

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.

Self-persistence

¹¹⁴ 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
¹¹⁷ 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
¹²⁰ criteria for self-persistence: $\text{LEP} \times \text{LR} \geq 1$. 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:

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

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

¹²³ 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).

¹²⁶ 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
¹²⁹ 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
132 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 con-
135 nectivity matrix λ_C be greater than 1: $\text{NP} = \lambda_C > 1$ (e.g. Hastings and Botsford,
2006; White et al., 2010; Burgess et al., 2014).

Defining recruit and census stage

138 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
141 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
144 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
147 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
150 covers (3.5-6 cm, Table A1).

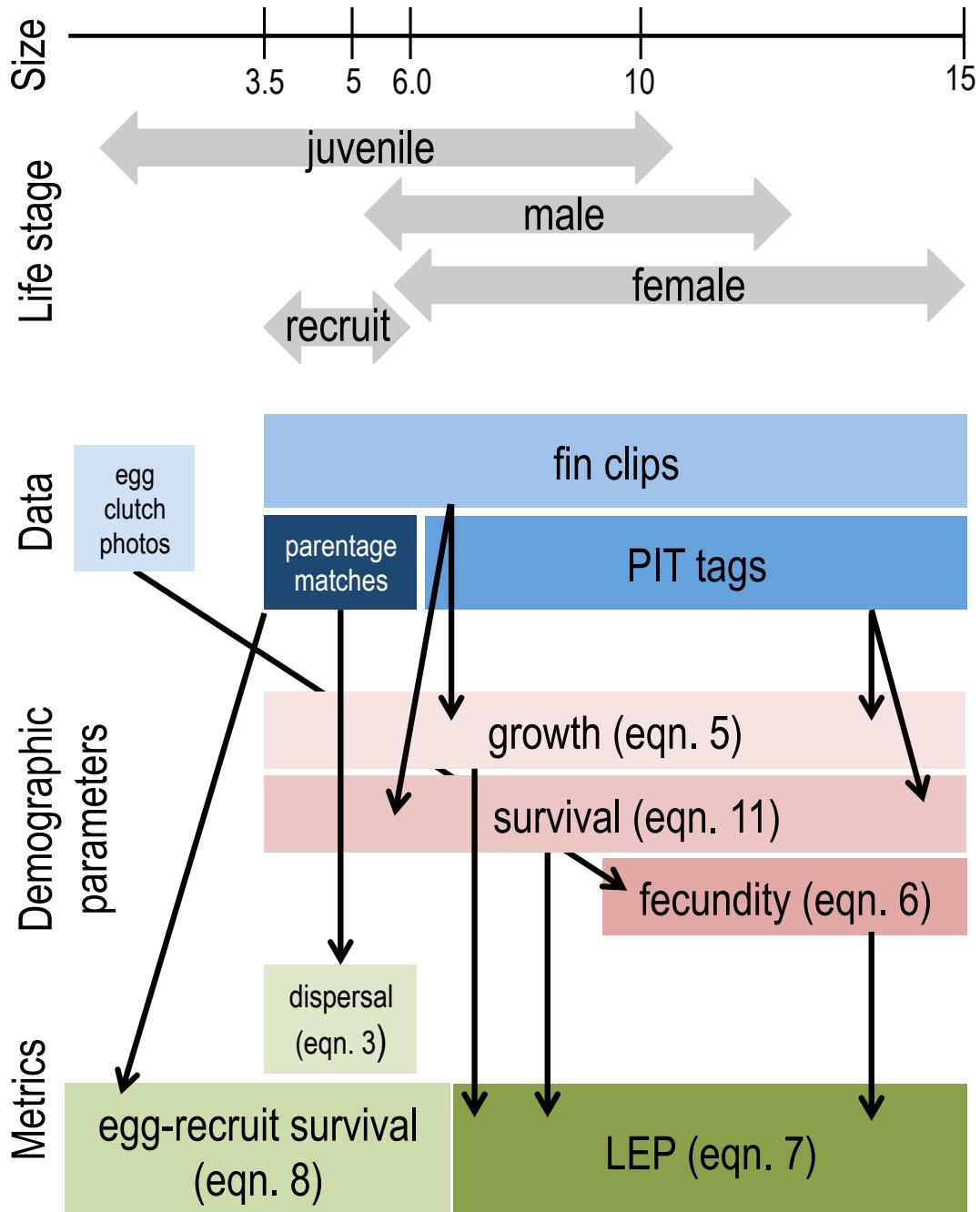


Figure 1: Here, we show the data collected for fish at each life stage (life stage boxes are not scaled by length of stage) and how the empirical data fit into our parameter
9 and metric calculations.

Study system

We focus on a tropical metapopulation of yellowtail clownfish (*Ampiprion clarkii*, Fig. 153 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 156 with anemones, where small colonies of fish live (Buston, 2003b; Fautin et al., 1992). Yellowtail clownfish are protandrous hermaphrodites and maintain a size-structured 159 hierarchy; within an anemone, the largest fish is the breeding female, the next largest is the breeding male, and any smaller fish are non-breeding juveniles. The fish on an anemone maintain a strict social and size hierarchy (Buston, 2003b), with fish moving up in rank to become breeders only after the larger fish have died. In the 162 tropical patch reef habitat of the Philippines, yellowtail clownfish spawn once per lunar month from November to May, laying clutches of benthic eggs that the parents protect and tend (Ochi, 1989; Holtswarth et al., 2017). Larvae hatch after about six days and spend 7-10 days in the water column before returning to reef habitat to 165 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 168 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 171 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
174 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
177 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
180 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).

183 **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
186 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
189 exceed that range. On the north edge, the sites are isolated from nearby habitat
with no substantial reef habitat for at least 20 km.

