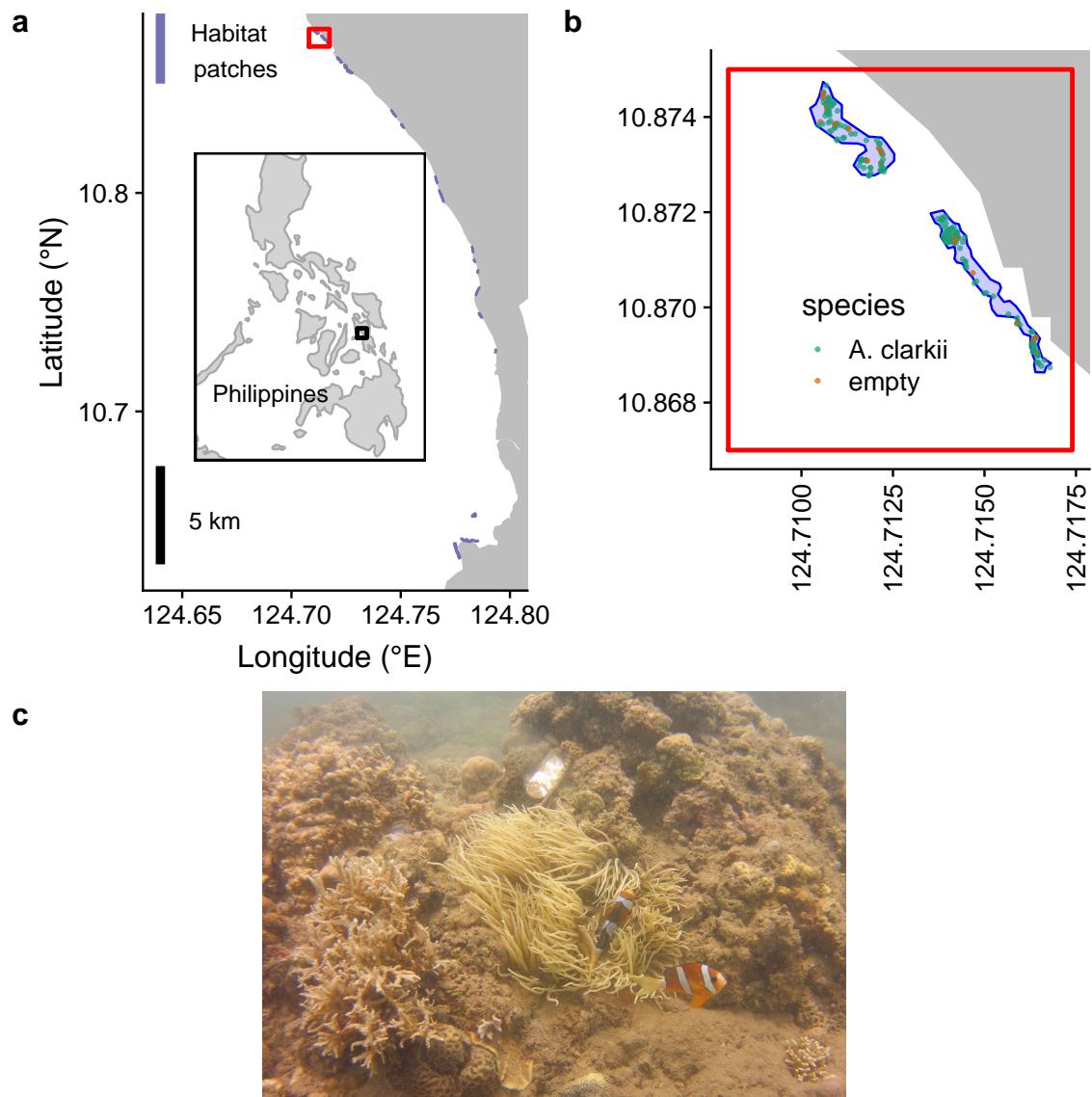


Figure 1: a) A map of the sites along the coast of Leyte in the Philippines. b) A zoomed-in map of Palanas and Wangag to show anemone arrangement for anemones occupied by *A. clarkii* (green) or unoccupied by clownfish (green). c) An example anemone occupied by *A. clarkii* in a typical habitat at the sites.

Since 2012, we have sampled fish and habitat at most of the sites annually (Table 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, 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 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 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

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 (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 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

distance d as measured in kilometers and parameters θ and k_d , which control the
 204 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
 $k_d = -1.84$ (Fig. 4a, estimated in (Catalano et al., in prep)).

207 The dispersal kernel is estimated using fish that have already recruited to a population and survived to be sampled so it gives the relative amount of dispersal given that a fish recruits somewhere, not the probability that a released larva will
 210 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 the middle of the origin site to the closest and farthest bounds of the destination site
 213 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 d_2 is the distance from the middle of A to the far edge of B, is:

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

²¹⁶ Estimating inputs from empirical data

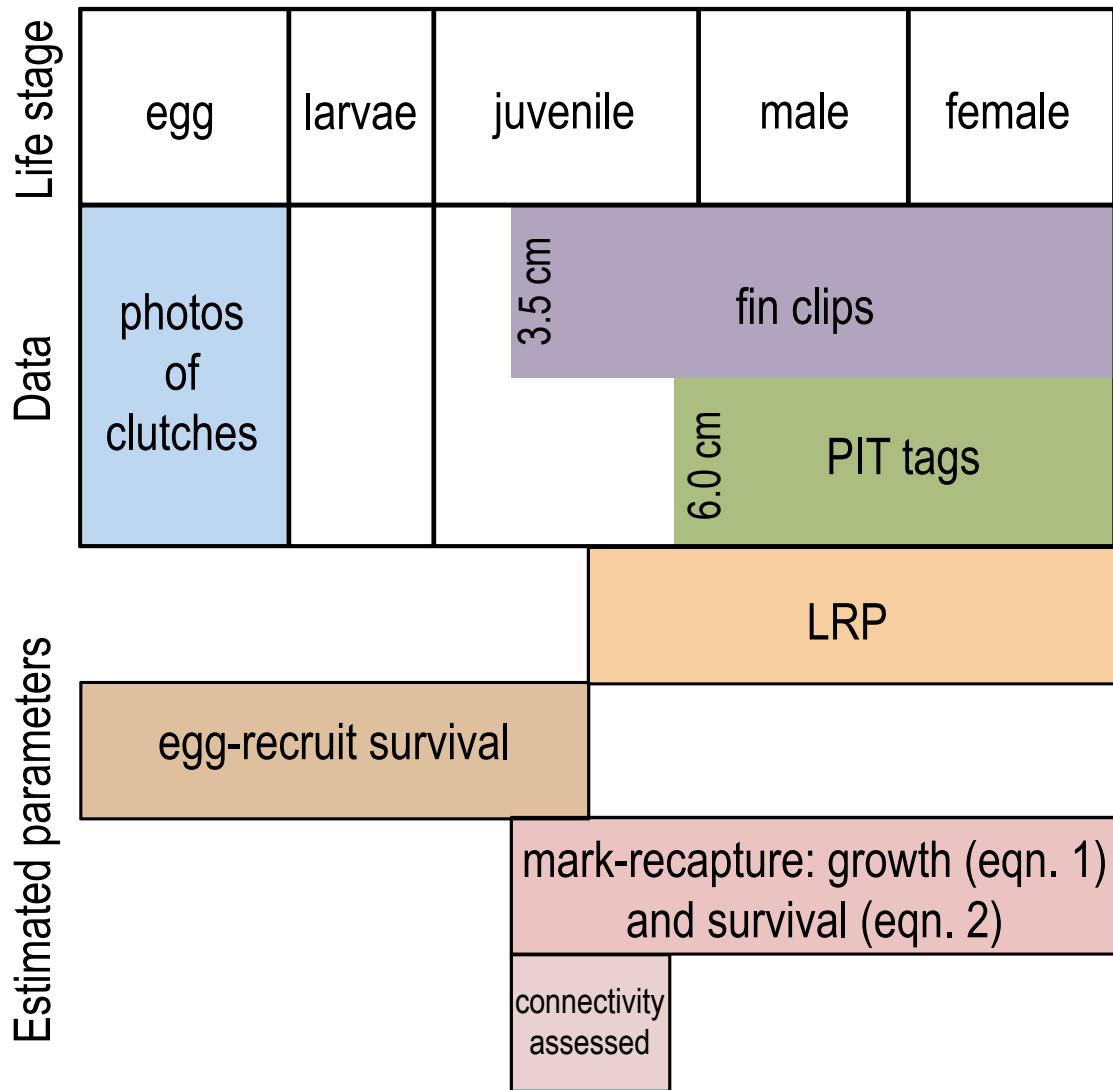


Figure 2: Here, we show the data collected for fish at each life stage (life stage boxes are not scaled by length of stage) and how the empirical data fit into our parameter and metric calculations.

Growth and survival: mark-recapture analyses

We mark fish through both genetic samples and PIT tags, allowing us to estimate
219 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 fish that includes size and stage at each capture time.

222 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 length at a later capture L_{t+1} (Hart and Chute, 2009), where L_∞ is the average
225 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 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 fish that were recaptured after a year (within 345 to 385 days) to estimate L_∞ and K .
228 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 this process 1000 times to generate a distribution.

231 We use the full set of marked fish to estimate annual survival ϕ and probability 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
237 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
240 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
to have a reasonable chance of capturing the fish on it. Therefore, we also consider a
243 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 (Table A2).

246 **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
249 (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:

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

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

255 We only consider reproductive effort once the fish has reached the female stage

and use the average size of first observation as female for recapture fish as the transition size L_f .

258 **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),
261 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
264 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
267 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.

