

Clownfish metapopulation persistence draft

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Introduction

Metapopulations exist along a continuum, with dynamics driven by the balance of

³ extinction and colonization of local patches at one extreme and focused on the bal-

ance of immigration and emmigration at constantly-occupied local patches at the other (Kritzer and Sale, 2006). Terrestrial metapopulations often show extinction-
6 colonization dynamics (e.g. Hanski, 1998), while marine metapopulations tend to exhibit immigration-emmigration dynamics where local extinction of patches is un-
common (Kritzer and Sale, 2006). For these marine metapopulations, dynamics and
9 persistence depend on connectivity among patches and the demographic rates at each patch (e.g. Hastings and Botsford, 2006; Hanski, 1998). Assessing levels of connectiv-
ity and demographic parameters has been particularly challenging for marine
12 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;
15 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
18 metapopulations might persist.

For any population to persist, individuals must on average replace themselves during their lifetime. Assessing replacement must take into account the demographic processes across the whole life cycle, including how likely individuals are to survive to the next age or stage, their expected fecundity at each stage, and the survival of any offspring produced to recruitment. In a spatially-structured population, as many marine populations are, in addition to assessing whether the reproductive output and survival of a population is sufficient, we must also consider how the offspring are distributed across space. Marine larvae were once thought to be well-mixed and dis-

²⁷ persed far on ocean currents (e.g. Roughgarden et al., 1988), suggesting widespread connectivity among patches and largely open populations. Recent advances in estimating connectivity through natural tags and genetics, however, suggest that dispersal may be more limited (e.g. D'Aloia et al., 2013; Hameed et al., 2016; Almany et al., 2017), and local persistence of marine populations on a small spatial scale is seeming more possible.

³³ Considering both the demographic processes within patches and the connectivity among them, a metapopulation can persist in two ways: 1) at least one patch can achieve replacement in isolation, or 2) patches receive enough recruitment to achieve replacement through multi-generational loops of connectivity with other patches in the metapopulation (Hastings and Botsford, 2006; Burgess et al., 2014). In the first case (termed self-persistence), enough of the reproductive output produced at one patch is retained at the patch for it 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 eventually send offspring back to the first in a future generation - provide the patch with enough recruitment to persist within the network. Though it has been challenging to estimate the parameters necessary to understand how actual metapopulations persist, a large work of theory developed in part to guide marine protected area design helps predict when each type of persistence is likely to occur (i.e., large patches relative to the mean dispersal distance are likely to be self-persistent, Botsford et al., 2001).

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

it increasingly possible to estimate both the demographic [ADD EXAMPLE CITATIONS] and the dispersal (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, as they lack nearby populations with which to exchange larvae and would go locally extinct if they did not achieve replacement. At isolated Kimbe Island in Papua New Guinea, Salles et al. (2015) find that the population of orange clownfish (*Amphiprion percula*) can likely persist without outside immigration. In contrast, populations of bicolor damselfish (*Stegastes partitus*) at a set of reef patches across four isolated islands in the Bahamas do not appear able to persist without outside input (Johnson et al., 2018). For populations that exist in patches along a continuous linear coastline, rather than on separate islands, however, how patches interact and what the scale of metapopulation persistence is are still open questions.

The number of studies estimating demographic rates and connectivity in marine metapopulations is growing (e.g. Salles et al., 2015; Johnson et al., 2018) (OTHER EXAMPLES), but most use data from one or a few years. Longer data sets enable better estimates of long-term average rates, rather than assuming the demographic and dispersal rates from a particular year or two are representative through time. More data is also useful for explicitly considering uncertainty, both to assess how well we understand persistence for a population and to see which parameters contribute most to our uncertainty. Finally, sampling over many years provides the possibility of comparing abundance trends to persistence metrics to see if they tell a consistent story.

Here, we further our understanding of metapopulation dynamics in a network of patches along a coastline through a study of yellowtail clownfish (*Amphiprion clarkii*) in the Philippines. We assess persistence for all patches of habitat within a 30 km stretch of coastline, which exceeds estimates of the dispersal spread for this species (Pinsky et al., 2010), suggesting the network is likely to operate as a contained metapopulation. With seven years of annual sampling data, we are able to estimate persistence metrics and replacement over the longer term and investigate abundance through time to compare with the replacement-based persistence metrics. We use our long-term data set from habitat patches on a continuous section of coastline to understand persistence within a local network.

Methods

84 Persistence theory and metrics

For a population to persist, individuals must be able to replace themselves on average at low abundance (CITATIONS). In non-spatially structured populations, we 87 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). For spatially-structured populations, we must also consider the spatial spread of offspring, often represented through a dispersal kernel or connectivity matrix (CITATIONS).

We consider three primary metrics to assess whether and how the population is persistent: 1) lifetime recruit production (LRP), to assess whether the population has enough surviving offspring to achieve replacement 2) self-persistence (SP), to assess whether any individual patch can persist in isolation without input from other patches, and 3) network persistence (NP), to assess whether the metapopulation is persistent as a connected unit. We explain each metric below in detail. To represent the uncertainty in our estimates, we calculate each metric 1000 times, pulling each input parameter from a distribution or range. In our results, we show the range of values of each persistence metric as well as our best estimate.

Lifetime production of recruits

We find the estimated number of recruits an individual recruit will produce (lifetime recruit production: LRP) by multiplying the total number of eggs a recruit-sized individual will produce in its lifetime (lifetime egg production: LEP) by the fraction of those eggs that will survive to become recruits (egg-recruit survival: S_e) (Fig. 1 Metrics):

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

If $\text{LRP} \geq 1$, the population has the possibility for replacement; individuals produce enough surviving offspring, before taking into account the probability of dispersal. If $\text{LRP} < 1$, the individuals are not replacing themselves and the population cannot persist without input from outside patches. We consider LRP for all recruits produced by our individuals, regardless of where they settle, which requires combining

¹¹⁴ with the dispersal kernel to understand persistence, and for recruits that settle only
at our sites, LRP_{local} . If $LRP_{local} \geq 1$, our group of sites is able to persist locally.

Self-persistence

¹¹⁷ A patch is able to persist in isolation (self-persistent) if individuals produce enough
offspring that survive to recruitment (LRP) and disperse back to the natal patch
(with probability of dispersal $p_{i,i}$) to replace themselves. Burgess et al. (2014) use
¹²⁰ LEP to represent offspring produced and local retention (LR) - the number of surviving
recruits that disperse back to the natal patch over the number of eggs produced
by the natal patch - to capture egg-recruit survival and dispersal combined in a
¹²³ criteria for self-persistence: $LEP \times LR \geq 1$. We modify this to use include egg-
recruit survival in the offspring term, using LRP in place of LEP, to assess whether
a particular patch i is self-persistent:

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

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

¹²⁶ 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).

¹²⁹ **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 distances between sites. We then ¹³² create a realized connectivity matrix C by multiplying the dispersal probabilities by the expected number of recruits an individual produces: $C_{i,j} = \text{LRP} \times p_{i,j}$ (Burgess et al., 2014, though we include egg-recruit survival in LRP, rather than in $p_{i,j}$ as they ¹³⁵ do). The diagonal entries of C , where the origin and destination are the same site, 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: $\text{NP} = \lambda_C > 1$ (e.g. Hastings and Botsford, ¹³⁸ 2006; White et al., 2010; Burgess et al., 2014).

Defining recruit and census stage

¹⁴¹ 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 itself with an individual that reaches the same life stage (Burgess et al., 2014). We ¹⁴⁴ define a recruit to be a juvenile individual that has settled on the reef within the previous year, which also encompasses the size we are first able to sample (3.5-6.0 cm for parentage studies). In theory, it does not matter how we define recruit as long ¹⁴⁷ as we use that definition in our calculations of both egg-recruit survival and LEP. In our system, however, while it is straightforward to calculate LEP from any size, we do not have enough tagged recruits to reliably estimate survival to different recruit

₁₅₀ 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
recruit sizes by pulling from a uniform distribution over the sizes the recruit stage
₁₅₃ covers (3.5-6 cm, Table A1).

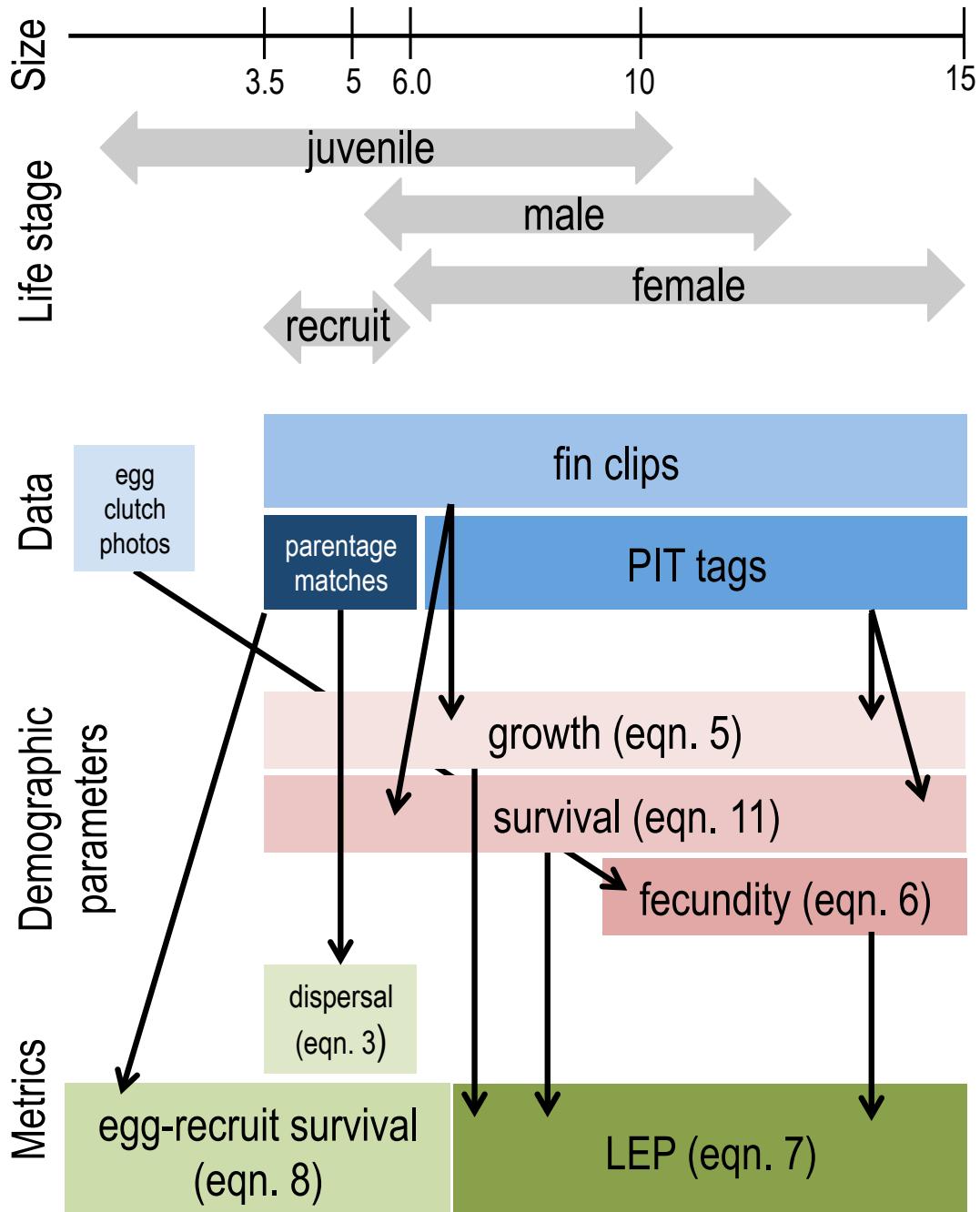


Figure 1: Here, we show the data collected for fish at each life stage (life stage boxes are not scaled by length of stage) and how the empirical data fit into our parameter
10 and metric calculations.

Study system

We focus on a tropical metapopulation of yellowtail clownfish (*Ampiprion clarkii*, Fig. 156 2c) on the west coast of Leyte island facing the Camotes Sea in the Philippines (Fig. 2a). Like many clownfish species, yellowtail clownfish have a mutualistic relationship 159 with anemones, where small colonies of fish live (Buston, 2003b; Fautin et al., 1992). Yellowtail clownfish are protandrous hermaphrodites and maintain a size-structured 162 hierarchy; within an anemone, the largest fish is the breeding female, the next largest is the breeding male, and any smaller fish are non-breeding juveniles. The fish on an anemone maintain a strict social and size hierarchy (Buston, 2003b), with fish 165 moving up in rank to become breeders only after the larger fish have died. 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 168 protect and tend (Ochi, 1989; Holtswarth et al., 2017). Larvae hatch after about six days and spend 7-10 days in the water column before returning to reef habitat to settle in an anemone (Fautin et al., 1992).

Clownfish are particularly well-suited to metapopulation studies due to their limited movement as adults and clearly patchy habitat. Once fish have settled, they 171 tend to stay within close proximity of their anemones [XX meters, CITATION]. This 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 174 to be the reef patch or the anemone territory of the fish, are clearly discrete and easily delineated (Fig. 2a, b), which makes determining the spatial structure

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

186 **Field data collection**

We focus on a set of seventeen patch reef sites spanning approximately 30 km along
the western coast of Leyte island (Fig. 2a). The sites consist of rocky patches of coral
189 reef and are separated by sand flats (Fig. 2b). Previous work using genetic isolation
by distance 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
192 exceed that range. On the north edge, the sites are isolated from nearby habitat
with no substantial reef habitat for at least 20 km.