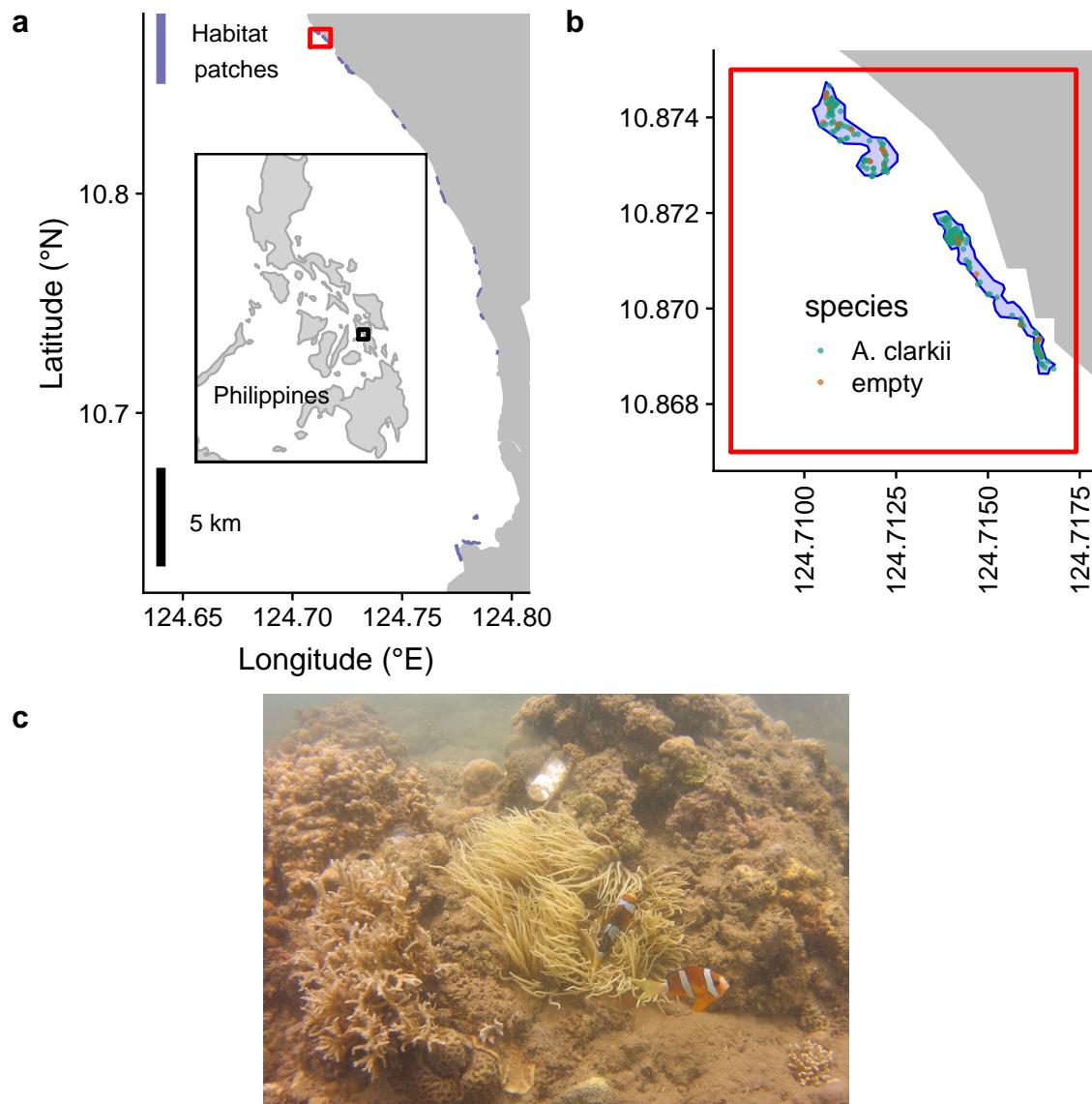


Figure 2: a) Map of the sites along the coast of Leyte in the Philippines. b) Zoomed-in map of the two northern-most sites, Palanas and Wangag, to show anemone arrangement, with anemones occupied by *A. clarkii* (green) or unoccupied by clownfish (orange). c) An example anemone occupied by *A. clarkii* 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 192 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, 195 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 198 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 201 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

204 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 207 (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, 210 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

213 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

- ²³¹ 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.
- ²³⁴

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:

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

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 .

²⁴⁰ ²⁴³ 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

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, 249 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. 252 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. 255 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 258 of the models (Table A3).

Fecundity

We use a size-dependent fecundity relationship, determined using photos of egg 261 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 264 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.

267 (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 270 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

273 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 276 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 279 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, 282 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 285 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 288 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
 291 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).

294 **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
 297 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
 300 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
 303 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

306 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
309 ($P_s = XX$, details in A.3) to avoid counting this mortality twice.

To incorporate uncertainty in our estimate of egg-recruit survival, we consider
uncertainty in the number of offspring assigned to parents during the parentage
312 analysis (R_m) and in the probability of capturing a fish (P_c). We generate a set
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
315 on each trial is the assignment rate of offspring from the parentage analysis (Catalano
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
318 recapture dives (details in A.2).

Accounting for density-dependence

Ideally we would assess persistence metrics when the population is at low abundance
321 and not limited by density-dependence. Clownfish have strong social hierarchies
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
324 clownfish, with anemones already occupied by *A. clarkii* settlers essentially
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
327 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
 330 present results both with and without this density-dependence modification.

Estimated abundance over time

We also consider trends in abundance of breeding females at each site over time to
 333 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
 336 probability of capturing a fish P_c :

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

We then fit a linear model through the time series for each site 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

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
 342 to be increasing or decreasing at our sites, eleven sites had a positive slope over 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,

³⁴⁵ Fig. 3b) and one has a negative slope (Sitio Baybayon, Fig. 3p) and the next two 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.