270 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
273 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;
276 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 estimate survival S_e from egg to recruit using the number of recruited offspring we can match back to genotyped parents as surviving individuals from genetically "tagged" eggs in a method similar to that in Johnson et al. (2018). We estimate the number of eggs produced by genotyped parent fish by multiplying the number of genotyped parents ($N_g = 913$) by the expected lifetime egg production of a parent fish LEP_p , using LEP calculated starting with an individual of 6 cm. We make the assumption that all recruited offspring originating from the genotyped parents end up in one of the sites we sample and estimate the total number of offspring that survive to recruit R_t by dividing the number of offspring matches we find ($R_m = 90$) by the proportion of our site habitat we sample cumulatively across all sampling years ($P_h = 0.34$) and the probability of capturing a fish if we sample an anemone P_c (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 of tagged eggs produced:

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

Persistence metrics

For a metapopulation to persist, at least one patch needs to achieve replacement,
 300 where the number of individuals entering the population balances those lost to mor-
 tality or emigration (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-
 gration and only need to assess whether fish produce enough offspring that survive to
 303 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
 306 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-
 309 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.

312 Estimated abundance over time

[Add brief section here.]

Lifetime production of recruits

³¹⁵ 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) ³¹⁸ by multiplying LEP by the estimated survival from egg to recruit S_e :

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

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.

³²¹ If $\text{LRP} < 1$, the individuals are not replacing themselves and the population cannot persist without input from outside patches.

Self-persistence

³²⁴ 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): $\text{LEP} * \text{LR} \geq 1$ (Burgess et al., 2014). Our ³²⁷ 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 ³³⁰ 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

metapopulation as a whole is persistent as well (Hastings and Botsford, 2006; Burgess 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 integrating the dispersal kernel (eqn. 3) 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: $C_{i,j} = LRP \times p_{i,j}$ (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.

Network persistence requires that the largest real eigenvalue of the realized connectivity 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).

Incorporating uncertainty

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

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

For the dispersal kernel, we keep the shape parameter θ constant and pull the scale
351 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 size_{recruit}, and therefore the transition of mortality being captured by
354 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
357 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
360 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 .

363 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
366 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)
369 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

³⁷² parameters α_{P_c} and β_{P_c} , found using the mean and variance of capture probabilities estimated from recapture dives across sites and sampling seasons (details in A.2).

Results

³⁷⁵ Our estimated abundance of females at each site over time is relatively constant [*add some sort of actual analysis here*] (Fig. 3), suggesting that our sample populations are stable over time.

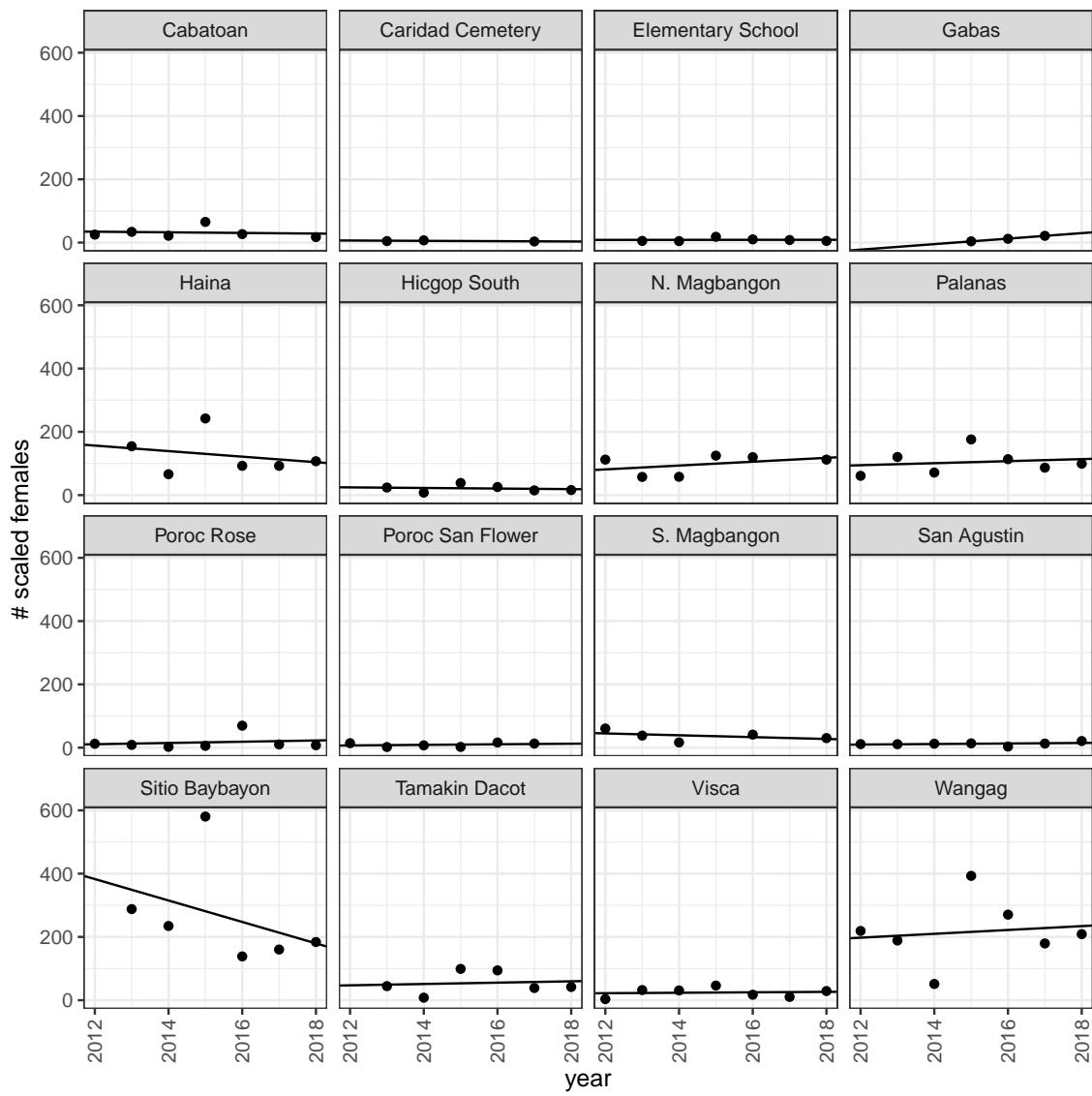


Figure 3: The estimated number of females at each site over the sampling years. The total number of females at each site was estimated by taking the number of females (fish > 5 cm with the yellow pointed tail indicating female) captured at each site in each year and scaling up by the proportion of habitat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

378 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. 4b,
381 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
384 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
387 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
390 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. 4, to the appendix and
reference here.]

393 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. 4d). [*Contextualize these values.*]

[*Not sure where to put this table - kind of a methods/results hybrid, or if it
396 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_{p_r}	intercept for recapture probability from mark-recapture analysis	17.93	± 0.858 standard error	not used in persistence estimates
b_1	size effect for re-capture	-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
$\text{size}_{\text{recruit}}$	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:

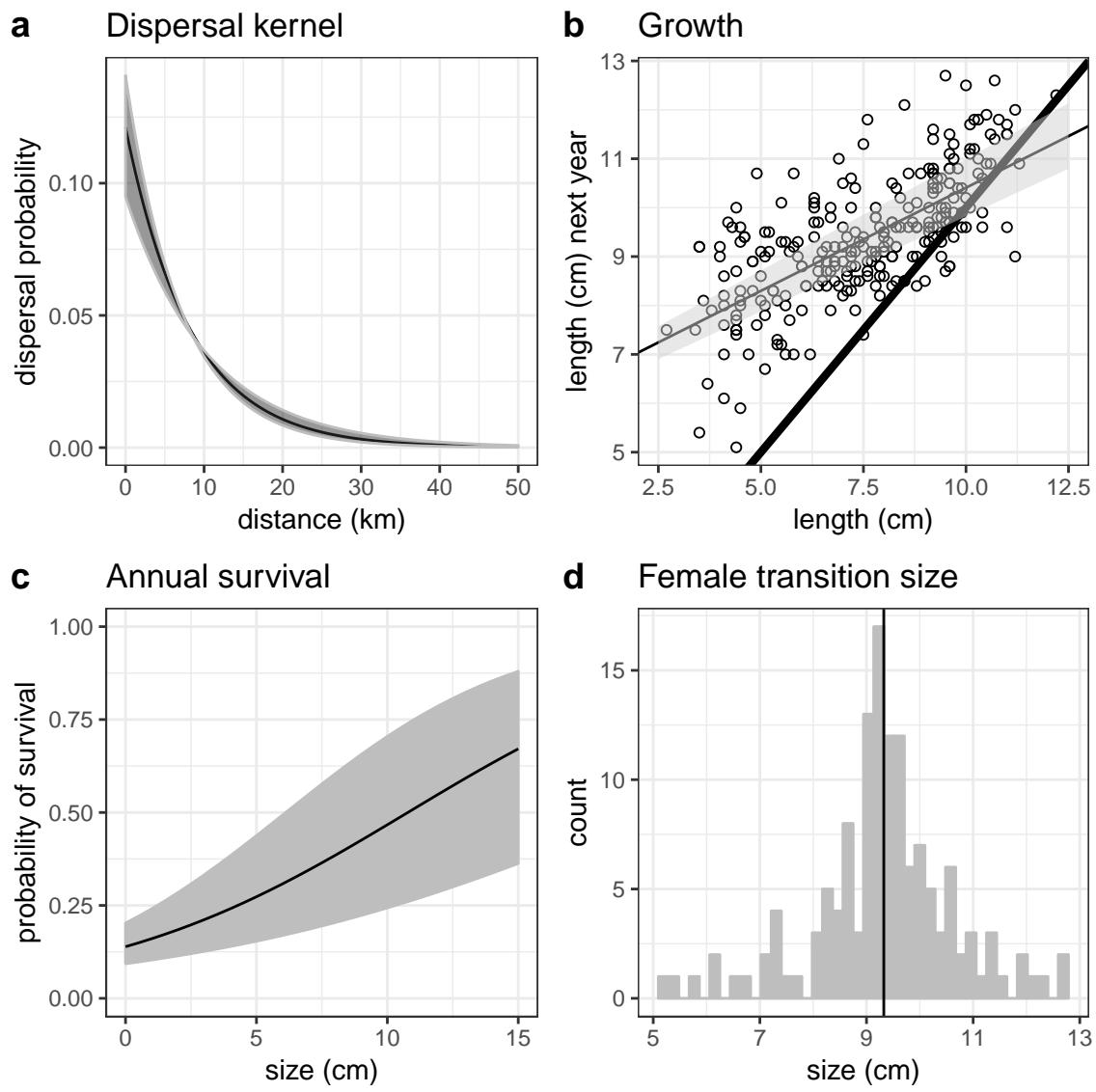


Figure 4: Best estimates (solid black line) and range included for uncertainty (gray) for dispersal (a), growth (b), post-recruit survival (c), and size at female transition (d) parameters.