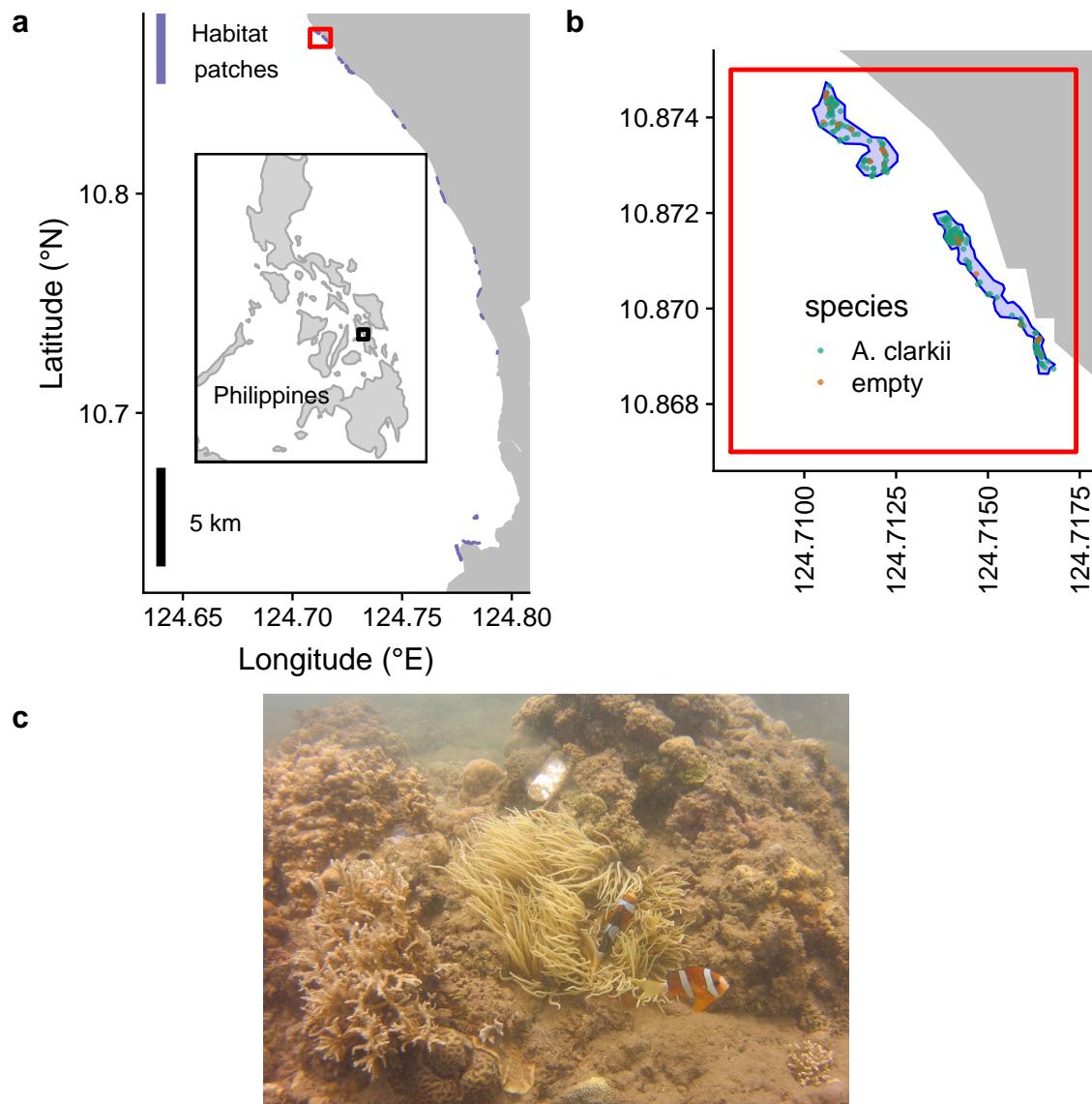


Figure 2: a) Map of the sites along the coast of Leyte in the Philippines. b) Zoomed-in map of the two northern-most sites, Palanas and Wangag, to show anemone arrangement, with anemones occupied by *A. clarkii* (green) or unoccupied by clownfish (orange). c) An example anemone occupied by *A. clarkii* in a typical habitat at the sites. The metal anemone tag is visible just above the anemone on the rock.

Since 2012, we have sampled fish and habitat at most of the sites annually (Table 195 A2). During sampling, divers using SCUBA and tethered to GPS readers swam the extent of each site. Divers visited each anemone inhabited by yellowtail clownfish, 198 tagging the anemone to track it 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 201 and larger were also tagged with a passive integrated transponder (PIT) tag, unless already tagged. Divers also looked for eggs around each anemone and measured and photographed any clutches found. In total, we took fin clips from XX fish and 204 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

207 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 210 (SNPs) using the program FreeBayes (*is there a citation for this?*) (details and results in Catalano et al., in prep). In total, we genotyped XX fish. We used the SNPs to identify parent-offspring matches with the software program COLONY2 (Wang, 213 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

216 distance d as measured in kilometers and parameters θ and $z = e^{k_d}$, which control
the shape and scale of the kernel:

$$p(d) = ze^{-(zd)^\theta}. \quad (3)$$

We use a Laplacian dispersal kernel with shape parameters $\theta = 1$ and scale parameter $k_d = -2.11$ (Fig. 4a, estimated in (Catalano et al., in prep)). To account for uncertainty in the dispersal kernel, we keep the shape parameter θ constant and pull the scale parameter k_d from a set capturing the 95% interval produced during kernel estimation 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 given that a fish recruits somewhere, not the probability that a released larva will travel a particular distance. To find the probability of fish dispersing among our sites, we numerically integrate the dispersal kernel (eqn. 3) using the distance from the middle of the origin site to the closest and farthest bounds of the destination site as the upper and lower bounds. For example, the probability of dispersal from site A to B, where d_1 is the distance from the middle of A to the closest edge of B and d_2 is the distance from the middle of A to the far edge of B, is:

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

Estimating inputs from empirical data

Growth and survival: mark-recapture analyses

- ²³⁴ 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 fish that includes size and stage at each capture time.
- ²³⁷

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 asymptotic size across the population and K controls the rate of growth:

²⁴⁰

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

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 .

²⁴³

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.

²⁴⁶

²⁴⁹

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, 252 2013). We consider several models with year, size, and site effects on the probability of survival on a log-odds scale (see full list in Table A3). For fish that are not recaptured in particular year, we estimate their size using our growth model (eqn. 255 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. 258 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 261 of the models (Table A3).

Fecundity

We use a size-dependent fecundity relationship, determined using photos of egg 264 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 267 eggs are old enough to have visible eyes:

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

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

270 (2017).

We only consider reproductive effort once the fish has reached the female stage and use the average size of first observation as female for recaptured fish as the 273 transition size $L_f = 9.32\text{cm}$. To incorporate uncertainty, we draw from the full set of sizes at which recaptured fish were first captured as female (5.2 cm - 12.7 cm).

Lifetime egg production

276 We use an integral projection model (IPM) (e.g. Rees et al., 2014) with size as the continuous structuring trait z to estimate lifetime egg production (LEP), the total number of eggs produced by one individual, starting at the recruit stage. We initialize 279 the IPM with one recruit-sized individual ($\text{size}_{\text{recruit}}$) at the initial time step ($t = 0$), then project forward for 100 time steps using the size-dependent survival (eqn. 11) and growth (eqn. 5) functions as the probability density functions that make up the 282 kernel to describe the survival and growth of the individual into the next time step. This gives us the size distribution at each time step, which represents the probability that the individual has survived and grown into each of the possible size categories, 285 ranging from a minimum of $L = 0\text{ cm}$ to a maximum of $U = 15\text{ cm}$. The probability that the individual is still alive and of any size decreases as the time steps progress; by using a large number of steps, we are able to avoid arbitrarily setting a maximum 288 age and instead let the probabilities become essentially zero.

We then multiply the size-distribution v_z at each time by the size-dependent fecundity f_z described above (eqn. 6) to get the total number of eggs produced at 291 each time step. We then integrate across time and size to get the total number of

eggs one individual is likely to produce in its lifetime:

$$\text{LEP} = \int_{t=0}^{100} \int_{z=L}^{z=U} v_{z,t} f_z dz dt. \quad (7)$$

To compute LEP, we discretize time and size and sum across the matrix. We
 294 use 0.1 as the standard deviation of size for a recruit ($\text{size}_{\text{recruit},sd}$) and estimate the standard deviation of the distribution of sizes of fish in the next year (size_{sd}) from our recapture data (A1).

297 **Survival from egg to recruit**

We estimate survival from egg to recruit (S_e) using parentage matches to estimate the number of surviving recruits produced by genotyped parents (similar to the
 300 method in Johnson et al., 2018). We scale the number of offspring we match back to parents ($R_m = XX$) by various ways we could have missed offspring (P_h , P_c , P_d , and P_s , described below), then divide by the estimated number of eggs produced by
 303 genotyped parents, found by multiplying the number of genotyped parents ($N_g = XXX$) by the expected lifetime egg production for a fish of parent size (LEP_{*p*}):

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

We scale the number of matched recruits we find by the cumulative proportion
 306 of habitat in our sites we sampled over time (P_h , details in A.1), the probability of capturing a fish if we sampled its anemone (P_c , see A.2 for details), and the proportion of the total dispersal kernel area from each our of sites covered within our

309 sampling region (P_d , calculation in A.2). Finally, because our dispersal kernel gives
the probability of dispersal given that a recruit settled somewhere but our sampling
region is not all habitat, we scale by the proportion habitat in our sampling region
312 ($P_s = XX$, details in A.3) to avoid counting this mortality twice.

To estimate $\text{LRP}_{\text{local}}$, we scale only by the proportion of habitat we cumulatively
sample in our sites and the probability of capturing a fish.

315 To incorporate uncertainty in our estimate of egg-recruit survival, we consider
uncertainty in the number of offspring assigned to parents during the parentage
analysis (R_m) and in the probability of capturing a fish (P_c). We generate a set
318 of values for the number of assigned offspring using a random binomial, where the
number of trials is the number of genotyped offspring and the probability of success
on each trial is the assignment rate of offspring from the parentage analysis (Catalano
321 et al., in prep). For the probability of capturing a fish, we pull values from a beta
distribution that captures the mean and variance of capture probabilities across
recapture dives (details in A.2).

324 Accounting for density-dependence

Ideally we would assess persistence metrics when the population is at low abundance
and not limited by density-dependence. Clownfish have strong social hierarchies
327 and juveniles on an anemone will prevent others from settling there as well (seen in
A. percula, Buston, 2003a). Each anenome, therefore, can only house one settling
clownfish, with anemones already occupied by *A. clarkii* settlers essentially
330 unavailable as habitat. We attempt to account for this density-dependent mortality

by multiplying our estimate of settling recruits (the numerator of eqn. 8) by the proportional increase (DD) in unoccupied anemones at our sites if all of the *A. clarkii* anemones were unoccupied, where p_A is the proportion of anemones occupied by *A. clarkii* and p_U is the proportion of unoccupied anemones: $DD = \frac{(p_U + p_A)}{p_U}$. We present results both with and without this density-dependence modification.

336 Estimated abundance over time

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

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

342 We then fit a linear model through the time series for each site i sampled in at least three years to assess whether the slope over time is positive or negative:

$$\# \text{ females}_i \sim \text{year} \quad (10)$$

Results

345 Our estimated abundance of females at each site over time does not suggest a clear trend in abundance (Fig. 3). In our very simple look at whether abundance seems to be increasing or decreasing at our sites, eleven sites had a positive slope over

³⁴⁸ time and five had a negative slope (Fig. 3q). For the two largest sites, with a mean estimated number of females of between 150-200, one has a positive slope (Wangag, Fig. 3b) and one has a negative slope (Sitio Baybayon, Fig. 3p) and the next two ³⁵¹ largest sites are also split (Palanas, Fig. 3a and Haina, Fig. 3o). Overall, there is not a clear directional change in abundance across the sites we sample over our sampling period.

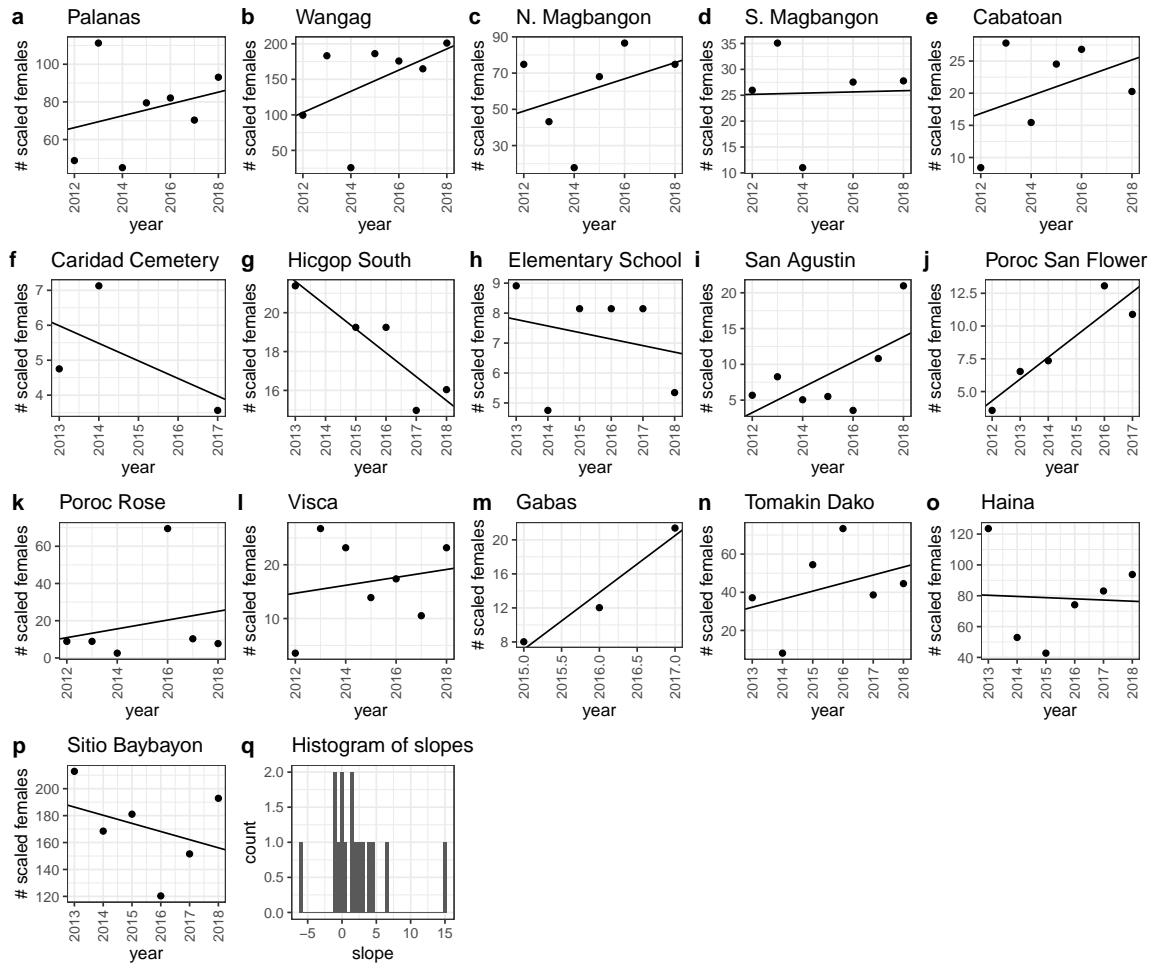


Figure 3: The estimated number of females at each site over the sampling years for sites sampled in at least three years. The total number of females at each site was estimated by scaling up the number of females captured at each site in each year by the proportion of habitat sampled at that site that season (see A.1 for details) and by the average probability of capturing a fish (see A.2). We show the estimated abundances and trend for each site individually (a-p) and a histogram of the slopes of abundance through time (q).