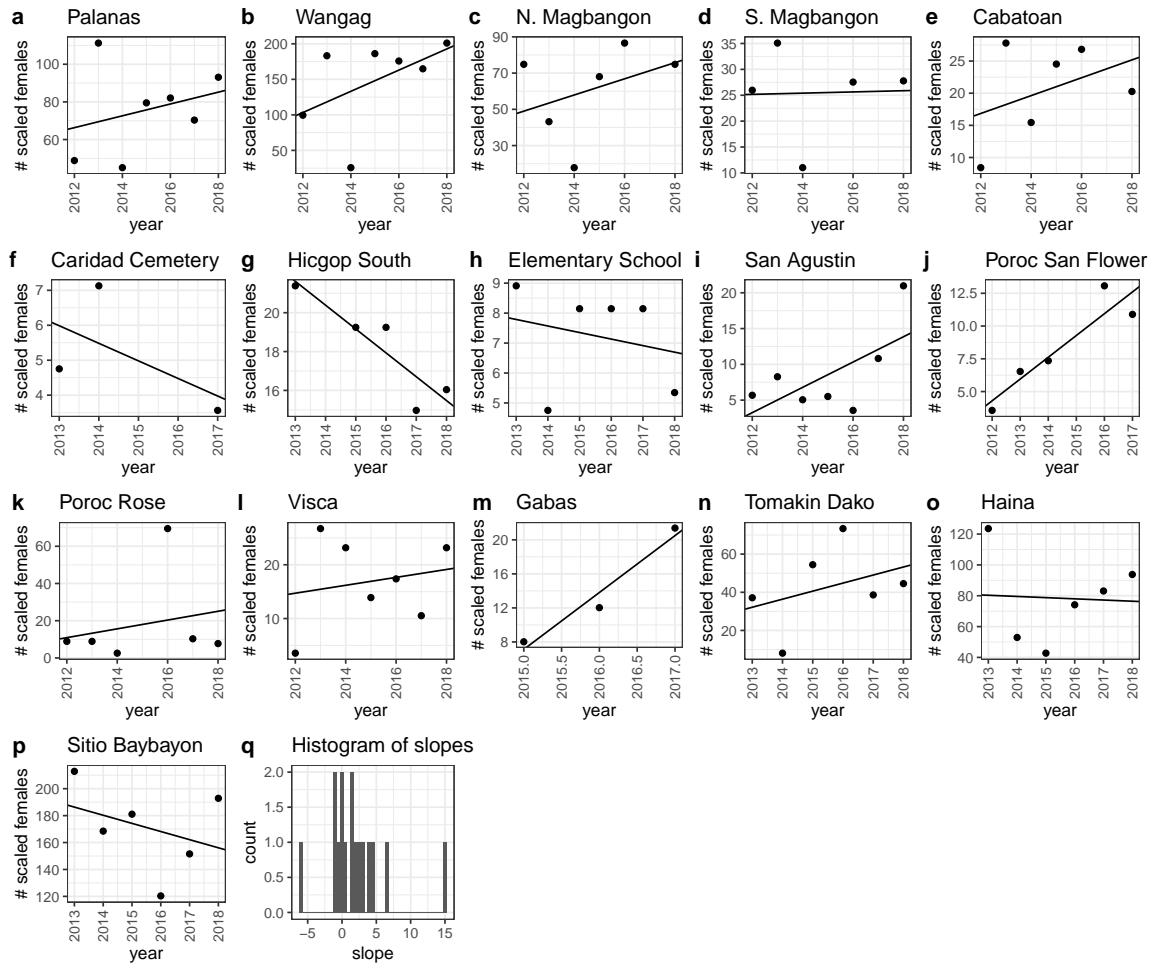


Figure 3: The estimated number of females at each site over the sampling years for sites sampled in at least three years. The total number of females at each site was estimated by scaling up the number of females captured at each site in each year by the proportion of habitat sampled at that site that 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).

From the mark-recapture analysis of tagged and genotyped fish, we estimate mean values of $L_\infty = 10.70\text{cm}$ (range of estimates 10.50 - 10.90 cm) and $K = 0.864$
 351 (range of estimates 0.785 - 0.944) for the von Bertalanffy growth curve parameters
 (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 $b_a = 0.169 \pm 0.028 \text{ SE}$
 354 and intercept $b_\phi = -1.83 \pm 0.231 \text{ SE}$. The accompanying best-fit model for log-odds recapture probability has a negative size effect and a negative effect of diver distance from the anemone (eqn. A.3, Fig. A.2).