399 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. 5a). The size at recruitment - the census point between egg-recruit survival and LEP - has the most effect on the value of LEP (Fig. B.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. 5b). Uncertainty in the size of transition to breeding female L_f has the largest effect on egg-recruit survival (Fig. B.6); 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.

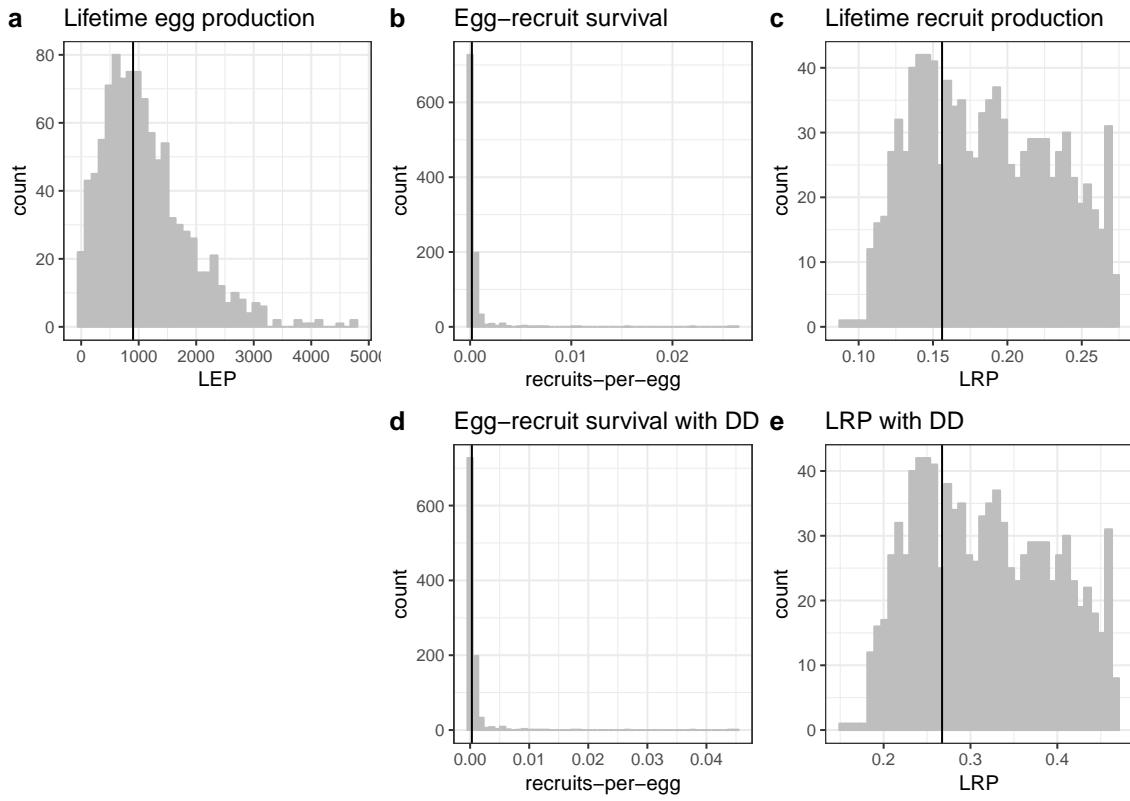


Figure 5: Estimates of a) LEP, b) egg-recruit survival, and c) LRP, showing the best estimate (black solid line) and range of estimates considering uncertainty in the inputs.

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

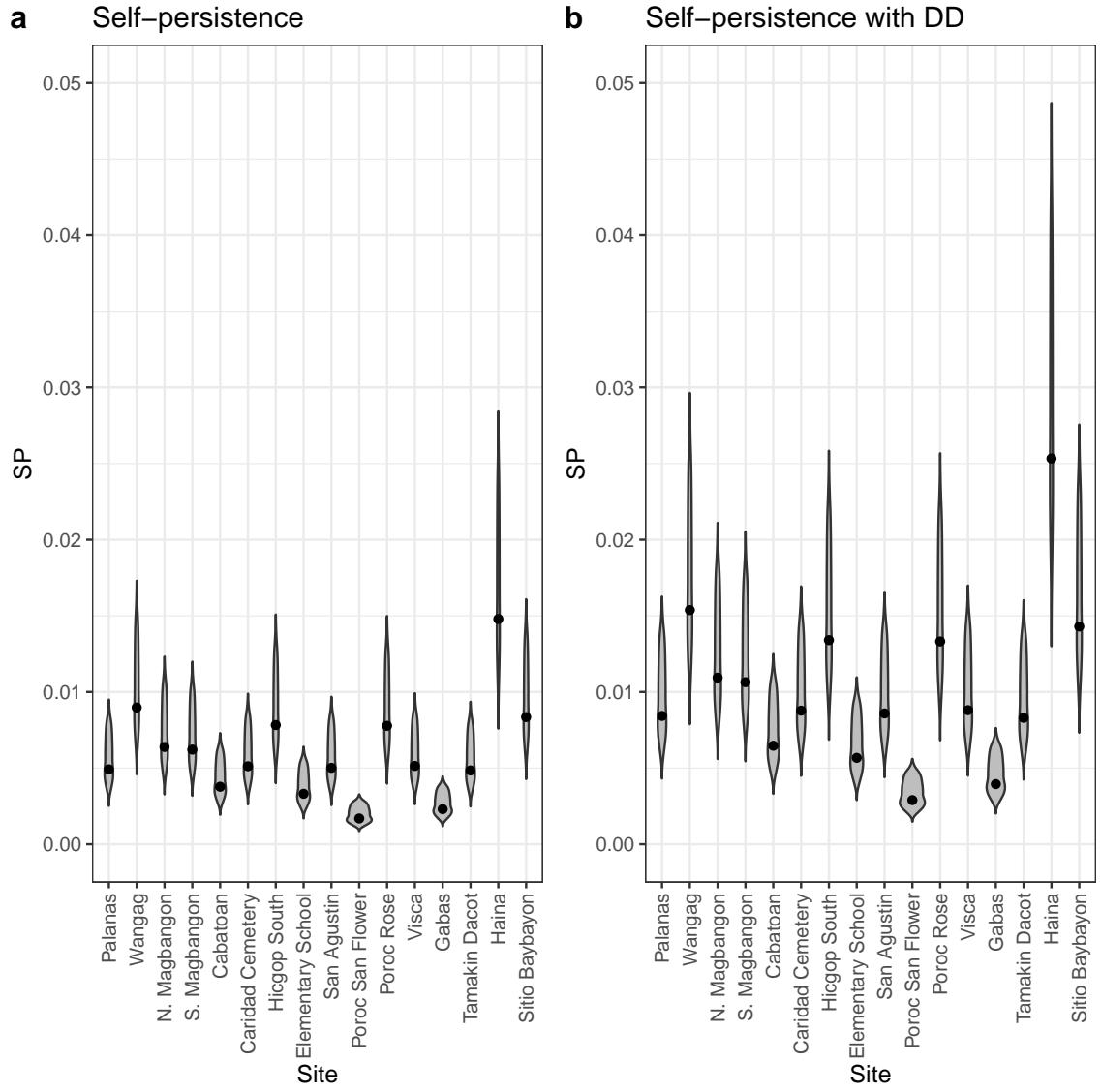


Figure 6: Values of self-persistence at each site, showing the best estimate (black point) and range of estimates considering uncertainty in the input parameters. No site reaches a value of $SP > 1$, necessary to be self-persistent.

423

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. 7a). We see that most of the connectivity occurs among
426 the sites in the northern part of our sample area, from Palanas to Caridad Cemetery.