354 From the mark-recapture analysis of tagged and genotyped fish, we estimate
 mean values of $L_\infty = 10.71\text{cm}$ (range of estimates 10.50 - 10.90 cm) and $K = 0.864$
 (range of estimates 0.785 - 0.944) for the von Bertalanffy growth curve parameters
 357 (Fig. 4b, Table A1). For juvenile and adult (post-recruitment) survival on a log-odds
 scale, the best-fit model has an effect of size, with coefficient $b_a = 0.169 \pm 0.028 \text{ SE}$
 and intercept $b_\phi = -1.83 \pm 0.231 \text{ SE}$. The accompanying best-fit model for log-odds
 360 recapture probability has a negative size effect and a negative effect of diver distance
 from the anemone (eqn. A.3, Fig. A.2).

$$\log\left(\frac{\phi}{1-\phi}\right) = b_\phi + b_a \text{size.} \quad (11)$$

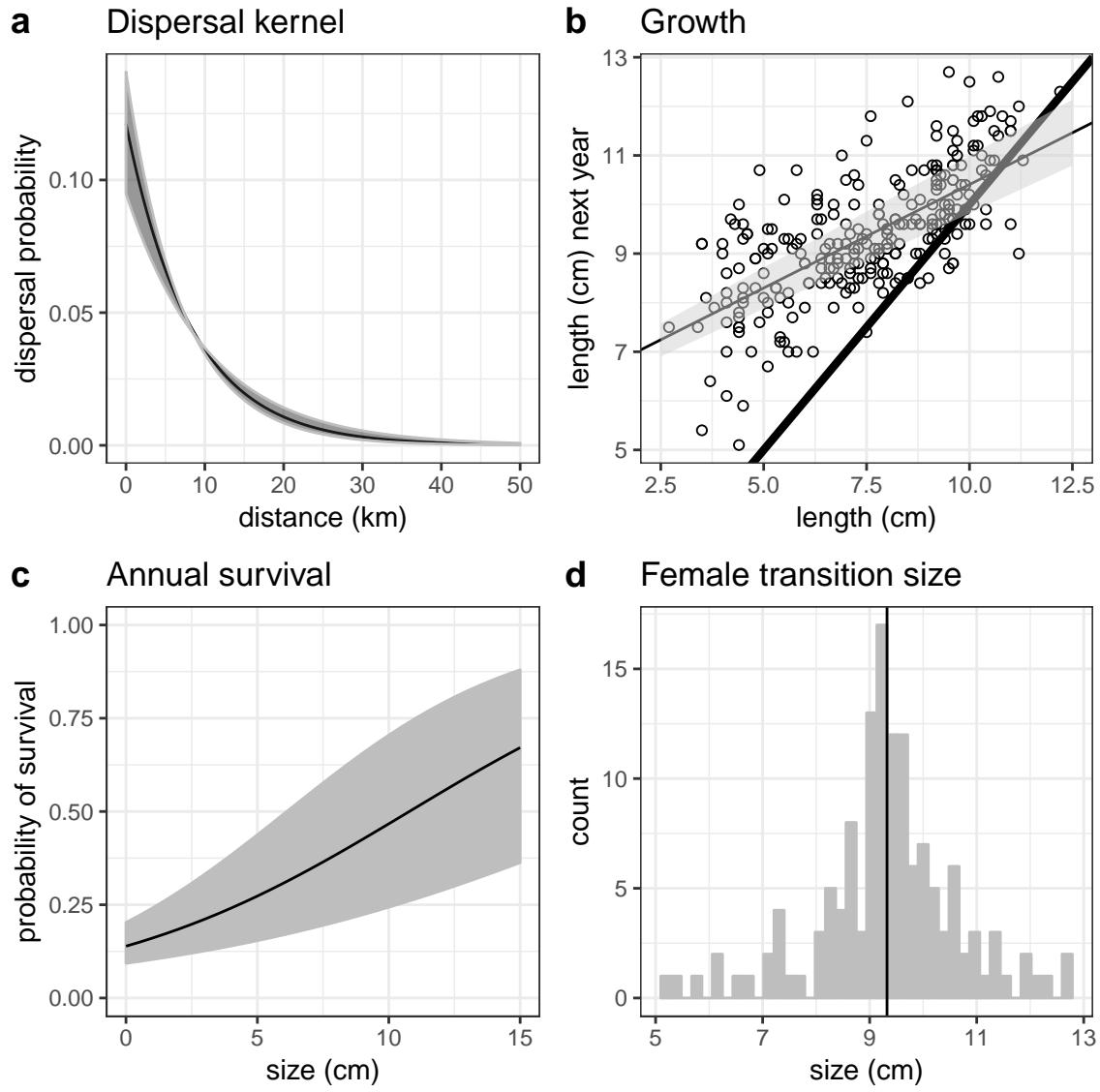


Figure 4: Best estimates (solid black line) and range included for uncertainty (gray) for dispersal (a), growth, including the 1:1 line in thick black (b), post-recruit survival (c), and size at female transition (d) parameters.

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

³⁶³ of LEP for 1061, ranging from 39 to 10345 when we consider uncertainty in the inputs (Fig. 5a). Adult survival has the most effect on the value of LEP (Fig. B.4), with higher values of LEP the higher annual survival of adults.

³⁶⁶ We estimate egg-recruit survival S_e to be 7.8e-04, ranging from 1.2e-04 to 0.033 when we include uncertainty in the number of offspring assigned to parents and the probability of catching a fish (Fig. 5b). When we compensate for density-dependence ³⁶⁹ in our data, we estimate S_e to be 0.0013, ranging from 2.1e-04 to 0.057. These are somewhat high values of egg-recruit survival compared to what we see elsewhere in the literature (e.g. Rumrill, 1990; Metaxas and Saunders, 2009) (though not unreasonable, e.g. White et al., 2014; Johnson et al., 2018) because we scale up by the amount of habitat in our sampling area and count mortality due to dispersal to non-habitat in the dipsersal probability, rather than in S_e . Uncertainty in the size of ³⁷⁵ transition to breeding female L_f has the largest effect on egg-recruit survival (Fig. B.7); 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 ³⁷⁸ by genotyped parents and the higher egg-recruit survival.

We estimate lifetime recruit production (LRP), the product of LEP and S_e , to be 0.83, with a range of 0.28 - 3.89 when we consider uncertainty in inputs. When ³⁸¹ we compensate for density-dependence, we estimate a value of 1.42 for LRP, with a range of 0.48 - 6.66. The value when we compensate for density-dependence and the range of uncertainty for both are above the threshold of one necessary for replacement ³⁸⁴ before considering dispersal. This mean that individuals at our sites produce enough surviving offspring before considering dispersal to be able to replace themselves, but

LRP does not tell us whether those offspring will settle within our sample sites, or
387 on habitat elsewhere, and drive persistence.

We also estimate replacement for recruits from our sites returning to our sites,
which implicitly includes dispersal mortality, LRP_{local} to be 0.09 (ranging from 0.03
390 to 0.44 when we include uncertainty) or 0.16 (0.05 to 0.76) when we compensate for
density-dependence. With a value well below one, this suggests individuals at our
sites do not replace themselves with recruits that settle in our sites, suggesting our
393 sites do not persist as an independent network.

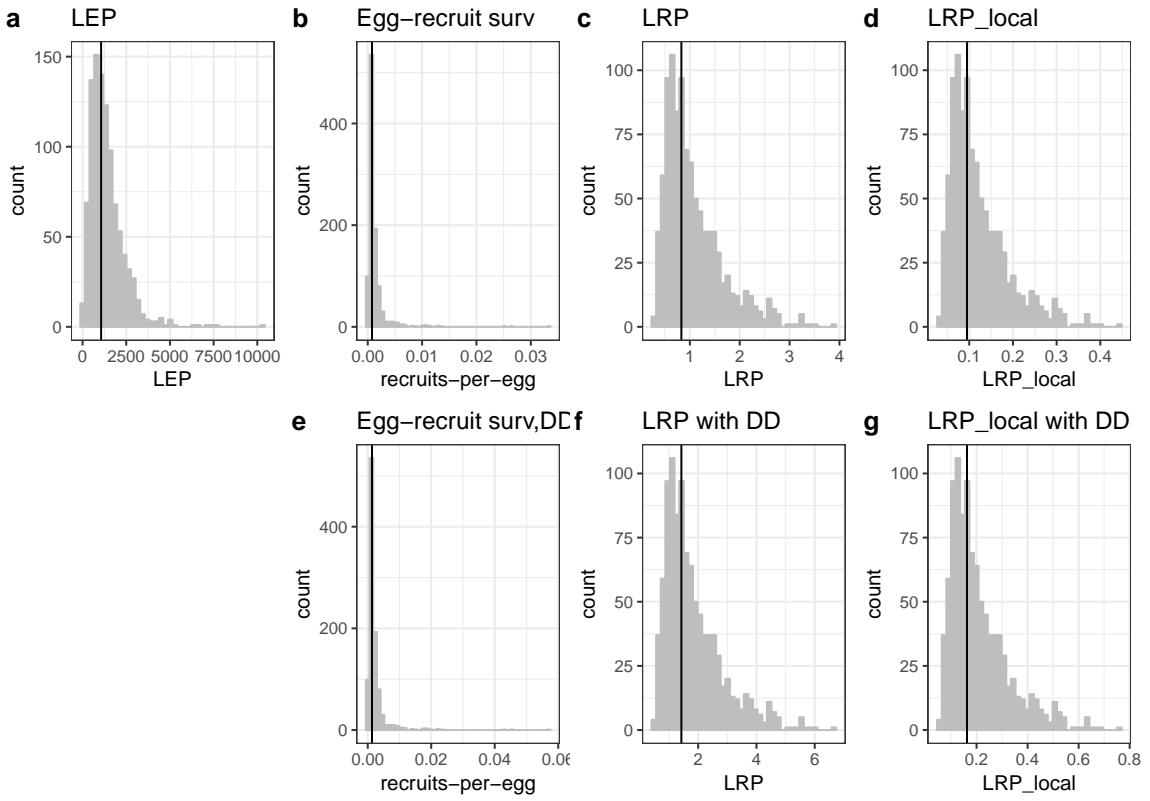


Figure 5: Estimates of a) LEP, b) egg-recruit survival, and c) LRP, and d) LRP_{local} , showing the best estimate (black solid line) and range of estimates considering uncertainty in the inputs. The estimates in e-g include our attempt to remove density-dependence in the early life stages, while the estimates in b-d do not. We only consider density-dependence in egg-recruit survival so LEP (a) estimates are the same in both cases.

We do not find any sites with $SP > 1$, whether we compensate for density-dependence or not (Fig. 6), indicating that no site could persist in isolation. Given
 396 that our best estimate of LRP does not suggest replacement and only a fraction

of those offspring stay at the natal site, this makes sense. We see the highest values of self-persistence at Haina ($SP = 0.079, 0.13$ when compensating for density-dependence) and Wangag ($SP = 0.048, 0.082$ when compensating for density-dependence),
our two widest sites.