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

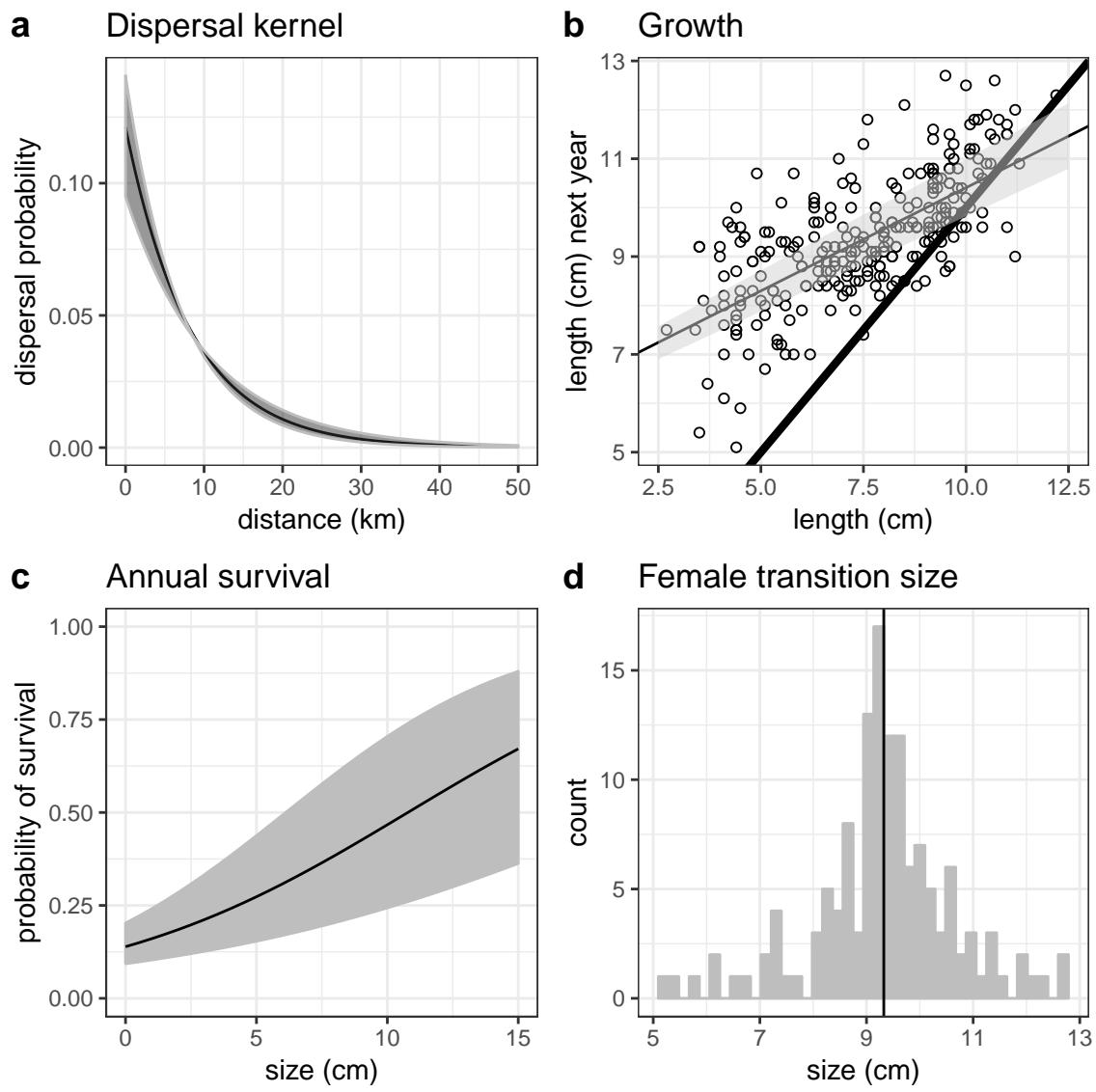


Figure 4: Best estimates (solid black line) and range included for uncertainty (gray) for dispersal (a), growth (b), post-recruit survival (c), and size at female transition (d) parameters.

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

of LEP for 1061, ranging from 29 to 8928 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.4), 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.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 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.

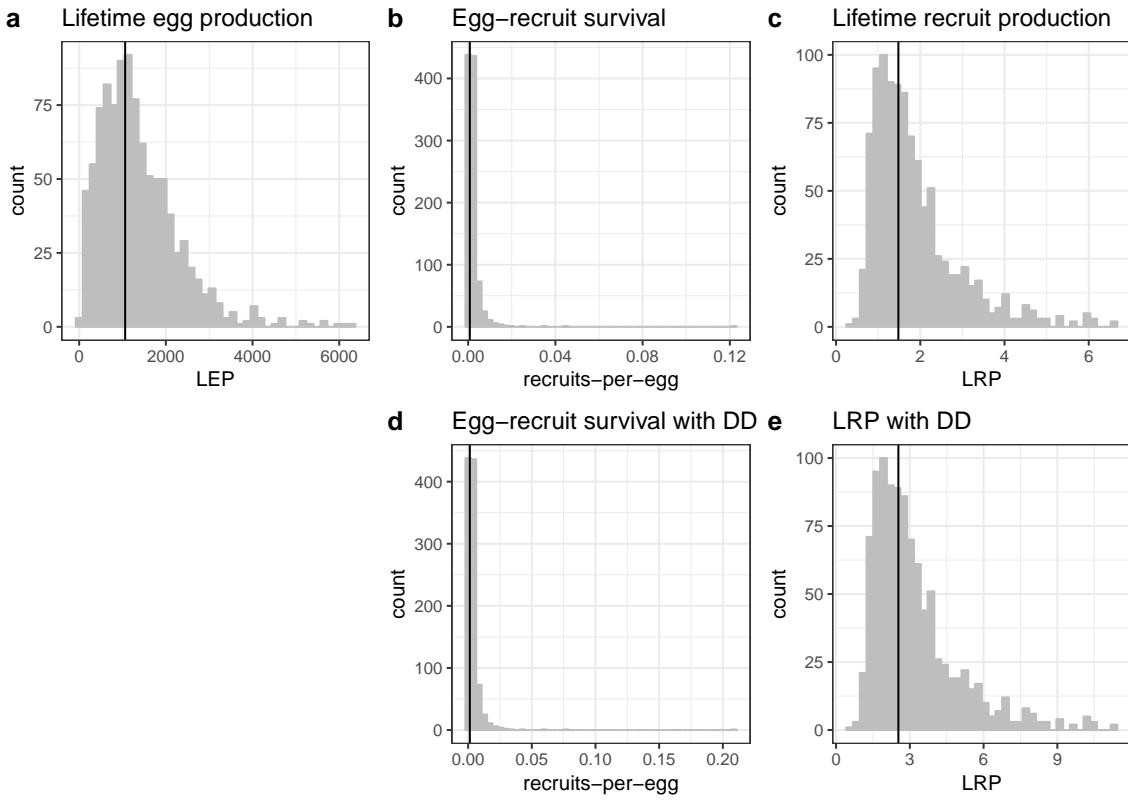


Figure 5: Estimates of a) LEP, b) egg-recruit survival, and c) LRP, showing the best estimate (black solid line) and range of estimates considering uncertainty in the inputs. The estimates in d-e include our attempt to remove density-dependence in the early life stages, while the estimates in b-c do 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 self-persistence values > 1 , indicating that no 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.