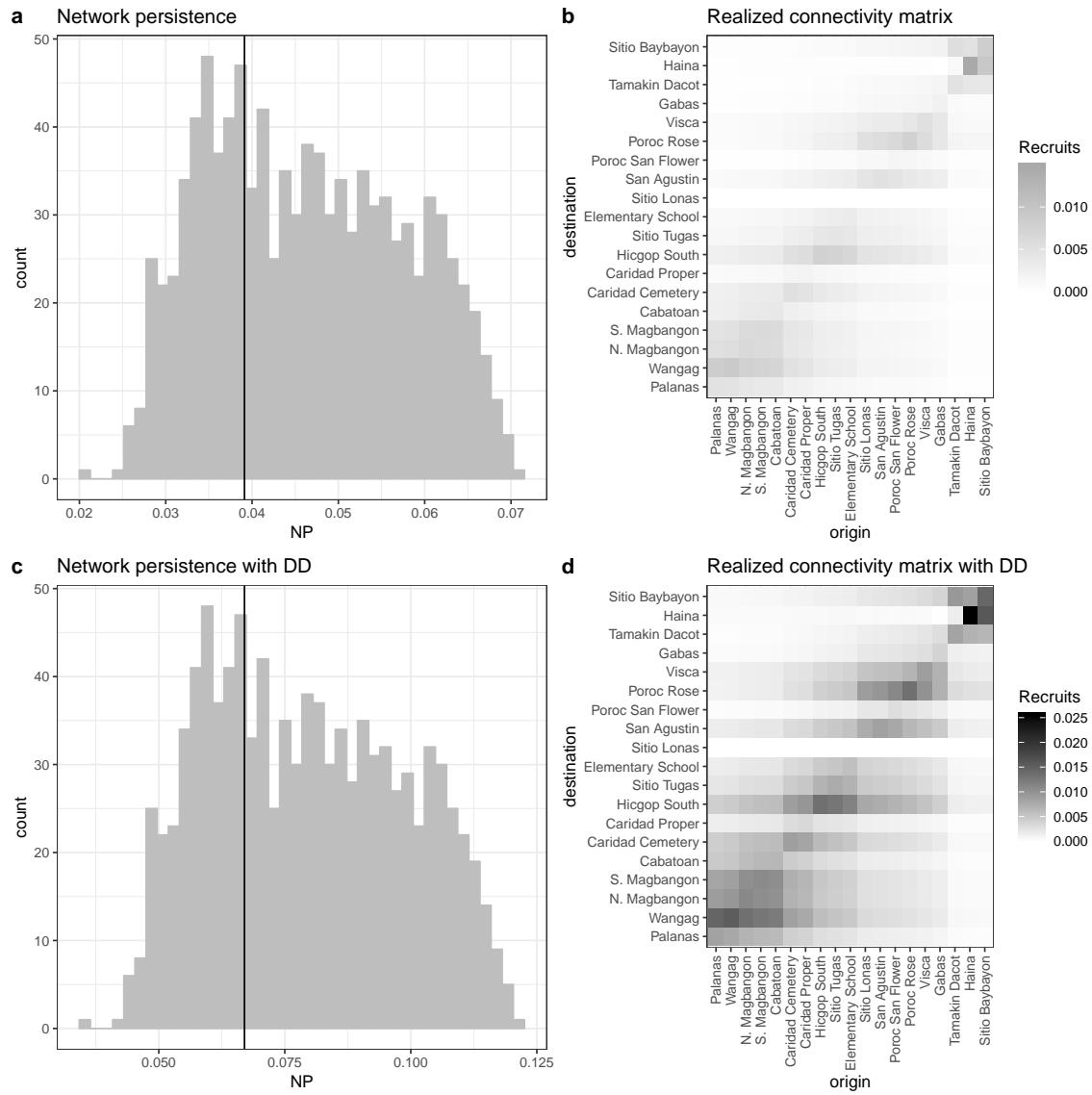


Figure 7: a) Network persistence values, showing the best estimate (black solid line) and range of estimates considering uncertainty. b) The realized connectivity matrix C , with sites arranged from north (Palanas) to south (Sitio Baybayon).

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
429 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
432 for replacement (Fig. 8a). 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. 8b). We see more of the distribution of estimates above 1, however,
435 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
438 of LEP or a value of LEP of XX with our estimated value of egg-recruit survival),
to $\lambda_c = 1$ and network persistence.

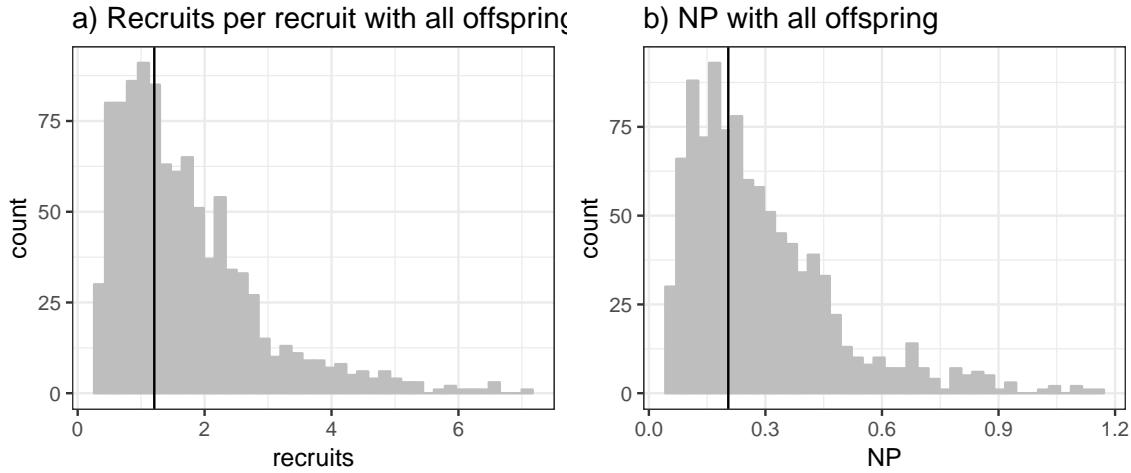


Figure 8: a) Recruits per recruit when we consider all arriving recruits to have originated from our sites. b) Range of values of NP considering all arriving recruits to be offspring from our sites, with the best estimate in a black solid line.

Discussion

⁴⁴¹ We do not see evidence for persistence in our metric estimates, either self-persistence where an individual site could persist alone or network persistence with exchange among sites. The abundances through time at our sites are relatively constant,

⁴⁴⁴ however, suggesting that the population at our sites is stable but relies on input of recruits from outside sites to persist. The portion of coastline we sampled is likely a portion of a larger metapopulation.

⁴⁴⁷ Big picture: What do our results mean for persistence in this system and our understanding of metapopulations generally?

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

450 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
453 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,
456 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)

459 • 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),
462 what we see for persistence when estimate recruits/recruits instead. Contextualize this with what other studies have found for these parameters, how
reasonable it would be to get better estimates in the field.

465 Persistence criteria, such as those detailed in Hastings and Botsford (2006) and
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
468 low abundances (CITATIONS, with the exception of xx density-dependence, like the
allee effect) so is not explicitly considered in persistence metrics. In real populations,
however, it can be challenging to estimate density-independent demographic rates,
471 as density-dependence is occurring in the population as it is sampled. In *A. clarkii*,

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, 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-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 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, which would increase LRP.

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, 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).

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
495 to settle without being chased off by already-settled recruits). But is it high
enough?

- Discuss site-specific demographic rates, why we don't estimate them in our system,
498 the importance they play in other studies, what we might need to go about resolving them, whether we would expect to see them.
- Contextualize our parameter estimates with those from other studies (esp. survival, growth, fecundity).
501

Broadening back out:

- What does this mean for moving forward in understanding metapopulation persistence more broadly? Stability in abundance doesn't mean the population would be able to persist in isolation. Area required seems to be much wider than dispersal kernel spread (particularly if LRP production is right around replacement). Even areas of habitat along a linear coastline seem to be drawing much of their recruitment from a larger surrounding area - even though we see some local retention, maybe broader connectivity is still the story in terms of receiving enough recruitment to persist.
504
507
510

Appendix

A Method details

513 A.1 Proportion of habitat sampled

We used tagged anemones to estimate the proportion of habitat sampled at each site in each year. We tagged each anemone with *A. clarkii*, using metal tags starting 516 in the spring of 2015. The metal tags are relatively permanent and easy to re-sight so we consider the total number of metal tags at each site to be the total number 519 of habitat anemones. We then divide the number of tagged anemones visited in a particular year by the total number of metal tags at 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 522 across the site - areas we did not visit are likely to have a lower density of anemones than the areas we did sample.

Add details about how sometimes it is >1 if the site doesn't have metal tags?

525 [Need to add in the details here]

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

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

Add in description

Proportion of dispersal kernel area sampled

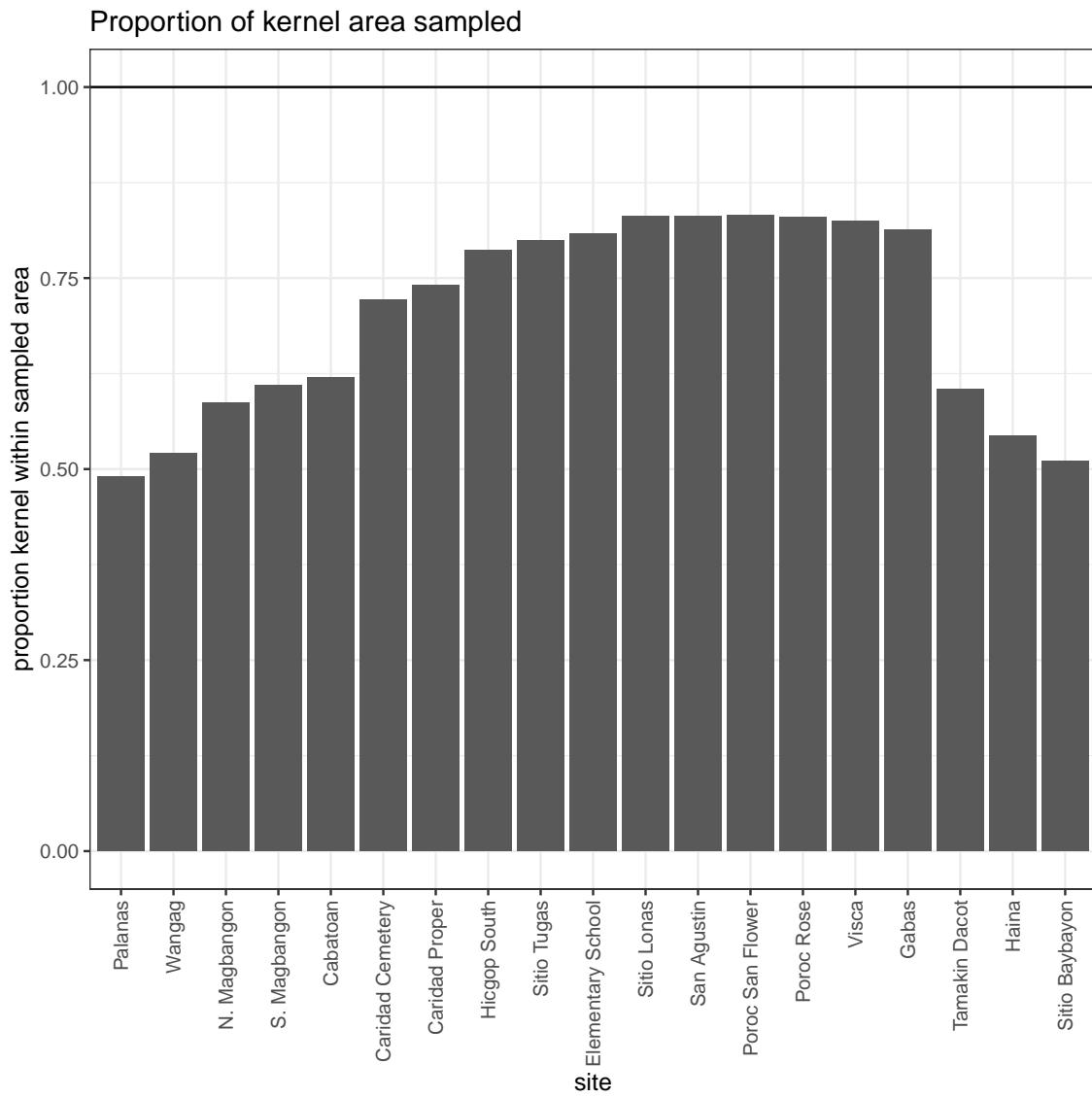


Figure A.1: Proportion of the dispersal kernel area from the center of each site covered by our sampling.