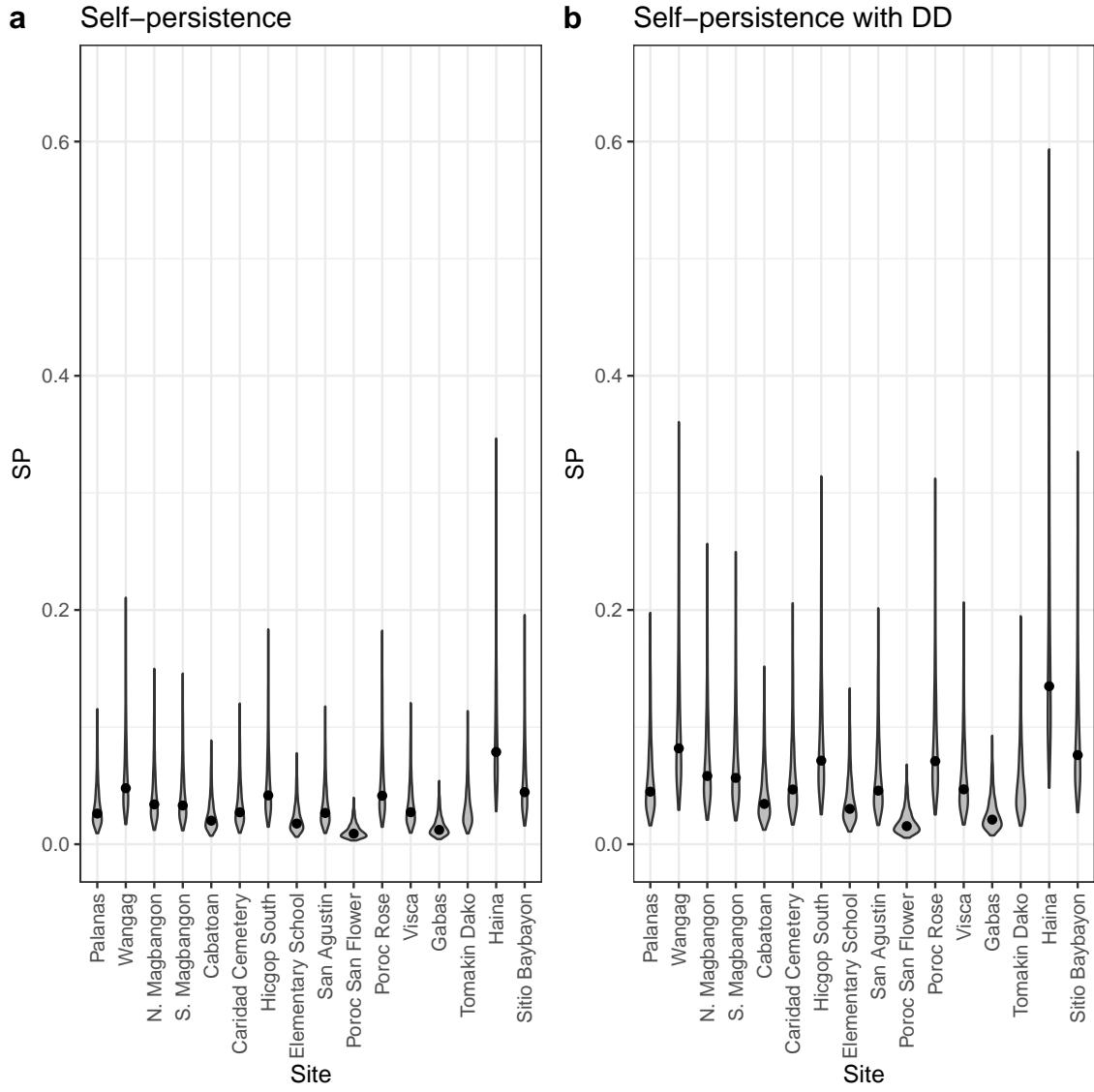


Figure 6: Values of self-persistence at each site, showing the best estimate (black point) and range of estimates considering uncertainty in the input parameters. No site reaches the value $SP \geq 1$ necessary to be self-persistent. The estimates in (b) attempt to compensate for density-dependence in early life stages in our data, while the estimates in (a) do not.

For network persistence, our best estimate of the dominant eigenvalue of the
402 realized connectivity matrix λ_c is 0.21 with a range of 0.07 - 0.92 with uncertainty
(Fig. 7a), or 0.36 with a range 0.12 - 1.58 with uncertainty when we compensate for
density-dependence (Fig. 7c). Our sites are likely not network persistent, as our best
405 estimates and most of the values we see in our runs with uncertainty are below one,
but network persistence is possible, as our range of estimates does exceed one when
we compensate for density-dependence. We see that most of the connectivity occurs
408 among the sites in the northern part of our sample area, from Palanas to Caridad
Cemetery, and at the southern part of our sample area from Tomakin Dako to Sitio
Baybayon (Fig. 7b, d).

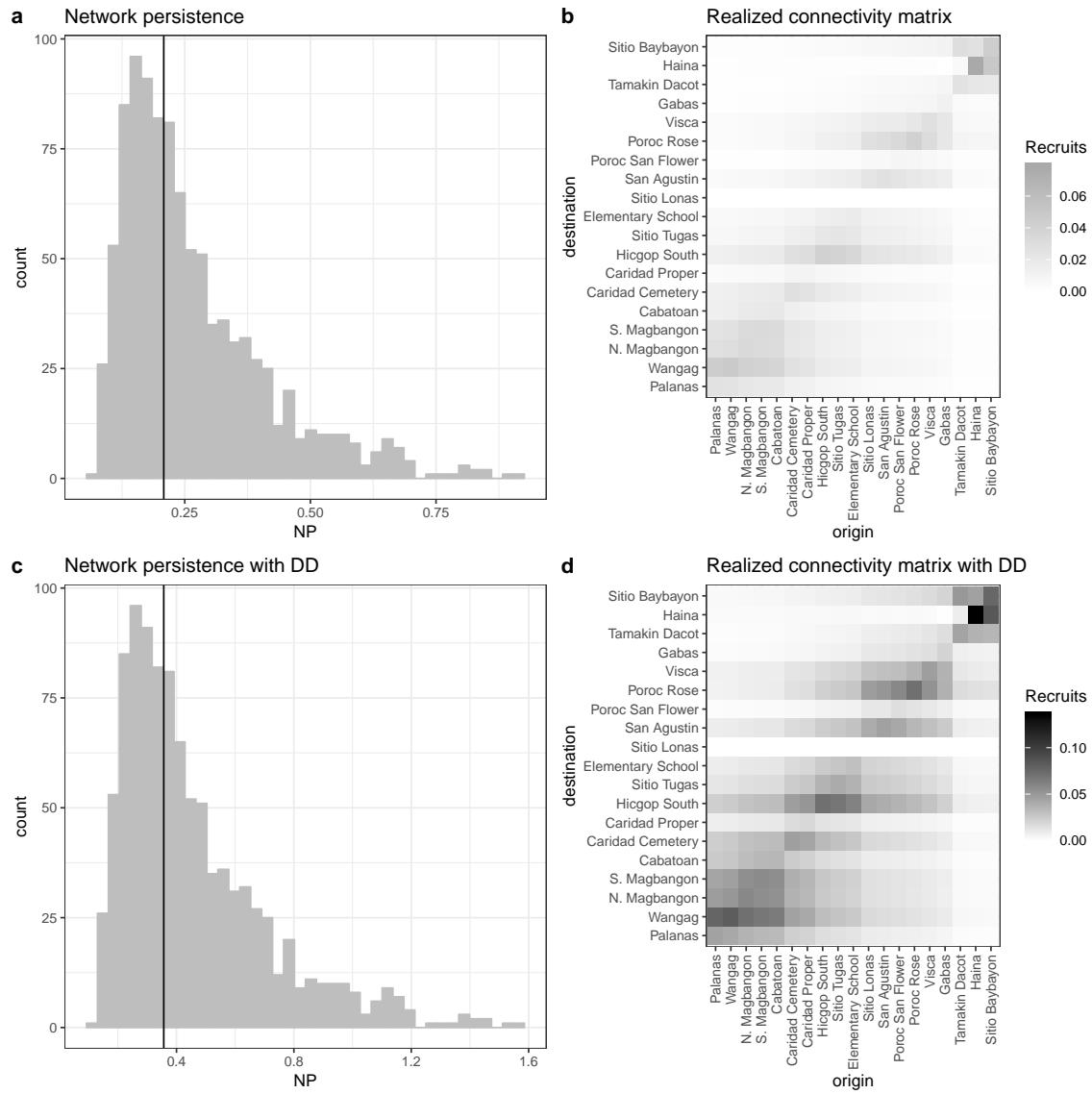


Figure 7: a) Network persistence values, showing the best estimate (black solid line) and range of estimates considering uncertainty, without accounting for density-dependence in our data. b) The realized connectivity matrix C , with sites arranged from north (Palanas) to south (Sitio Baybayon), without accounting for density-dependence in our data. Plots c) and d) show the network persistence values and realized connectivity matrix with attempts to compensate for density-dependence in early life stages in our data.

411 Based on our estimates of LRP, LRP_{local} , SP, and NP, it is possible but not likely
that our set of sites is able to persist in isolation as a closed system. To explore what
would be required for persistence in our best estimates, we consider a hypothetical
414 scenario in which we assume that all of the recruits arriving at our sites came from
adults at our sites. In this case, we find a value of $LRP = 1.2$, or 2.06 when we
compensate for density-dependence, higher the value of 1 necessary for replacement
417 (Fig. B.1a), and a corresponding higher value of λ_c in our best estimate ($NP = 0.30$,
 0.52 when compensating for density-dependence) (Fig. B.1b). The best estimate
does not indicate network persistence but we do see NP values greater than one in
420 the high end of the uncertainty range both with and without density-dependence
compensation, suggesting that the sites might persist if all recruits received came
from within. With our site configuration and dispersal kernel estimate, we would
423 need a value of LRP of 3.99 (an egg-recruit survival of 0.0038 with our estimated
value of LEP or a value of LEP of 5095 or 2975 with our estimated egg-recruit
survival compensating and not compensating for density-dependence, respectively),
426 to have a best estimate of $\lambda_c = 1$ and network persistence.

Discussion

We do not see strong evidence for persistence in our metric estimates. We see no
429 evidence for self-persistence where an individual site could persist alone and weak
evidence for network persistence, with network persistence possible at the upper end
of our range of estimates with uncertainty but not suggested by most of the estimate
432 range or our best estimates. The abundances through time at our sites are relatively

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

For our sites to be able to persist as a network on their own, the number of surviving recruits produced by an average recruit - LRP - would likely need to be
438 higher. With our estimated connectivity among the sites, LRP would need to be at least 3.99 to see network persistence among our sites, which is within the top of our range of uncertainty but about 4.8 times higher than our best estimate and 2.8 times
441 higher than our best estimate when we compensate for density-dependence. Our best estimate of LRP when we compensate for density-dependence is greater than one, so higher connectivity and retention of offspring among our sites could lead to
444 network persistence. At our best estimate without density-dependence compensation, however, LRP is less than one for our sites - the average recruit only replaces itself with 0.83 of a surviving recruit of the same stage - no amount of increased
447 retention or connectivity, even retaining all of the recruits produced from our sites, would lead to network persistence. Similarly, if other surrounding patch populations had a similar LRP, increasing the area of the network to include them would also not
450 achieve network persistence. If nearby sites have higher egg production or survival to recruit, however, it might not take much of an increase in area considered to create a persistence network. Nearby sites such as Quatros Isles and XX have higher quality
453 habitat and could be contributing recruits to our sites.

We see considerable uncertainty in our estimate of persistence metrics, depending on the particular input values we use, with LRP values ranging from XX to XX and

456 NP values from XX to XX. We see a factor of XX between our highest and lowest
457 LRP values and our best estimate of LRP is only XX times away from suggesting our
458 population is network persistent. Measuring demographic and dispersal parameters
459 in the field is challenging, particularly egg-recruit survival, which also has a large
460 effect on our persistence metric estimates. and accounting for our uncertainty clearly
461 helps us understand XX. While none of our estimates even with uncertainty indicate
462 persistence and our population is likely subsized by outside input and unable to
463 persist as a network on its own,

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

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

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

⁴⁷⁷ WITH OTHER VALUES OF SURV, GROWTH, FECUNDITY. The reef health
and habitat quality in our sites in generally low, due anthropogenic effects such as
pollution and silt from a nearby gravel mining operations and habitat disturbance
⁴⁸⁰ due to storms. Our sites are in an area that was hit by Typhoon XX, the strongest
typhoon ever to make landfall, early in our sampling period, which destroyed much
of the reef habitat in some of our northern sampling areas. This recent disturbance
⁴⁸³ and generally low habitat quality could contribute to low production of surviving
recruits in our sites, necessitating subsidation by outside populations. RAP-UP,
CONCLUDING SENTENCE OR TWO!

⁴⁸⁶ 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
⁴⁸⁹ 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,
⁴⁹² 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
⁴⁹⁵ 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
⁴⁹⁸ 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
501 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 and increase
504 LRP.

Our estimates of persistence metrics do not suggest that the region of site we
sample are able to persist as a network without outside input, despite covering an area
507 larger than the estimated mean dispersal distance for our focal species. Our below-
one estimate of LRP, even when we consider uncertainty, suggests that dispersal
is not the primary reason our sites do not persist as a network: our sites do not
510 produce enough offspring for replacement regardless of dispersal patterns, possibly
due to worsening habitat quality. This is a reminder that dispersal is only part of the
persistence story for metapopulations; even areas of habitat that seem large enough
513 to contain a persistent network based on dispersal distance will not be able to persist
in isolation if they have low production and survival of offspring. We do find recruits
coming back to our region, and even to their natal site, but broader connectivity to
516 more productive sites enables our sites to persist.

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

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

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

525 • They can both be true at the same time - maybe fish from our sites don't
disperse very far but others in sites nearby have access to different currents,
etc. send recruits farther and into our sites.

528 • It's a linear coastline but within a big bay - could have some interesting connec-
tivity patterns via currents/eddies/etc. (reference how far the drifters went?)

Are there some citations on this?

5) Caveats paragraph

531 • Density-dependence - likely plays a larger role throughout the life cycle, not just
at early life - particularly important in this species (and others with strong
social hierarchies)

534 • Site-specific demographic rates - coming in the future as get more of a handle on
predator densities and such. Not have enough data from some of the sites and
some of the params (fecundity) to get site-specific rates, though those have
been interesting/important in other systems. If our larger sites had higher
537 production/survival, might see persistence.

6) Wrap-up paragraph

540 • How does this contribute to our understanding of metapopulation persistence?
Where do we go from here?

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

543 where an individual site could persist alone or network persistence with exchange
among sites. The abundances through time at our sites are relatively constant,
however, suggesting that the population at our sites is stable but relies on input of
546 recruits from outside sites to persist. The portion of coastline we sampled is likely a
portion of a larger metapopulation.