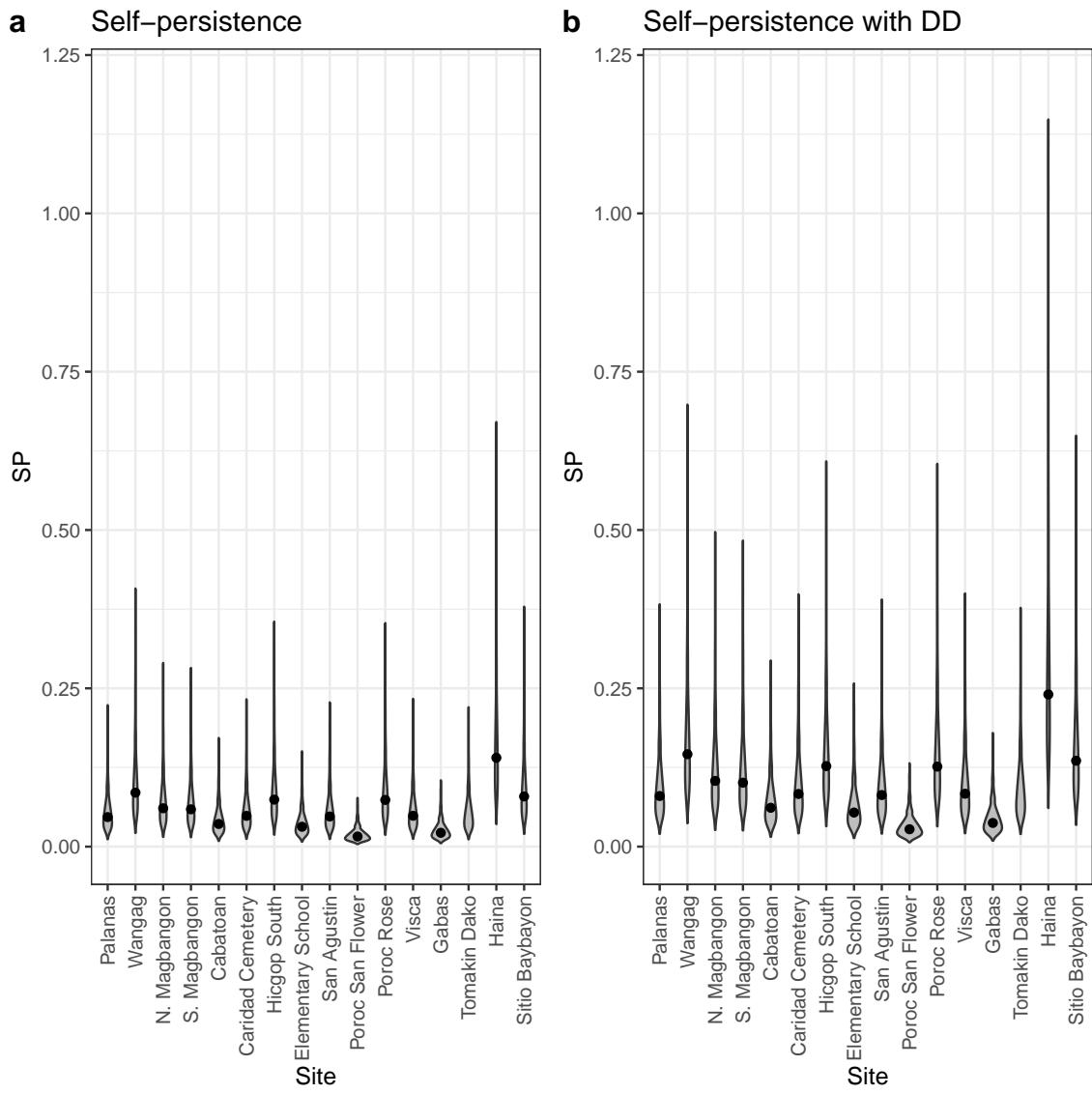


Figure 6: Values of self-persistence at each site, showing the best estimate (black point) and range of estimates considering uncertainty in the input parameters. No site reaches a value of $SP > 1$, necessary to be self-persistent. The estimates in (b) attempt to compensate for density-dependence in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

³⁸¹ 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). The value of λ_c rises to XX when we compensate for
³⁸⁴ density-dependence (Fig. 7c) but still below network persistent. We see that most
of the connectivity occurs 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
³⁸⁷ Tomakin Dako to Sitio Baybayon (Fig. 7b).