528 **A.2 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), 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 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. 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 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 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 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 the appropriate α_{P_c} and β_{P_c} parameters, where

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

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

549 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
 552 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
 555 the length of the number of runs.

A.3 Full set of MARK models

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:

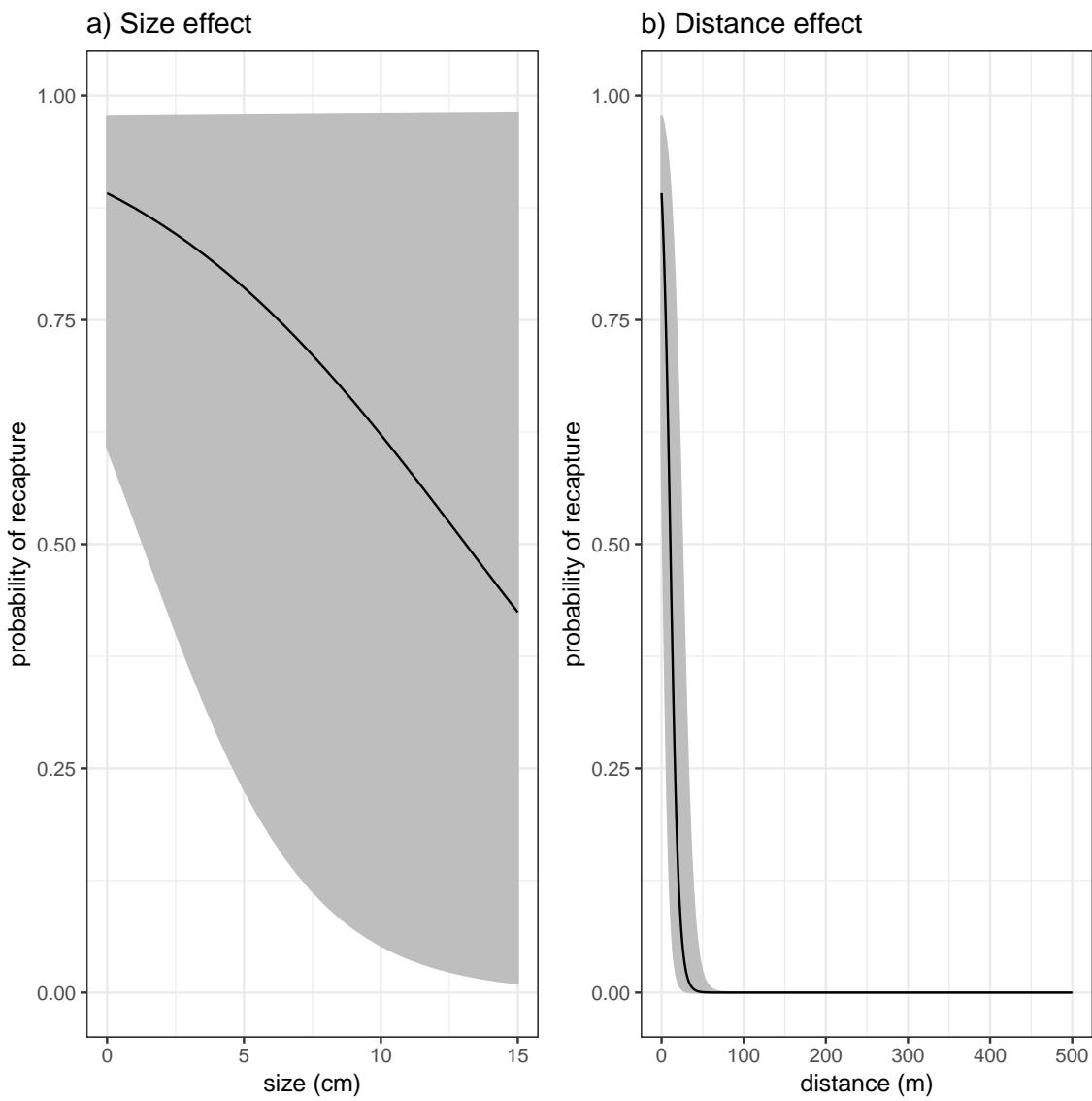


Figure A.2: Effects of a) fish size and b) minimum distance between divers and the anemone where the fish was first caught on the probability the fish will be recaptured, estimated along with survival in a mark-recapture analysis. Size has a slightly negative effect on the probability of recapture -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

558 **B Uncertainty details**

B.1 Sensitivity to parameters

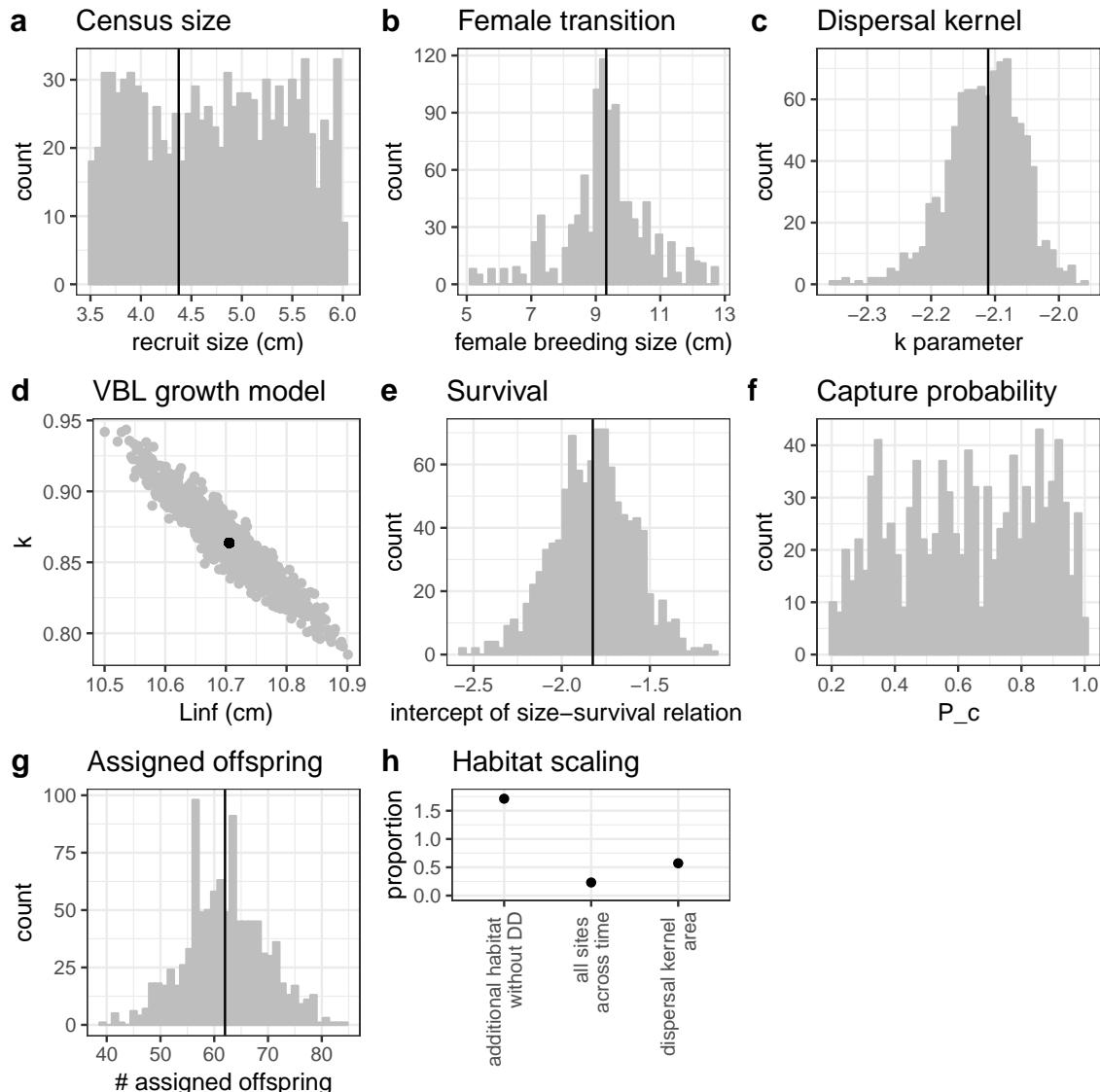


Figure B.1: Range of parameter inputs for uncertainty runs with all uncertainty included: a) $\text{size}_{\text{recruit}}$, the census size at which fish are considered to have recruited after egg-recruit survival occurs; b) L_f , the size at which fish transition from male to female and their reproductive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