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

- So we don't see persistence in our metrics, either self-persistence or network
552 persistence but our abundances don't seem to be changing. Suggests that
this is just a portion of a larger metapopulation, rather than a self-contained
metapopulation. Maybe it is a sink? Persistent in terms of constant abundance
but relies on outside immigration to persist.
- How does dispersal spread (estimated to be within our sites) interact with scale
555 of a self-contained metapopulation? How do we reconcile this in our system,
where we don't estimate dispersal that far but don't see network persistence
in an area range that spans the estimated spread? (This point might change,
558 depending on mean dispersal distance from the new kernels)
- Sensitivity - how would our parameters need to change to see persistence?
561 Egg-recruit survival is a big one. Discuss limitations of how we calculated it
(offspring going outside our pops not included - though we might change this),
what we see for persistence when estimate recruits/recruits instead. Context-

564 tualize this with what other studies have found for these parameters, how
reasonable it would be to get better estimates in the field.

Persistence criteria, such as those detailed in Hastings and Botsford (2006) and
567 Burgess et al. (2014), ask whether a population at low abundance can grow and
recover rather than going extinct. Density-dependence is assumed to not exist at
low abundances (CITATIONS, with the exception of xx density-dependence, like the
570 allee effect) so is not explicitly considered in persistence metrics. In real populations,
however, it can be challenging to estimate density-independent demographic rates,
as density-dependence is occurring in the population as it is sampled. In *A. clarkii*,
573 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,
576 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-
579 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
582 on our estimate of egg-recruit survival but other estimates, particularly growth and
survival, would also likely be higher in the absence of density-dependence and increase
LRP.

585 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,
588 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).

591 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
594 DD isn't happening, that really matter for persistence. Egg-recruit-survival is probably higher in that case than our estimate of it here (b/c larvae able to settle without being chased off by already-settled recruits). But is it high enough?
- Discuss site-specific demographic rates, why we don't estimate them in our system, the importance they play in other studies, what we might need to go about resolving them, whether we would expect to see them.
600
- Contextualize our parameter estimates with those from other studies (esp. survival, growth, fecundity).

603 Broadening back out:

- What does this mean for moving forward in understanding metapopulation persistence more broadly? Stability in abundance doesn't mean the population
606 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.

609

Appendix

Summary of parameters

[Need to clarify somewhere what kind of distributions are going into the uncertainty
 615 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
$\text{size}_{\text{recruit}}$	size (cm) of recruited offspring	mean of size of offspring in parentage analysis = 4.4 cm	3.5 - 6.0 cm	

$\text{size}_{\text{recruit},sd}$	standard deviation of size of a recruit	0.1		used in discretization of IPM for LEP
size_{sd}	standard deviation distribution of sizes of a fish in the next year			used in discretization of IPM for LEP, estimated from range of sizes for fish starting at 7.4-7.6 cm and recaptured a year later
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_h	proportion of sites sampled cumulatively across time			details in A.1
P_d	proportion of dispersal kernel area from each site covered by our sampling region			details in A.2
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
P_s	proportion of our sampling region that is habitat			details in A.3

DD	proportion of habitat that would be available without density- dependence at settlement			
p_U	proportion of anemones un- occupied by clownfish			used to estimate DD
p_A	proportion of anemones oc- cupied by <i>A.</i> <i>clarkii</i>			used to estimate DD

Table A1:

A Method details

A.1 Proportion of habitat sampled

618 We used tagged anemones to estimate the proportion of habitat sampled at each site
in each year ($P_{h_{i,t}}$). We tagged each anemone that is home to *A. clarkii*, with a metal
tag, which is relatively permanent and easy to re-sight (the anemone tag is visible
above the anemone in Fig. 2c), so we consider the total number of metal tags at each
site to be the total number of anemones that are habitat. We divide the number of
tagged anemones visited each sampling year by the total number of metal tags at
that site to get the proportion of habitat sampled. We use proportion of anemones
rather than proportion of total site area because anemones, and therefore habitat
quality, are unevenly distributed across the site; areas we did not visit are likely to
have a lower density of anemones than the areas we did sample.
624
627

For scaling the number of tagged recruited offspring to account for areas of our
sites we did not sample, we use the overall proportion habitat sampled across all sites
and sampling years (P_h). We sum the metal-tagged anemones we visited across all
sites and years to get the total number of metal-tagged anemones we visited while
sampling. We then divide that by the number of anemones we could have sampled,
the sum of total metal-tagged anemones across all sites multiplied by the number of
sampling years, to get the overall proportion habitat sampled across our sites and
sampling years.
630
633

636 *Add details about how sometimes it is $\neq 1$ if the site doesn't have metal tags?*

Mention plastic tags?

		% Habitat surveyed							
Site	# Total anems	2012	2013	2014	2015	2016	2017	2018	
Cabatoan	26	42	58	58	65	73	0	62	
Caridad Cemetery	4	0	75	50	0	50	50	50	
Elementary School	8	0	100	38	88	88	88	100	
Gabas	9	0	0	0	44	44	67	0	
Haina	104	0	6	13	13	10	56	80	
Hicgop South	18	0	67	22	28	56	83	78	
N. Magbangon	105	5	12	40	63	63	0	5	
S. Magbangon	34	41	56	32	0	65	0	71	
Palanas	137	29	58	47	63	85	86	86	
Poroc Rose	13	100	100	69	31	23	69	69	
Poroc San Flower	11	100	82	73	73	55	82	64	
San Agustin	17	94	65	71	65	100	82	76	
Sitio Baybaon	260	0	14	30	33	30	41	80	
Tomakin Dako	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 A2: Table showing the percent of metal-tagged anemones surveyed at each site in each sampling year.

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

639 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
645 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
648 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 : $P_c = \frac{m_2}{n_2}$.

651 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
654 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
657 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

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

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

The mean of the individual capture probability values is $\mu_{P_c} = 0.56$, with variance
 660 $V_{P_c} = 0.069$, 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
 values larger than the lowest value of P_c estimated in an individual dive (0.20), to
 663 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
 the length of the number of runs.

666 Proportion of dispersal kernel area sampled

[Add in description of calculation and equation]

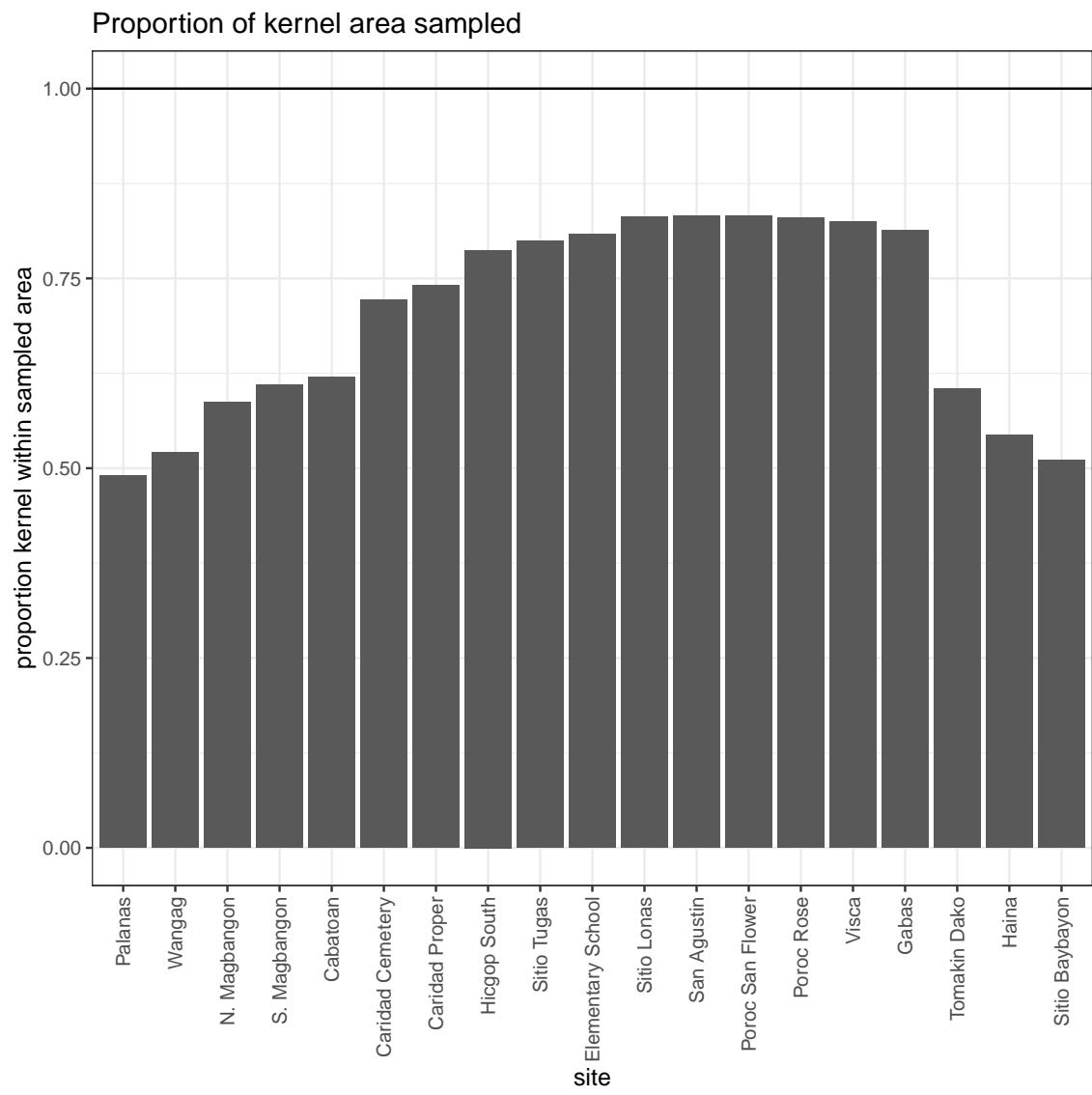


Figure A.1: Proportion of the dispersal kernel area from the center of each site covered by our sampling.

A.3 Proportion habitat in sampling area

669 We assume that larvae are unable to navigate to habitat if they attempt to settle
on an unsuitable patch, though clownfish larvae do likely have some ability both to
sense habitat (CITATIONS) and move toward it (CITATIONS)). To avoid counting
672 mortality due to settling on non-habitat twice - once in scaling up our matched
recruits, which only includes those who settled on habitat, and once in integrating
the dispersal kernel, we scale our estimate of total surviving recruits from our patches
675 by the proportion of our sampling region that is habitat (P_s). We find P_s by summing
the lengths of all of our sites, which run approximately north-south, and dividing
that by the total distance north-south of our sampling region, giving $P_s = 0.20$.

678 **A.4 Full set of MARK models**

We consider the following set of models in MARK [*Need to add in models*]:

A.4.0.1 Recapture model

- 681 The best model for log-odds recapture probability, accompanying the survival model in eqn. 11, has a size effect ($b_1 = -1.816 \pm 0.080$ SE, Fig. A.2a) and a negative effect of diver distance from the anemone ($b_2 = -0.171 \pm 0.021$ SE, Fig. A.2b), with 684 intercept $b_{p_r} = 17.93 \pm 0.858$ SE:

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

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.

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 A3:

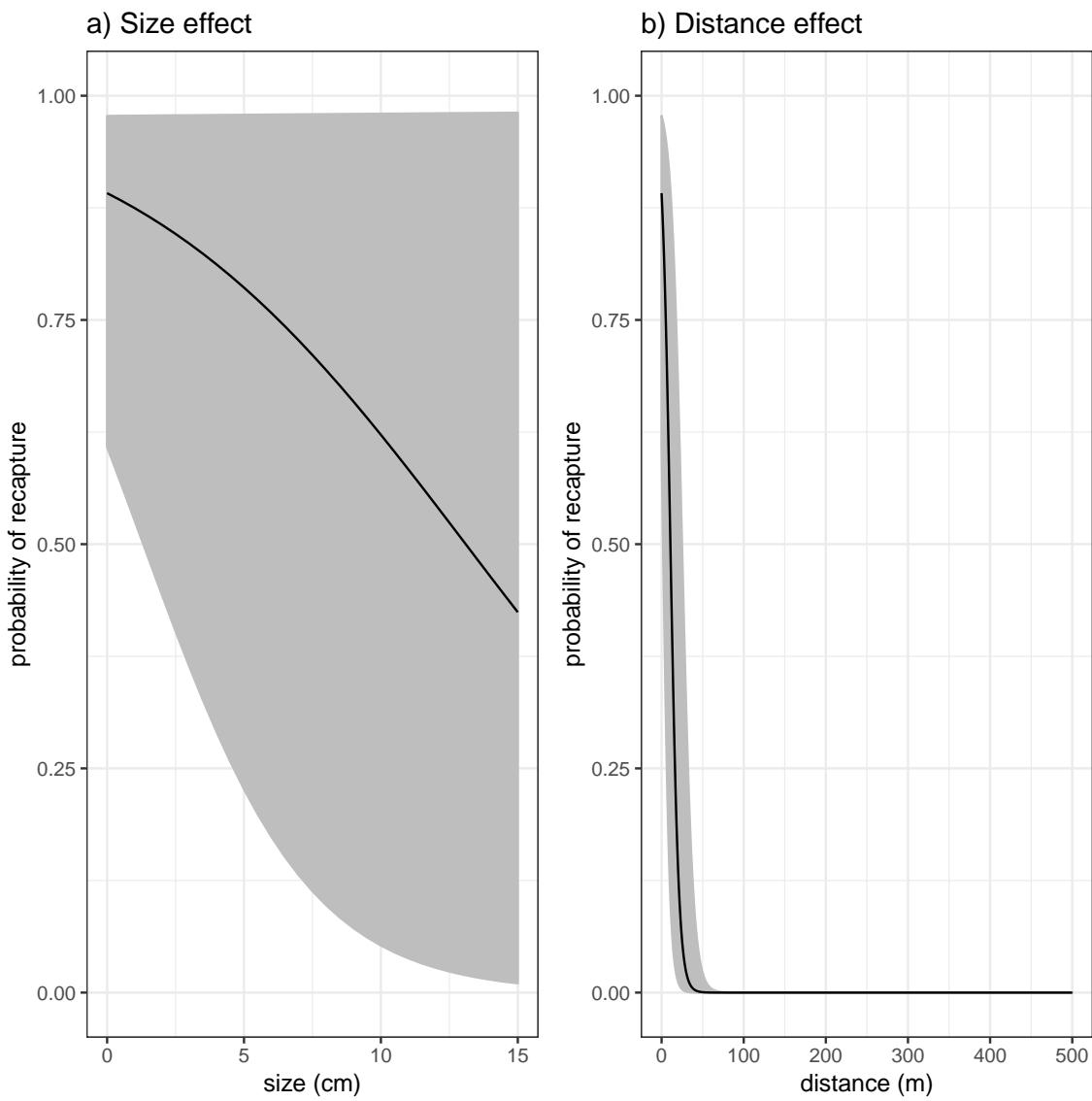


Figure A.2: Effects of a) fish size and b) minimum distance between divers and the anemone where the fish was first caught on the probability the fish will be recaptured, estimated along with survival in a mark-recapture analysis. Size has a slightly negative effect on the probability of recapture -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