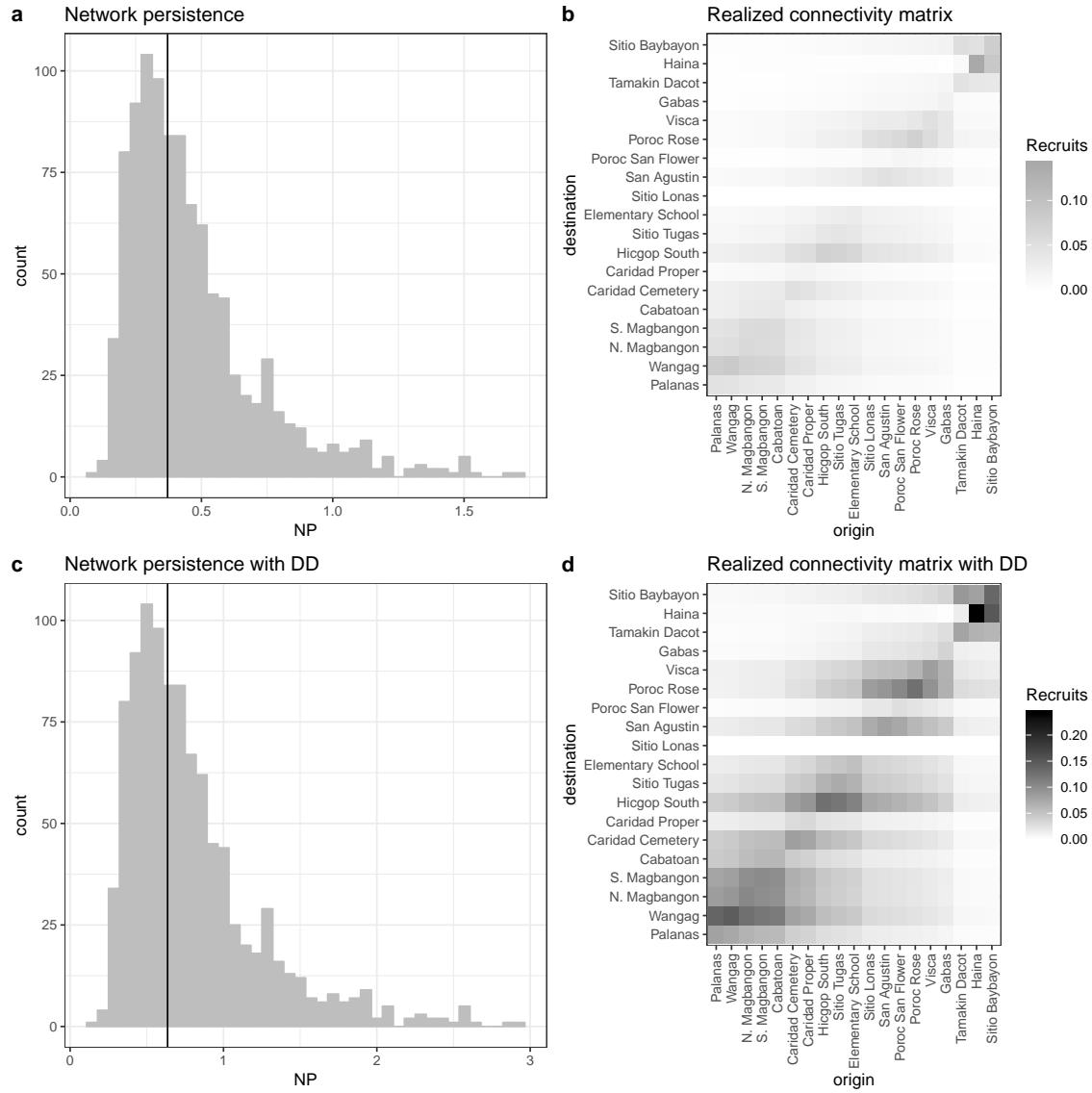


Figure 7: a) Network persistence values, showing the best estimate (black solid line) and range of estimates considering uncertainty, without accounting for density-dependence in our data. b) The realized connectivity matrix C , with sites arranged from north (Palanas) to south (Sitio Baybayon), without accounting for density-dependence in our data. Plots c) and d) show the network persistence values and realized connectivity matrix with attempts⁸⁹ to compensate for density-dependence in early life stages in our data.

Based on our estimates of LRP, SP, and NP, we do not expect that our set of sites is able to persist in isolation as a closed system. To explore what would be required for persistence, we consider a hypothetical scenario in which we assume that all of the recruits arriving at our sites came from adults at our sites. In this case, we find a value of $LRP = 1.21$, above the value of 1 necessary for replacement (Fig. B.1a). When we add in the connectivity, we see a higher value of λ_c in our best estimate ($NP = 0.20$) but still not high enough to indicate network persistence (Fig. B.1b). We see more of the distribution of estimates above 1, however, suggesting that network persistence is within our range of uncertainty in this case, though not likely. With our site configuration and dispersal kernel estimate, we would need a value of LRP of XX (an egg-recruit survival of XX with our estimated value of LEP or a value of LEP of XX with our estimated value of egg-recruit survival), to $\lambda_c = 1$ and network persistence.

Discussion

We do not see evidence for persistence in our metric estimates, neither self-persistence where an individual site could persist alone nor network persistence accounting for exchange among sites. The abundances through time at our sites are relatively constant, however, suggesting that the population at our sites is stable but relies on input of recruits from outside sites to persist. The portion of coastline we sampled is likely a sink portion of a larger metapopulation.

For our sites to be able to persist as a network on their own, the number of surviving recruits produced by an average recruit - LRP - would need to be higher.

With our estimated connectivity among the sites, LRP would need to be at least XXX
411 to see network persistence among our sites, about XXX times higher than our best
estimate and XXX times higher than the top of our range of uncertainty. To achieve
that value of LRP, either production of eggs would need to increase to an LEP of XX
414 or egg-recruit survival would need to be at least XX. Our estimate of LEP is XXX
compared to estimates for similar fish (e.g. CITATIONS) and our estimate of egg-
recruit survival is XXX compared to other estimates (e.g. CITATIONS), making a
417 rise of XX for either XX. Since LRP is less than one for our sites - the average recruit
only replaces itself with XX of a surviving recruit of the same stage - no amount
of increased retention or connectivity, even retaining all of the recruits produced
420 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 achieve network persistence. If nearby sites have higher egg
423 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 habitat and could be contributing recruits to our sites.

426 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
NP values from XX to XX. We see a factor of XX between our highest and lowest
429 LRP values and our best estimate of LRP is only XX times away from suggesting our
population is network persistent. Measuring demographic and dispersal parameters
in the field is challenging, particularly egg-recruit survival, which also has a large
432 effect on our persistence metric estimates. and accounting for our uncertainty clearly

helps us understand XX. While none of our estimates even with uncertainty indicate persistence and our population is likely subsized by outside input and unable to persist as a network on its own,

435 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
438 field
- Important to do this b/c not going to get a point estimate
- Think more about what the point of this paragraph is

441 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
distance of *A. clarkii* (10 km Pinsky et al., 2010) and those from our 2012-2018
444 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
of our sites. Our below-replacement estimate for LRP, however, suggests that lack
447 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
WITH OTHER VALUES OF SURV, GROWTH, FECUNDITY. The reef health
450 and habitat quality in our sites in generally low, due anthropogenic effects such as
pollution and silt from a nearby gravel mining operations and habitat disturbance
due to storms. Our sites are in an area that was hit by Typhoon XX, the strongest
453 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
and generally low habitat quality could contribute to low production of surviving
456 recruits in our sites, necessitating subsidation by outside populations. RAP-UP,
CONCLUDING SENTENCE OR TWO!

Persistence criteria, such as those detailed in Hastings and Botsford (2006) and
459 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
462 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*,
465 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,
468 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-
471 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
474 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.

477 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
larger than the estimated mean dispersal distance for our focal species. Our below-
480 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
produce enough offspring for replacement regardless of dispersal patterns, possibly
483 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
to contain a persistent network based on dispersal distance will not be able to persist
486 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
more productive sites enables our sites to persist.

489 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 field

492 • Important to do this b/c not going to get a point estimate

- Think more about what the point of this paragraph is

495 4) How do we reconcile this with the finding that mean dispersal distance is

within the reach of our sites but they don't persist as a contained metapopulation?

- They can both be true at the same time - maybe fish from our sites don't disperse very far but others in sites nearby have access to different currents,

498 etc. send recruits farther and into our sites.

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

501 Are there some citations on this?

5) Caveats paragraph

- 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)

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

6) Wrap-up paragraph

- How does this contribute to our understanding of metapopulation persistence?

513 Where do we go from here?

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, 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
519 portion of a larger metapopulation.

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

- 522 • So we don't see persistence in our metrics, either self-persistence or network
persistence but our abundances don't seem to be changing. Suggests that
this is just a portion of a larger metapopulation, rather than a self-contained
525 metapopulation. Maybe it is a sink? Persistent in terms of constant abundance
but relies on outside immigration to persist.
- 528 • How does dispersal spread (estiamted to be within our sites) interact with scale
of a self-contained metapopulation? How do we reconcile this in our system,
where we don't estimate dispersal that far but don't see network persistence
in an area range that spans the estimated spread? (This point might change,
531 depending on mean dispersal distance from the new kernels)
- 534 • Sensitivity - how would our parameters need to change to see persistence?
Egg-recruit survival is a big one. Discuss limitations of how we calculated it
(offspring going outside our pops not included - though we might change this),
what we see for persistence when estimate recruits/recruits instead. Contextualize this with what other studies have found for these parameters, how
reasonable it would be to get better estimates in the field.
537

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

540 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
allee effect) so is not explicitly considered in persistence metrics. In real populations,
543 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*,
density-dependence is likely most important in early life stages, as for many fish
546 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
549 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
552 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 and increase
555 LRP.