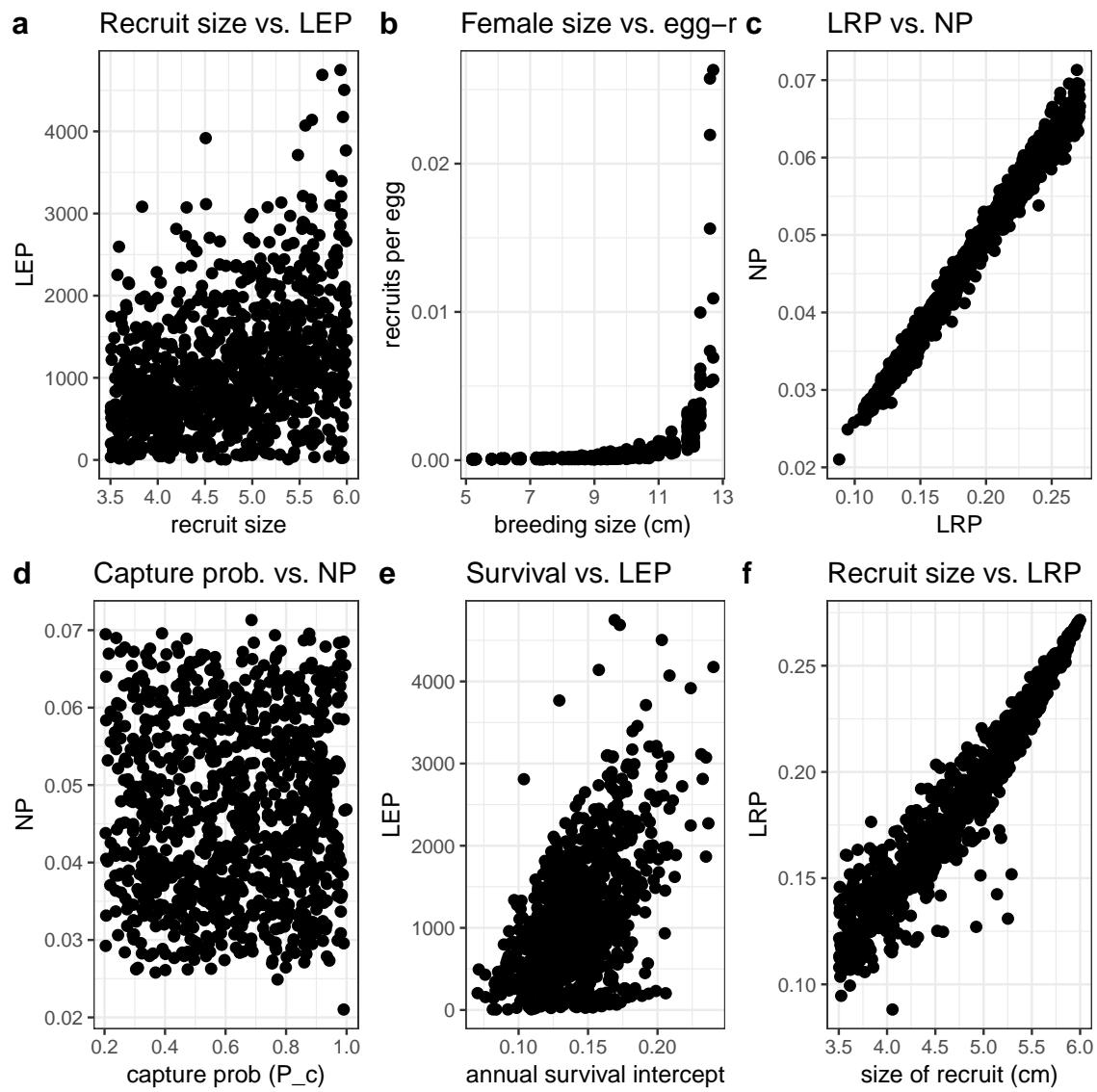


Figure B.2: Relationships among parameters and metrics.

B.2 Effects of different types of uncertainty on metrics

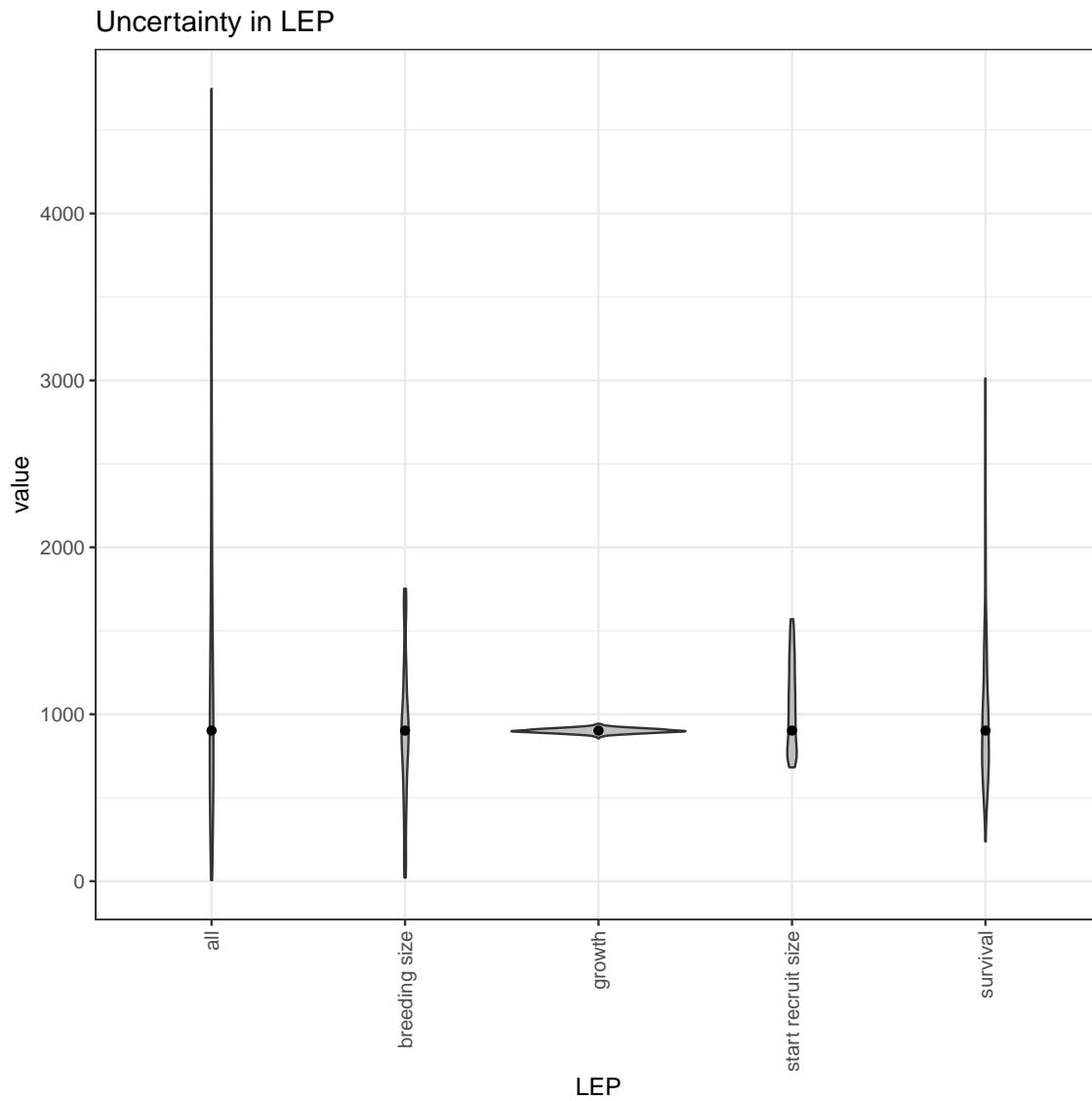


Figure B.3: The contribution of different sources of uncertainty in LEP.

Uncertainty in LRP

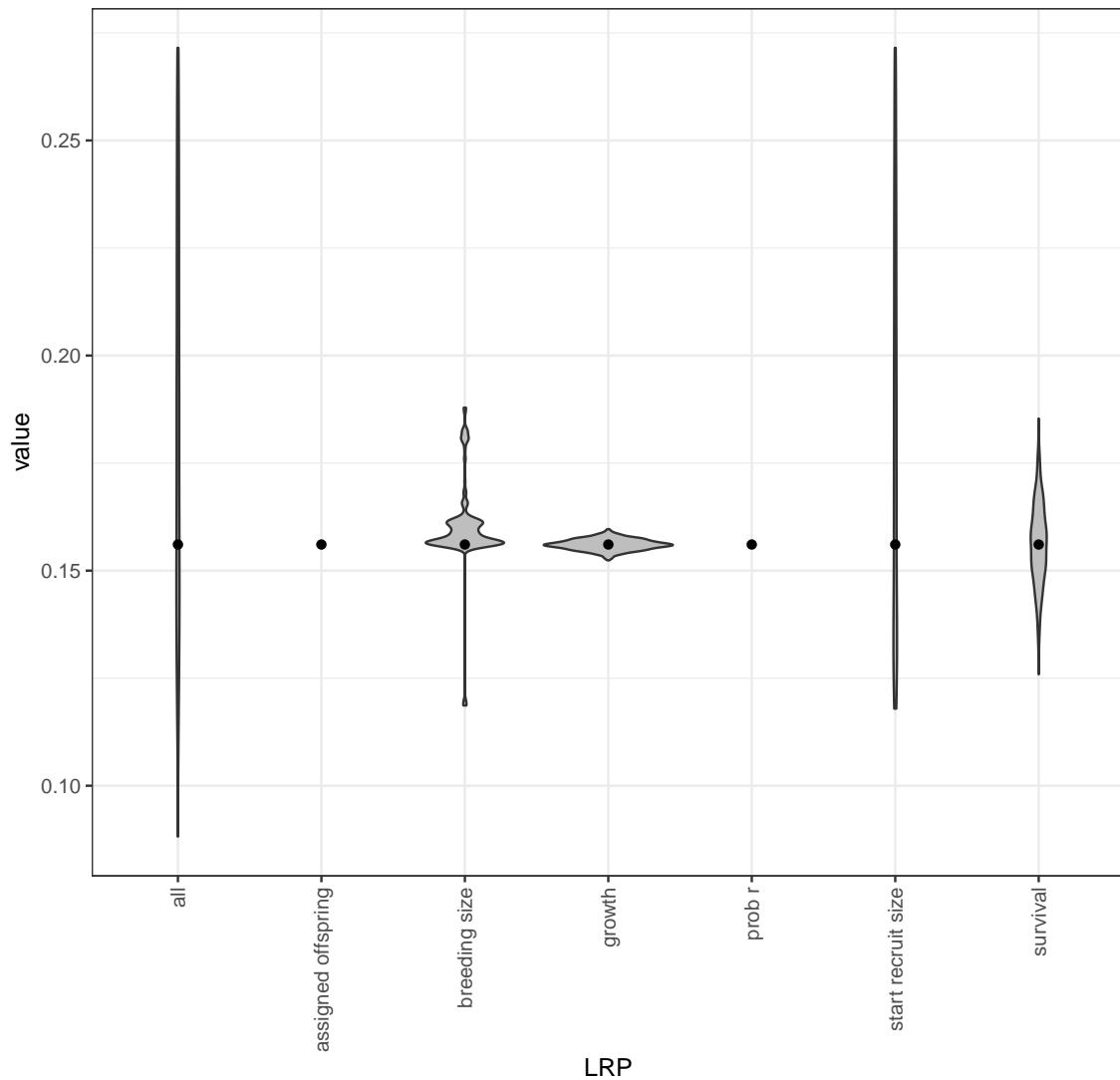


Figure B.4: The contribution of different sources of uncertainty in LRP.