687 **B Uncertainty and sensitivity**

B.1 What-if analyses

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

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

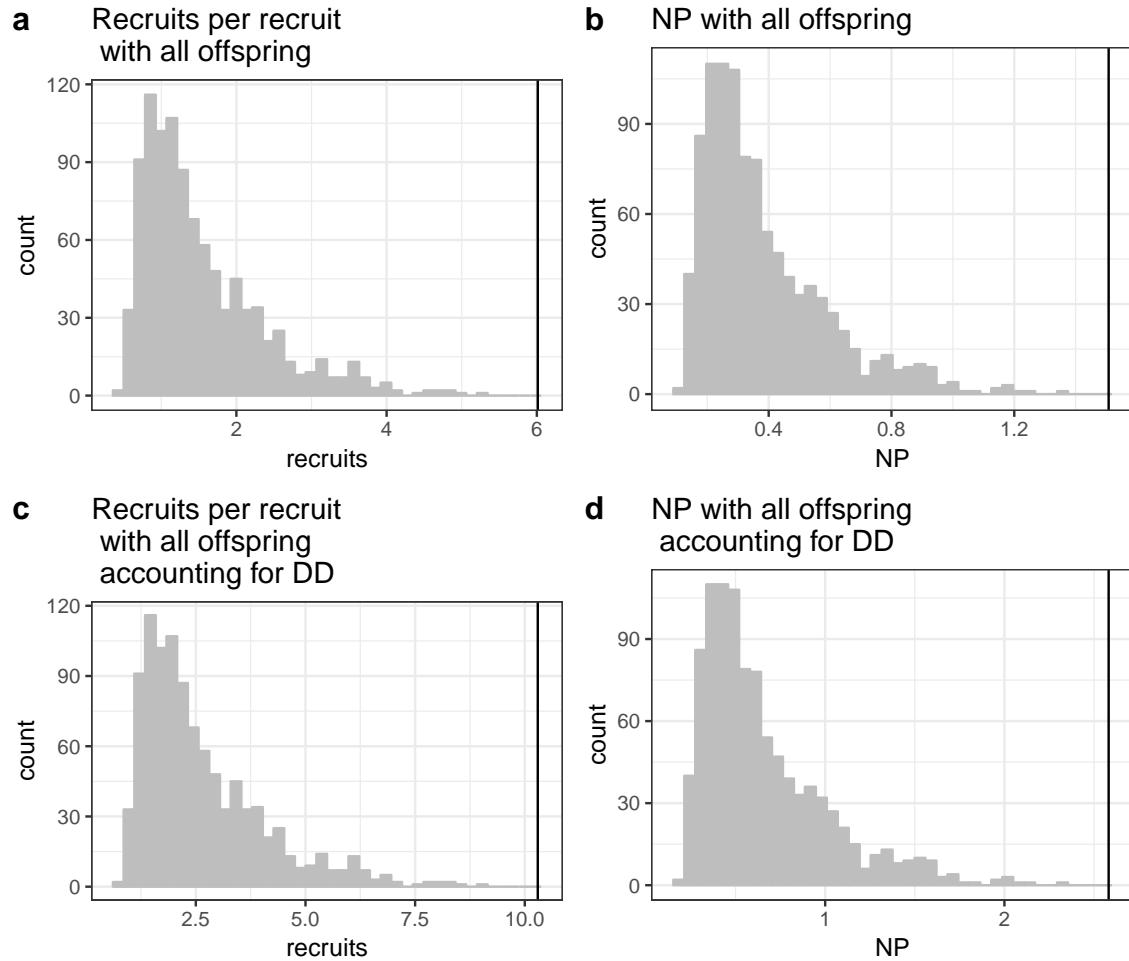


Figure B.1: a) Recruits per recruit when we consider all arriving recruits to have originated from our sites. b) Range of values of NP considering all arriving recruits to be offspring from our sites, with the best estimate in a black solid line.

B.2 Sensitivity to parameters

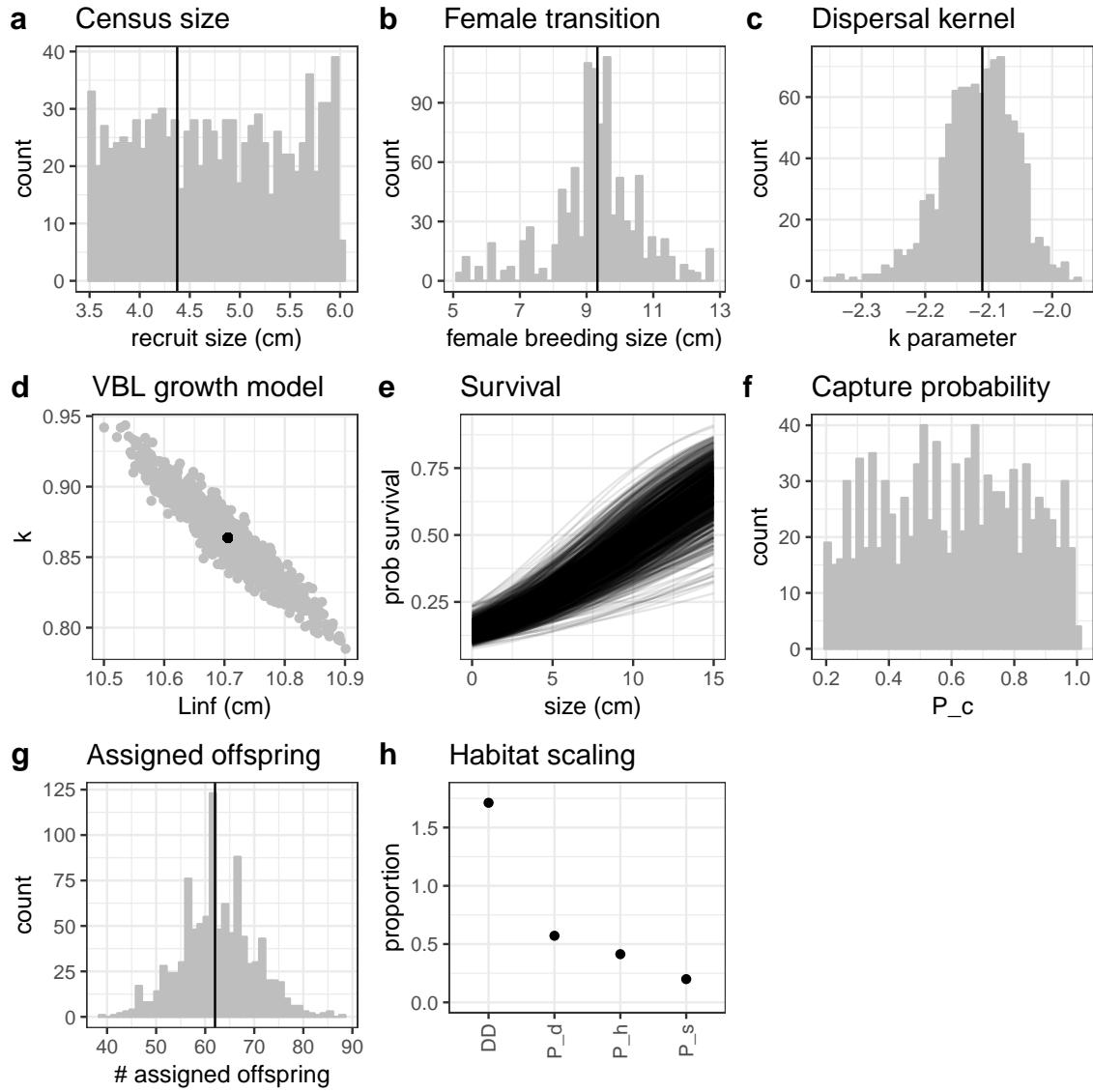


Figure B.2: Range of parameter inputs for uncertainty runs with all uncertainty included: a) $\text{size}_{\text{recruit}}$, the census size at which fish are considered to have recruited after egg-recruit survival occurs; b) L_f , the size at which fish transition from male to female and their reproductive output 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; g) number of offspring assigned back to parents in the parentage analysis.

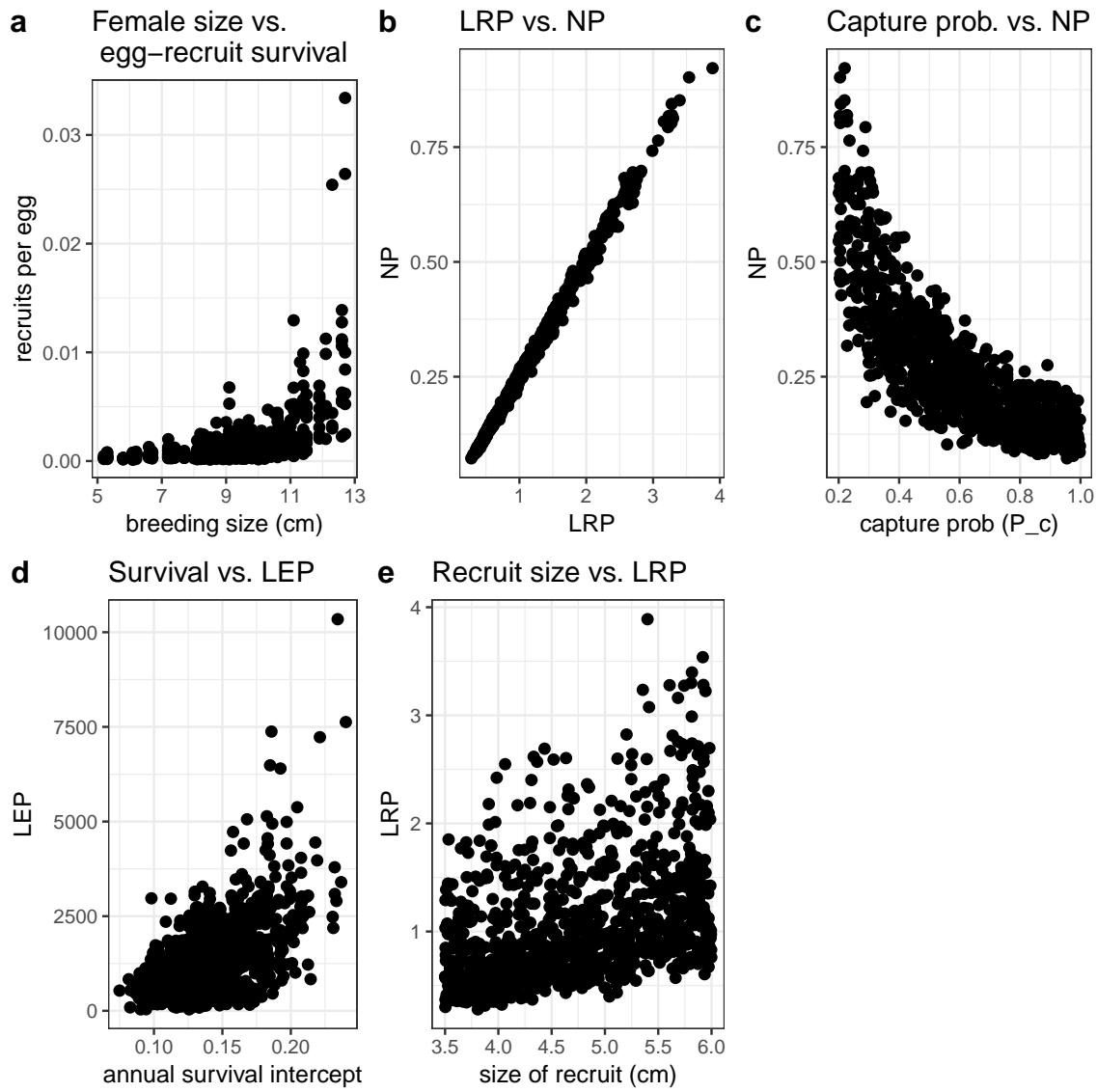


Figure B.3: Relationships among parameters and metrics. a) We only count reproductive effort by fish in the female stage so the higher the transition size to breeding female, the fewer eggs parents are considered to produce, which increases the estimated egg-recruit survival. b) LRP strongly affects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

₆₉₉ **B.3 Effects of different types of uncertainty on metrics**

B.3.0.1 Lifetime egg production (LEP)

Annual survival post-recruitment provides drives most of the uncertainty in LEP,
₇₀₂ as lower survivals keep fish from reaching and staying at large breeding sizes, with
higher fecundity. The transition size to breeding female also drives uncertainty in
LEP - the higher the transition size to female, the less time the fish has at a size
₇₀₅ where its reproduction is counted in LEP.