Our estimates of survival probabilities are similar to those estimated for other
558 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
561 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:

- 564 ● 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
567 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?
- 570 ● Discuss site-specific demographic rates, why we don't estimate them in our sys-
tem, the importance they play in other studies, what we might need to go
about resolving them, whether we would expect to see them.
- 573 ● Contextualize our parameter estimates with those from other studies (esp. sur-
vival, growth, fecundity).

Broadening back out:

- 576 ● 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
579 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
582 some local retention, maybe broader connectivity is still the story in terms of
receiving enough recruitment to persist.

Appendix

⁵⁸⁵ Summary of parameters

[Need to clarify somewhere what kind of distributions are going into the uncertainty runs (drawn from data, uniform across a range, 95% confidence bounds, etc.)]

Parameter	Description	Best estimate	Range in uncertainty runs	Notes
k_d	scale parameter in dispersal kernel	-1.36	-2.03 to -0.96	estimated using methods in Bode et al. (2018) in Catalano et al. (in prep)
θ	shape parameter in dispersal kernel	0.5	NA	estimated using methods in Bode et al. (2018) in Catalano et al. (in prep)
L_∞	average asymptotic size in von Bertalanffy growth curve	10.58 cm	10.39 to 10.75 cm	

K	growth coefficient in von Bertalanffy growth curve	0.928	0.854 to 1.025	
b_ϕ	intercept for adult survival	-4.83	± 0.340 standard error	
b_a	size effect for adult survival	0.74	± 0.060 standard error	
b_{pr}	intercept for recapture probability from mark-recapture analysis	17.93	± 0.858 standard error	not used in persistence estimates
b_1	size effect for recapture	-1.816	± 0.080 standard error	not used in persistence estimates
b_2	distance effect for recapture	-0.171	± 0.021 standard error	not used in persistence estimates
$\text{size}_{\text{recruit}}$	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:

588 **A Method details**

A.1 Proportion of habitat sampled

We used tagged anemones to estimate the proportion of habitat sampled at each site
591 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
594 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
597 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.

600 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
603 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
606 sampling years, to get the overall proportion habitat sampled across our sites and
sampling years.

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

609 *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

We use mark-recapture data from recapture dives done within a sampling season to
612 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
615 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.
618 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
621 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
624 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
627 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
630 the appropriate α_{P_c} and β_{P_c} parameters, where

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

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

- The mean of the individual capture probability values is $\mu_{P_c} = 0.56$, with variance $V_{P_c} = 0.069$, which gives beta distribution parameters $\alpha_{P_c} = 1.44$ and $\beta_{P_c} = 1.13$.
- 633 We sample 1000 values from the beta distribution, then truncate the sample to only values larger than the lowest value of P_c estimated in an individual dive (0.20), to avoid extremely low values that are sometimes sampled but are unrealistically low.
- 636 We then sample with replacement from the truncated set to get a vector of values the length of the number of runs.

Proportion of dispersal kernel area sampled

639 [Add in description of calculation and equation]