Uncertainty in LRP accounting for DD

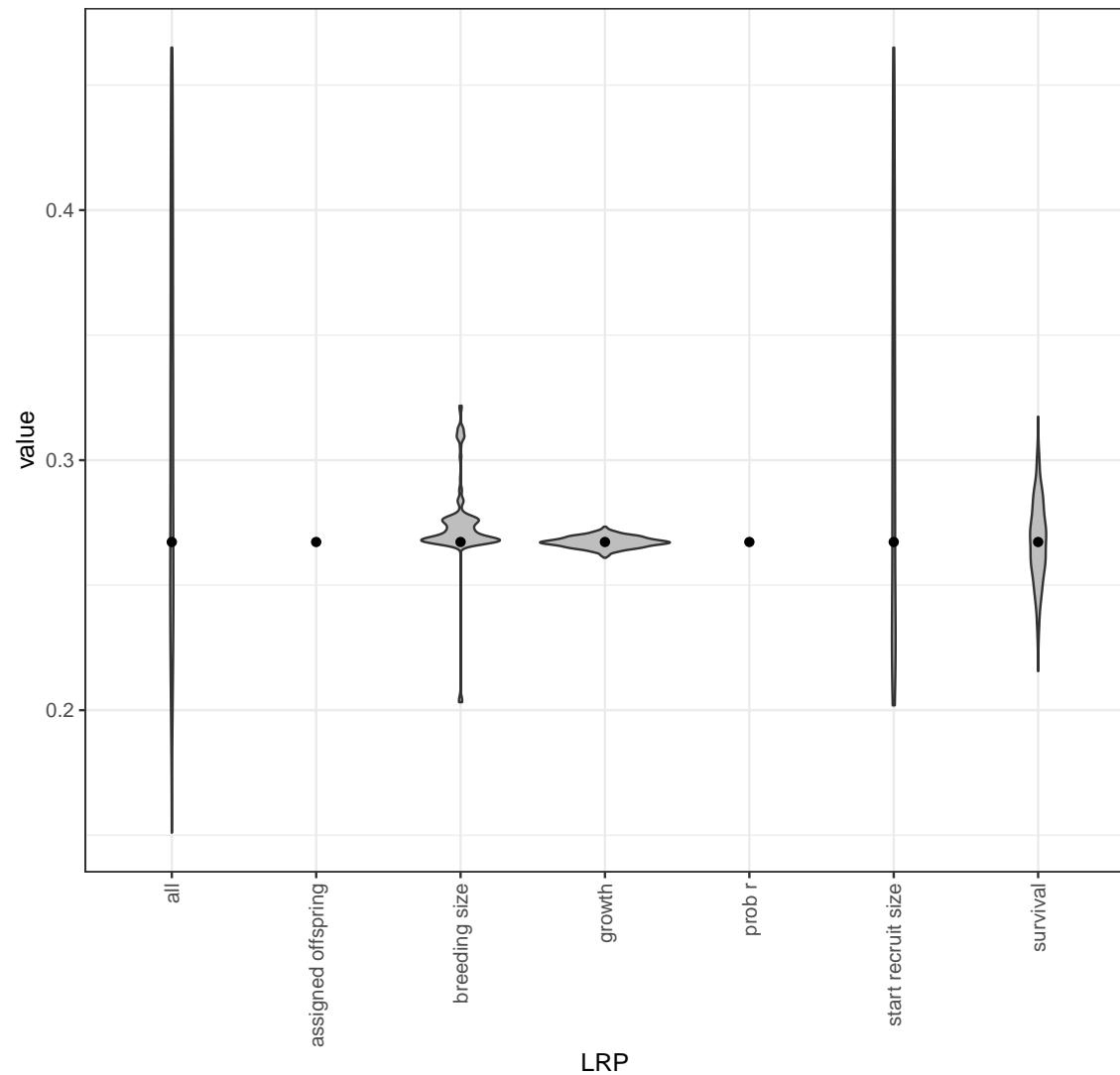


Figure B.5: The contribution of different sources of uncertainty in LRP, when we account for density-dependence in egg-recruit survival.

Uncertainty in egg–recruit survival

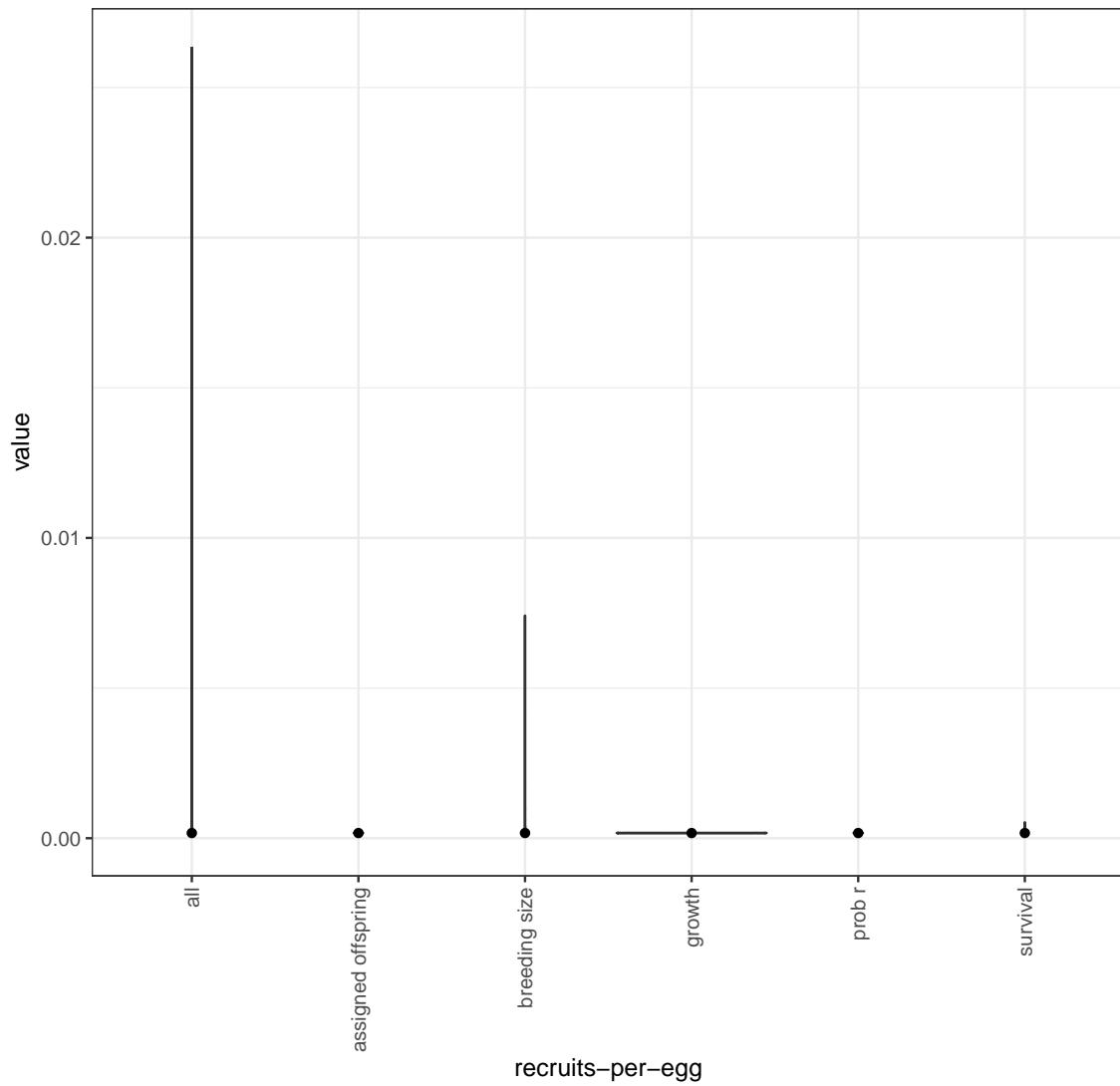


Figure B.6: The contribution of different sources of uncertainty in egg-recruit survival.