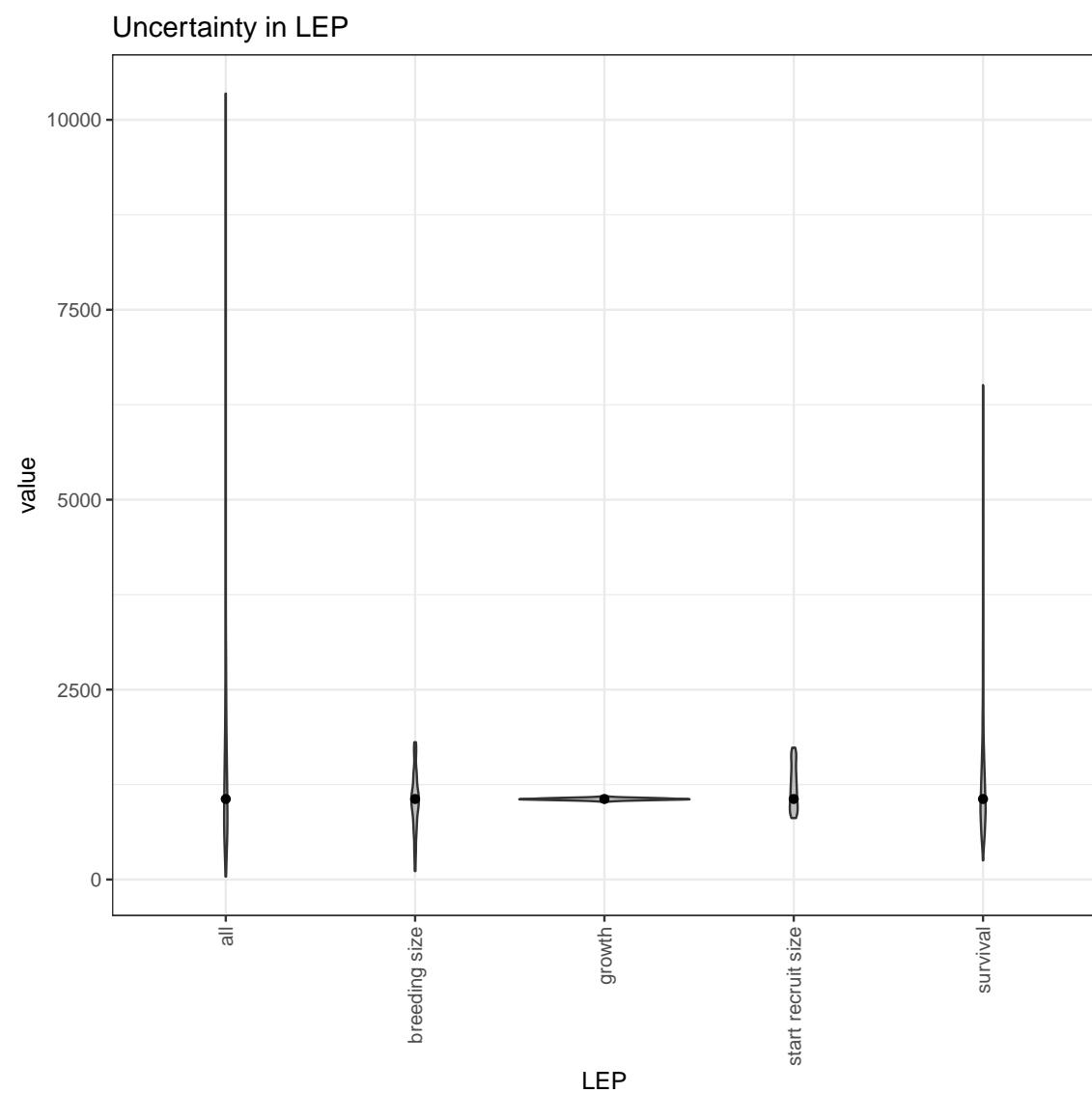


Figure B.4: The contribution of different sources of uncertainty in LEP.

B.3.0.2 Lifetime recruit production (LRP)

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

Uncertainty in LRP

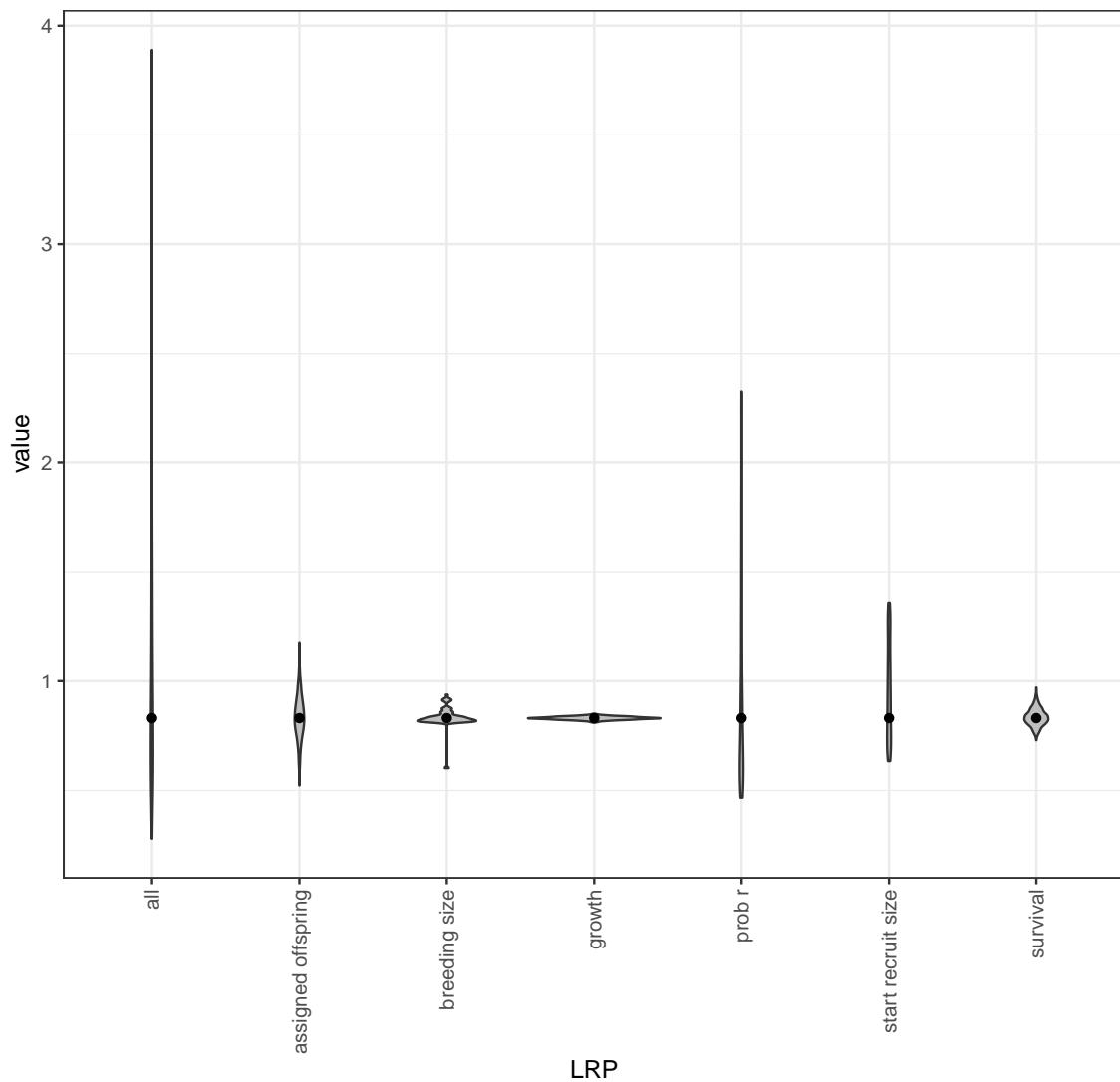


Figure B.5: The contribution of different sources of uncertainty in LRP.

Uncertainty in LRP accounting for DD

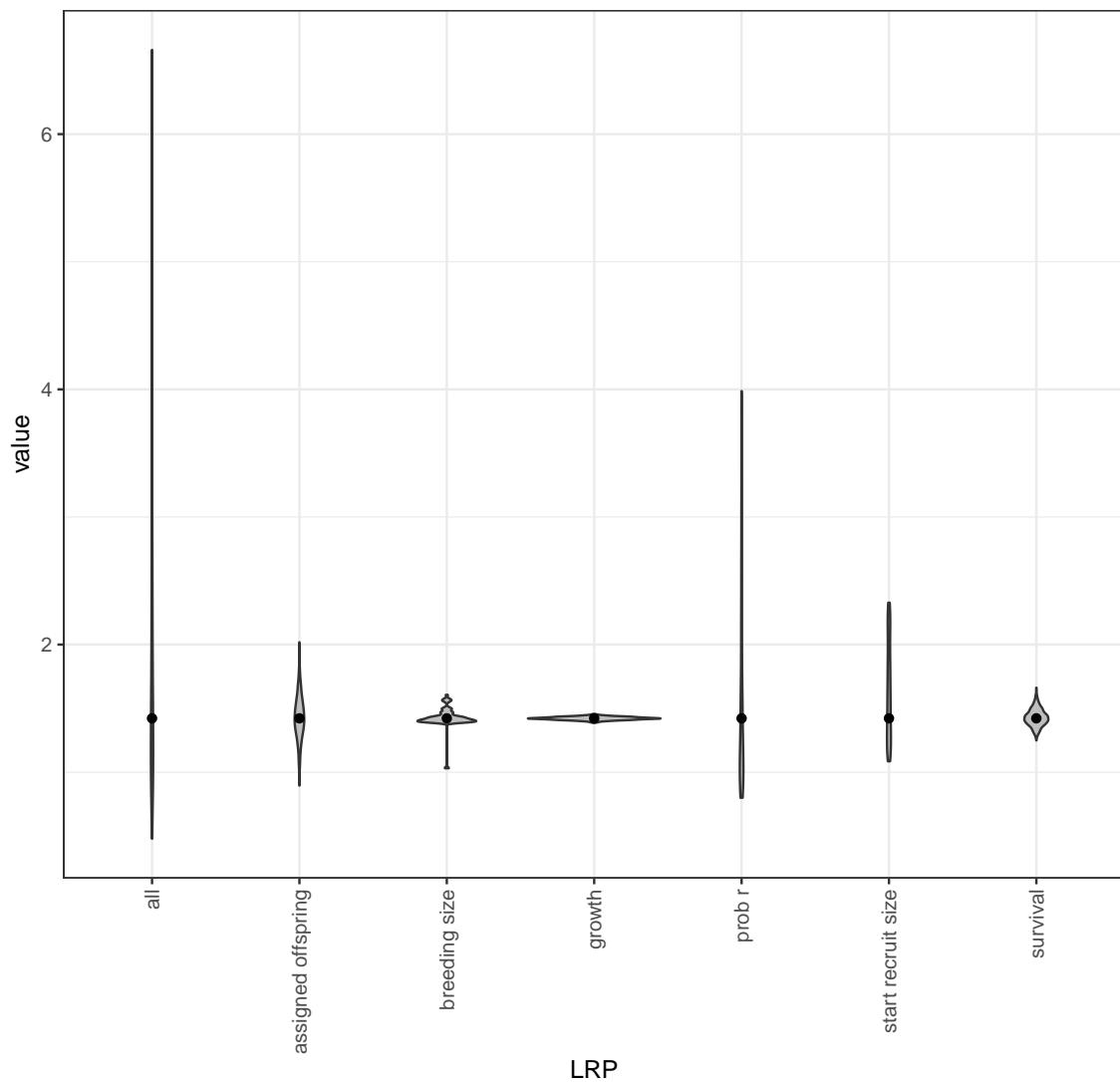


Figure B.6: The contribution of different sources of uncertainty in LRP, when we account for density-dependence in egg-recruit survival.

B.3.0.3 Egg-recruit survival (S_e)

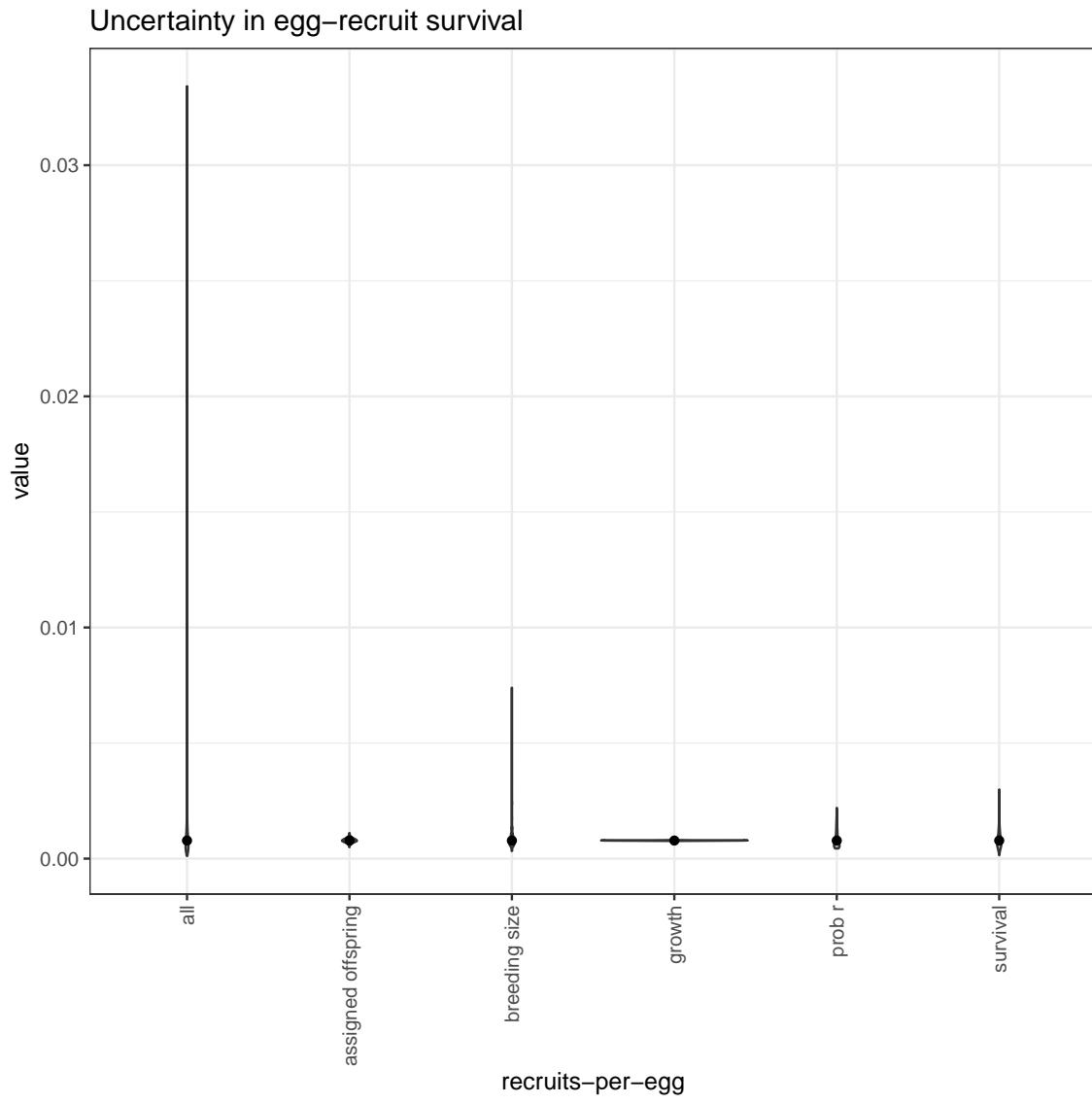


Figure B.7: The contribution of different sources of uncertainty in egg-recruit survival.

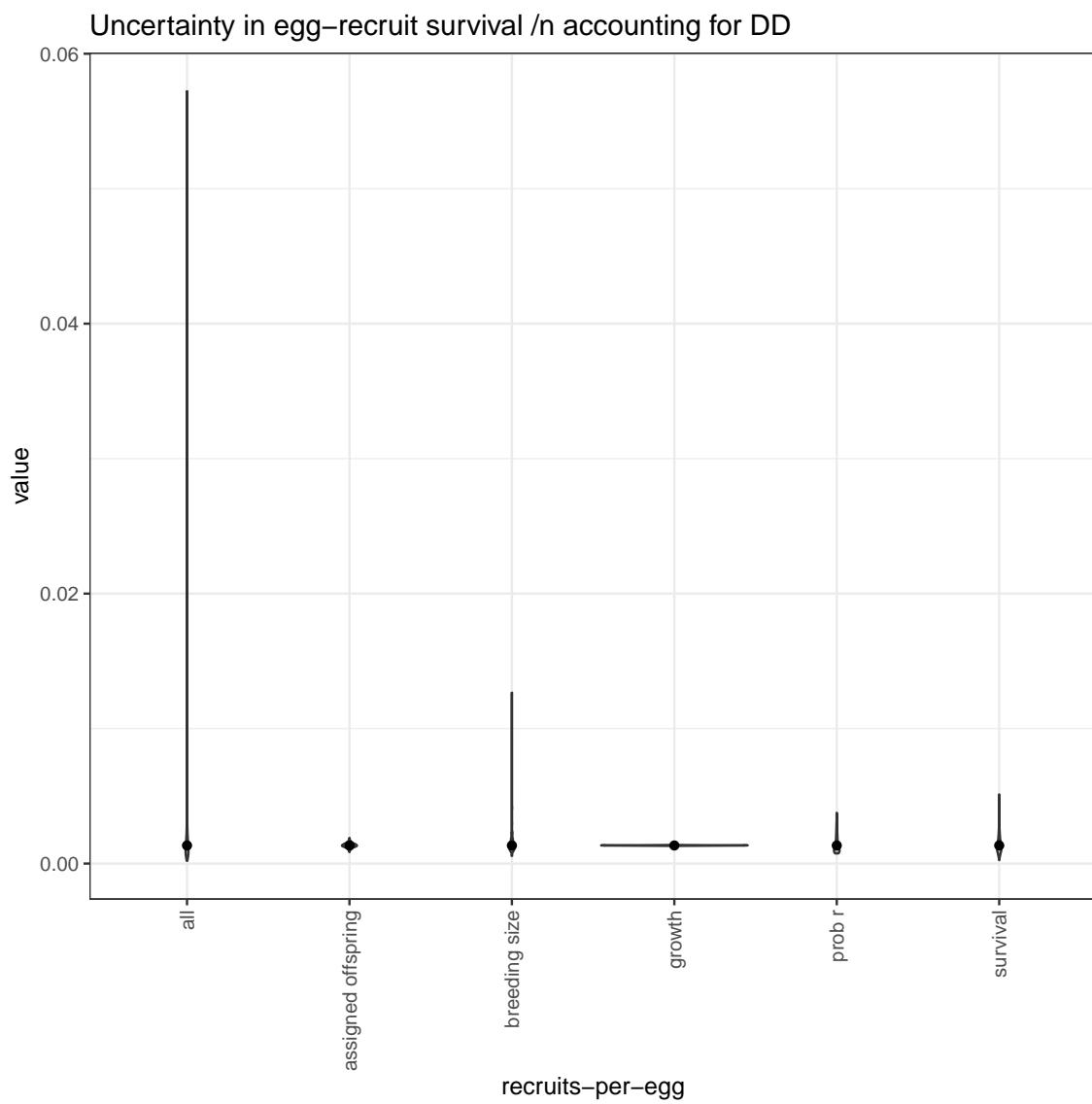


Figure B.8: The contribution of different sources of uncertainty in egg-recruit survival when we account for density-dependence in egg-recruit survival.

B.3.0.4 Network persistence (NP)

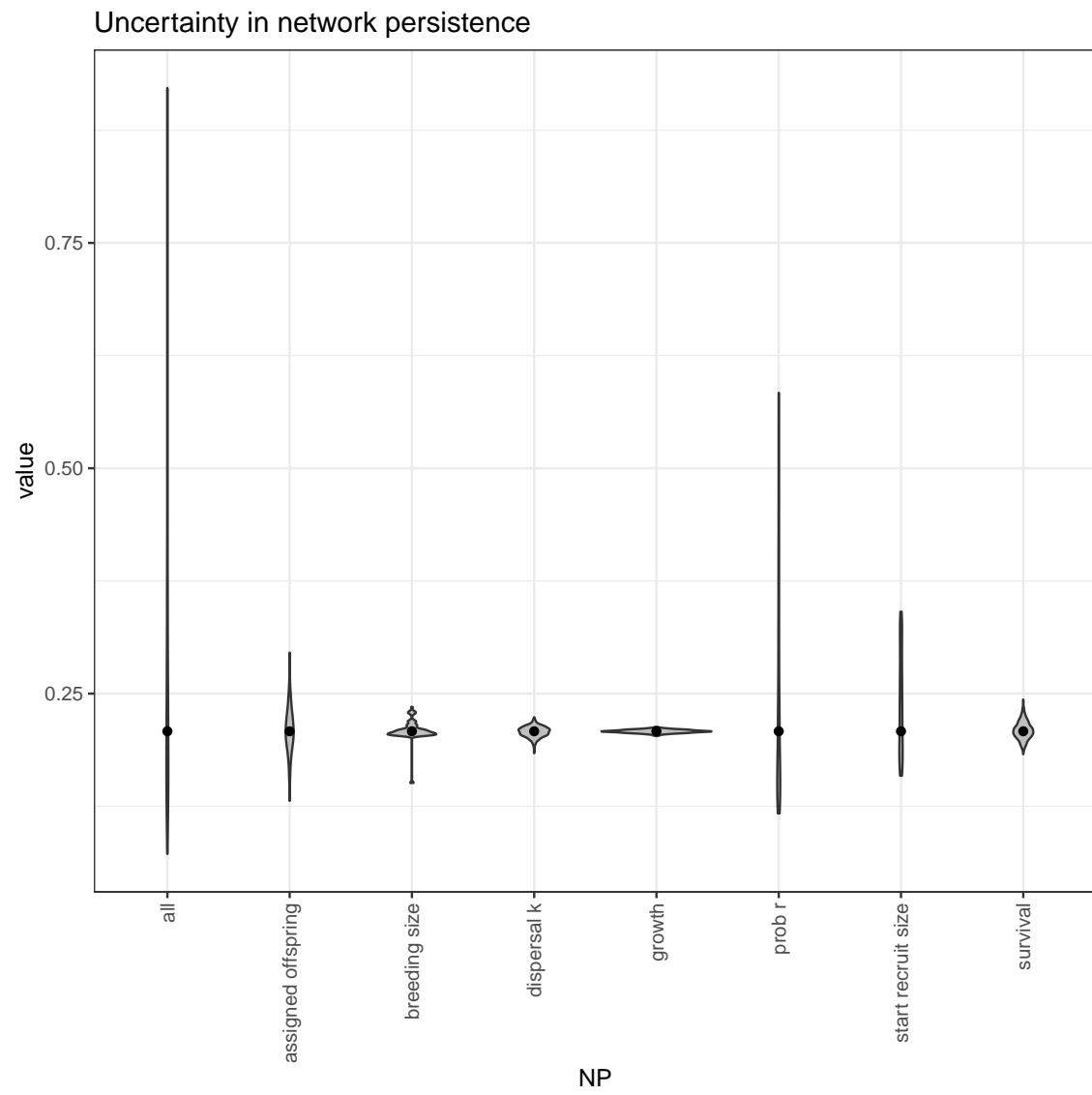


Figure B.9: The contribution of different sources of uncertainty in NP.

Uncertainty in network persistence /n accounting for DD

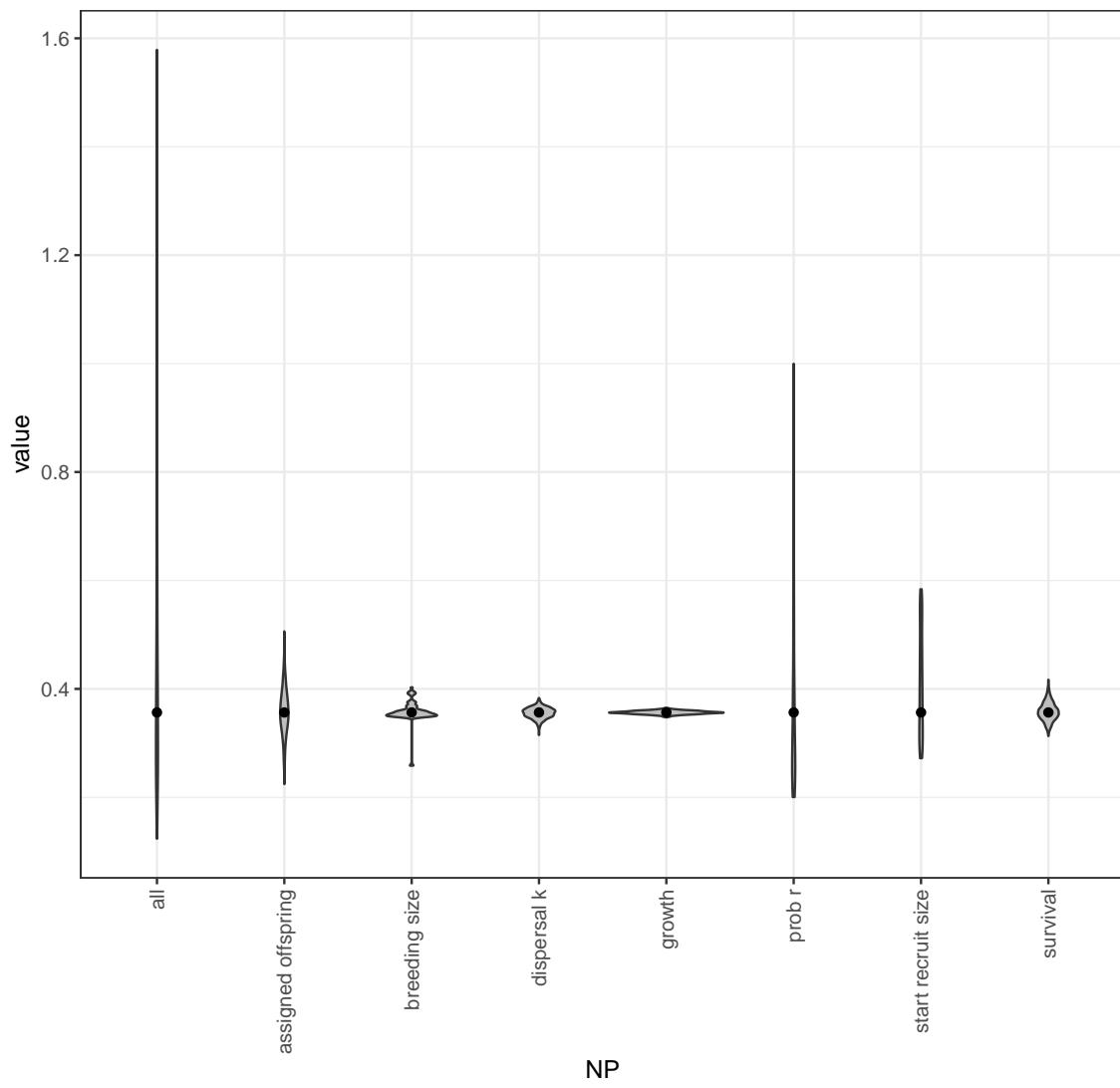


Figure B.10: The contribution of different sources of uncertainty in NP when we account for density-dependence in egg-recruit survival.

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