Uncertainty in egg–recruit survival /n accounting for DD

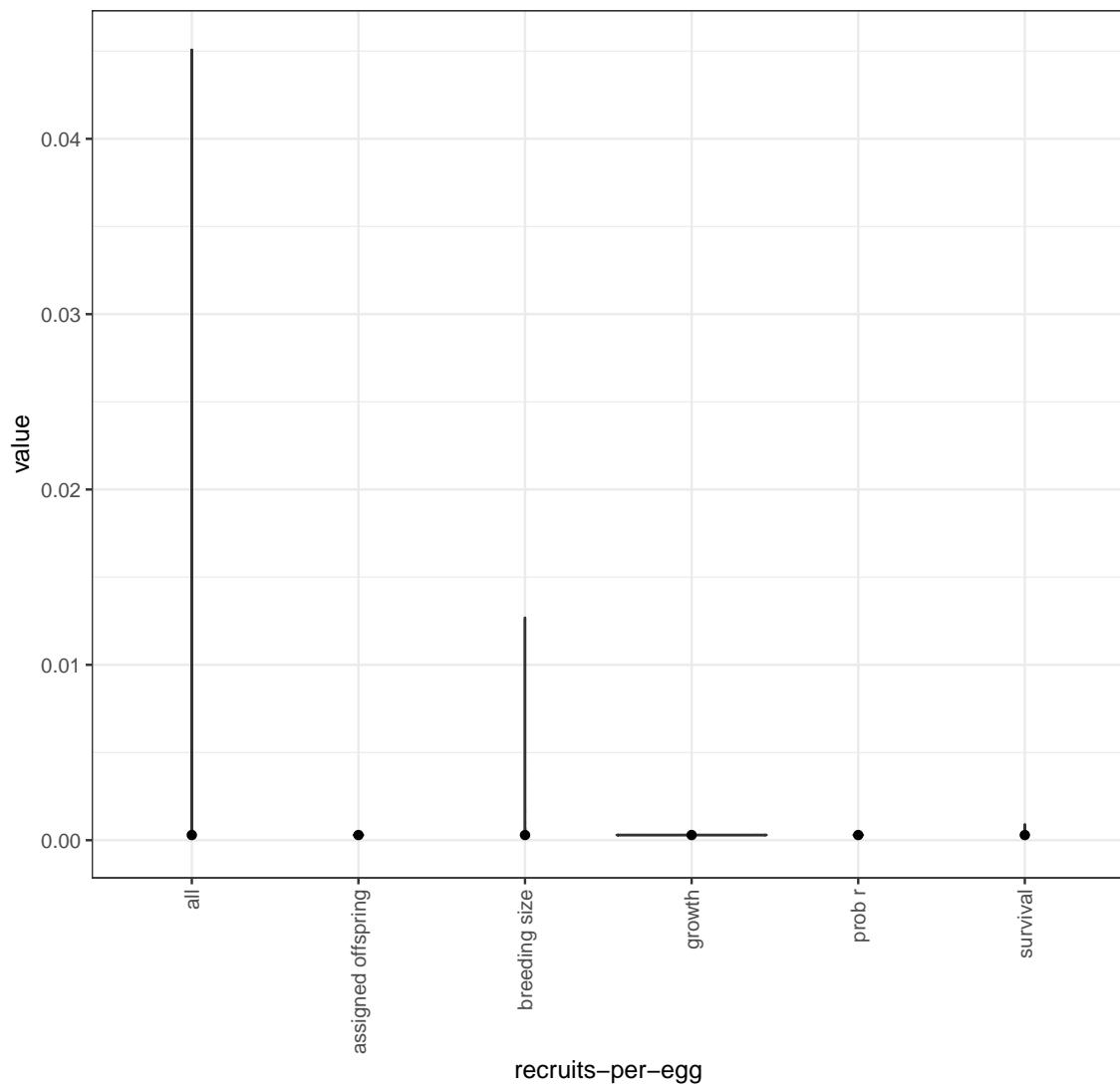


Figure B.7: The contribution of different sources of uncertainty in egg-recruit survival when we account for density-dependence in egg-recruit survival.

Uncertainty in network persistence

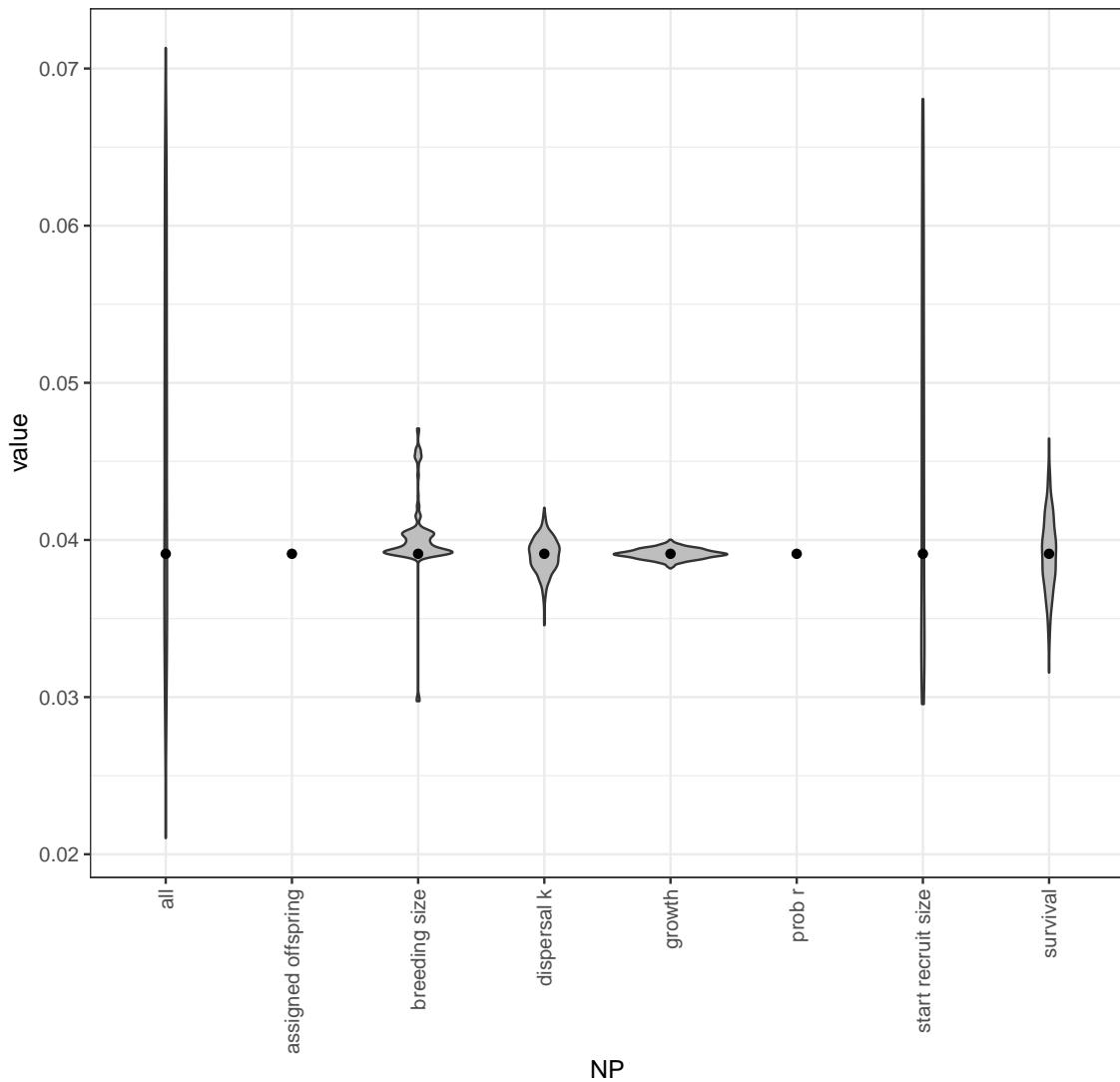


Figure B.8: The contribution of different sources of uncertainty in NP.

Uncertainty in network persistence /n accounting for DD

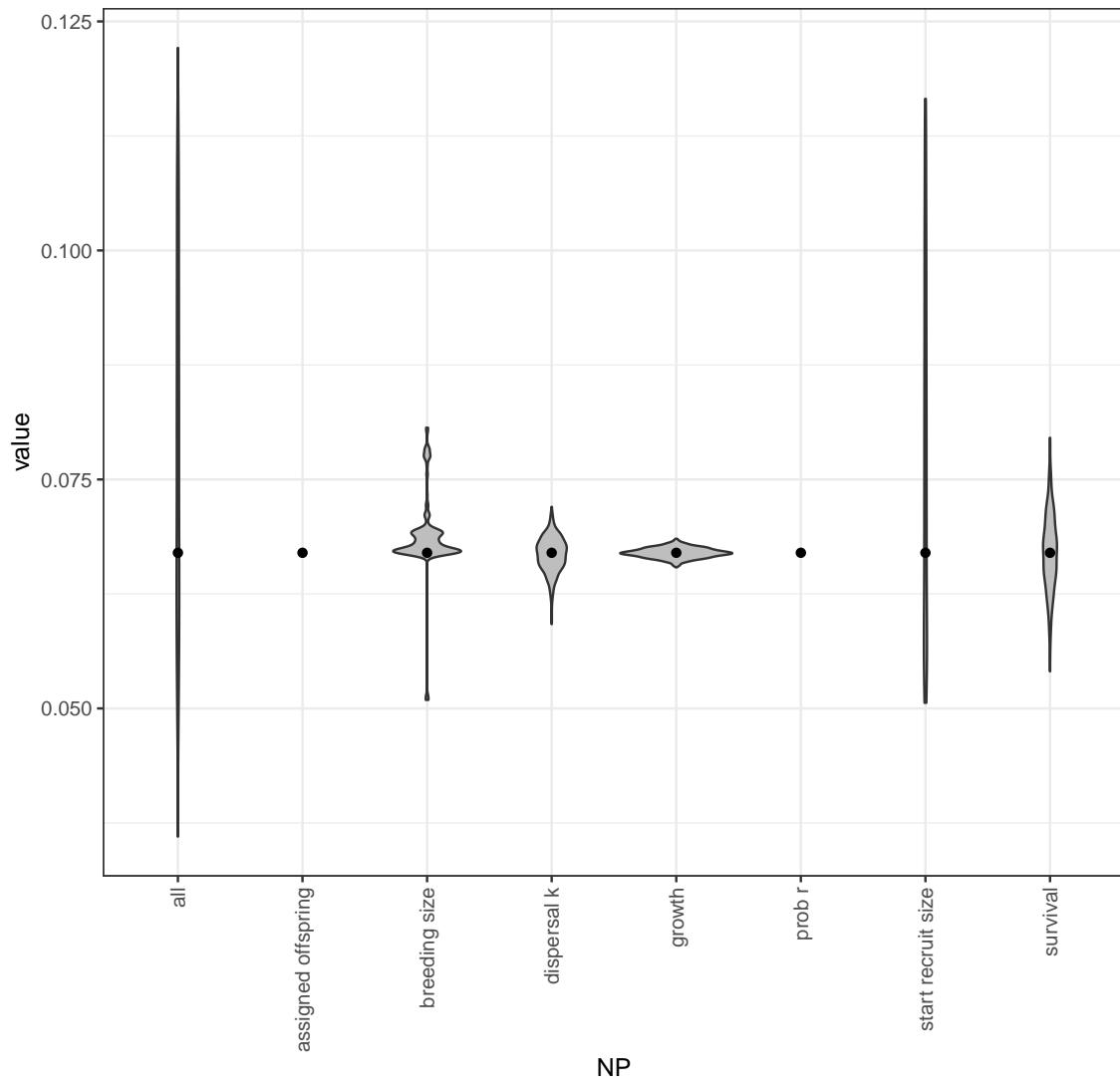


Figure B.9: The contribution of different sources of uncertainty in NP when we account for density-dependence in egg-recruit survival.

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