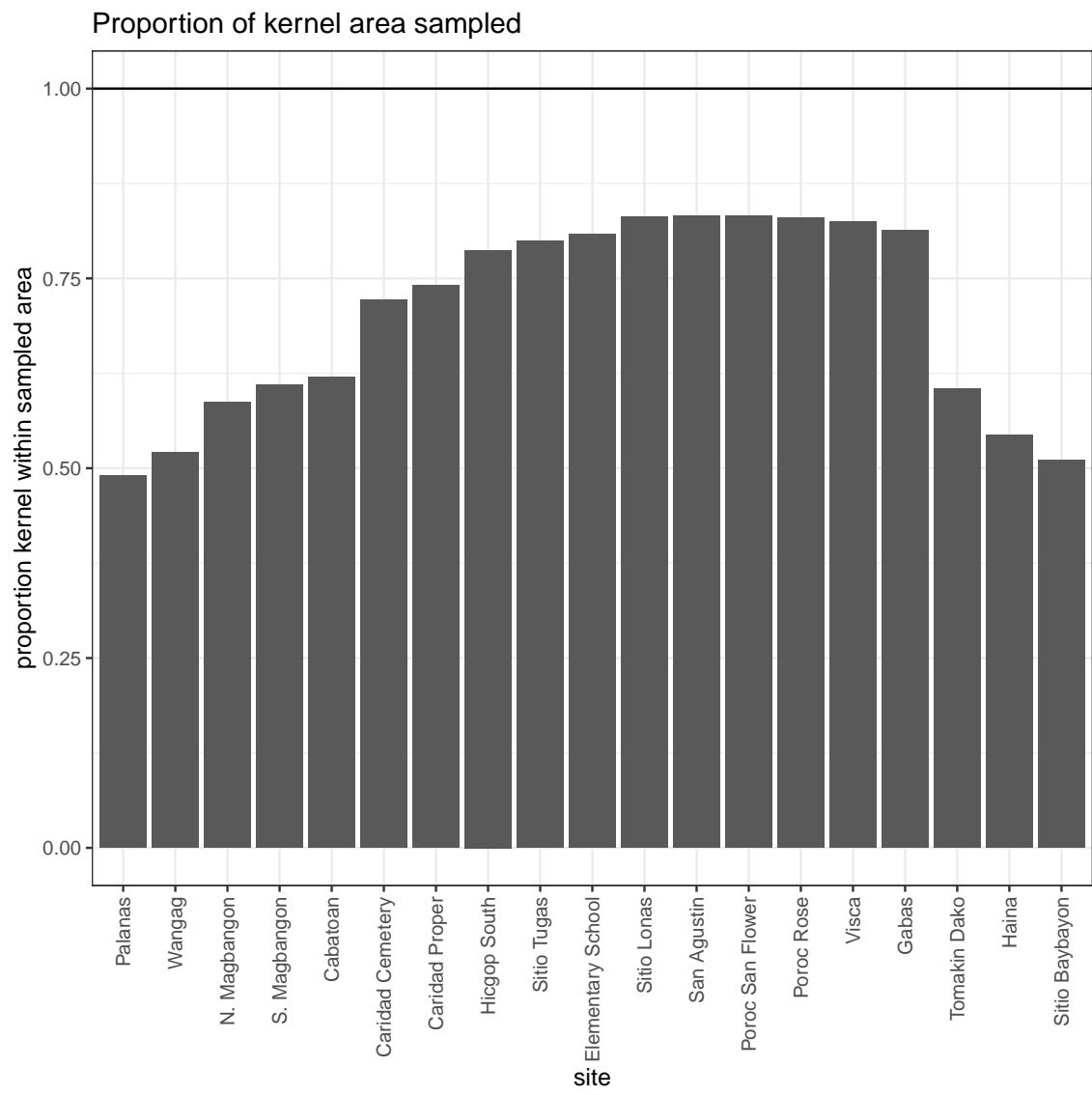


Figure A.1: Proportion of the dispersal kernel area from the center of each site covered by our sampling.

A.3 Proportion habitat in sampling area

We assume that larvae are unable to navigate to habitat if they attempt to settle
642 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
mortality due to settling on non-habitat twice - once in scaling up our matched
645 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
by the proportion of our sampling region that is habitat (P_s). We find P_s by summing
648 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 $P_s = 0.20$.

A.4 Full set of MARK models

⁶⁵¹ We consider the following set of models in MARK [*Need to add in models*]:

A.4.0.1 Recapture model

The best model for log-odds recapture probability, accompanying the survival model

⁶⁵⁴ 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 intercept $b_{pr} = 17.93 \pm 0.858$ SE:

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

⁶⁵⁷ 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:

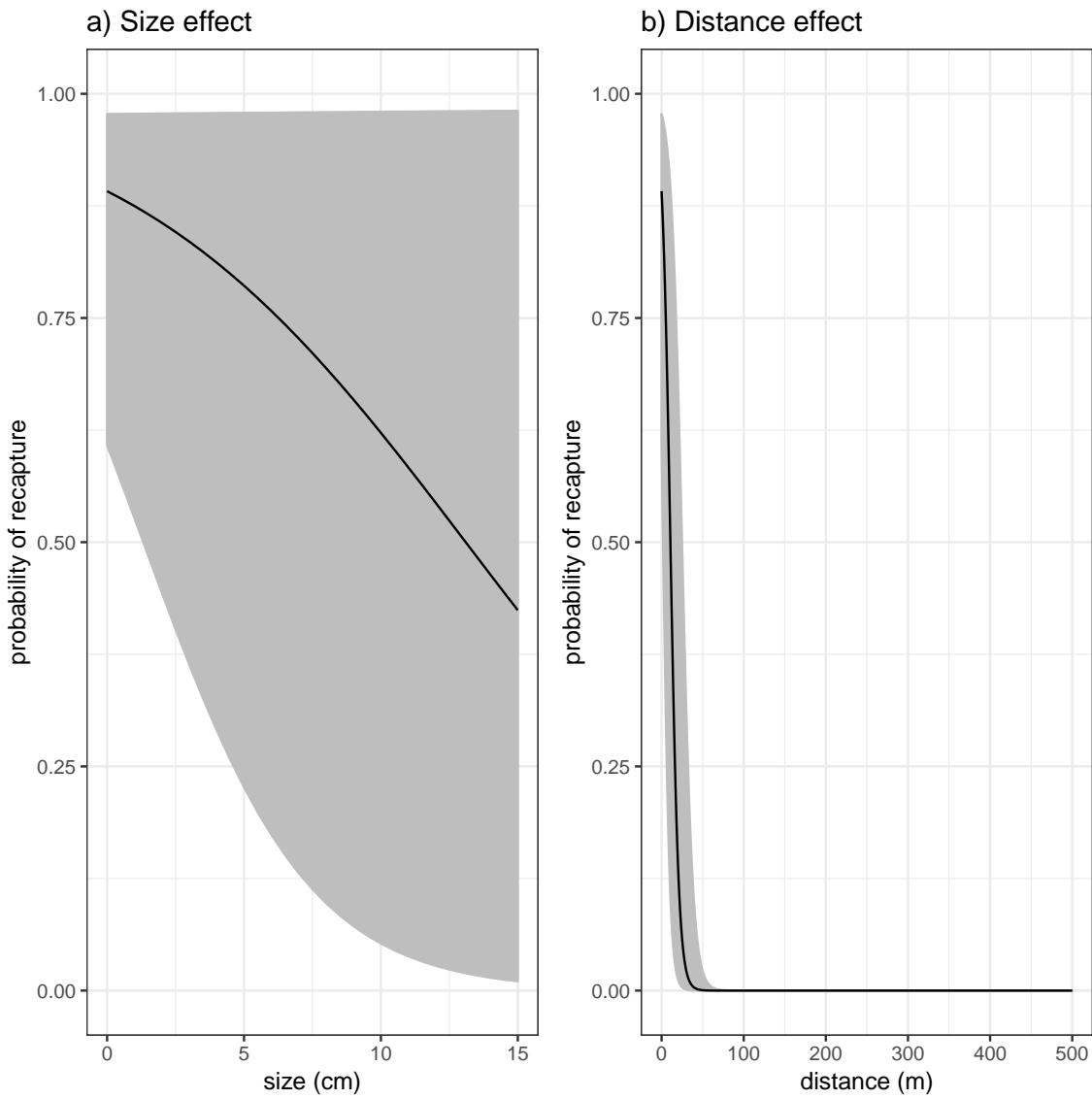


Figure A.2: Effects of a) fish size and b) minimum distance between divers and the anemone where the fish was first caught on the probability the fish will be recaptured, estimated along with survival in a mark-recapture analysis. Size has a slightly negative effect on the probability of recapture -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

B Uncertainty and sensitivity

660 B.1 What-if analyses

To compare our replacement-based persistence results, which do not suggest that our sites make up a persistent metapopulation, with our abundance trends (Fig. 3, 663 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, regardless of the origin of the arriving recruits. We repeat our metric estimates but 666 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 tagged offspring. We see XXX, which means YYY.

⁶⁶⁹ B.1.0.1 All genotyped offspring at our sites originated from our sites

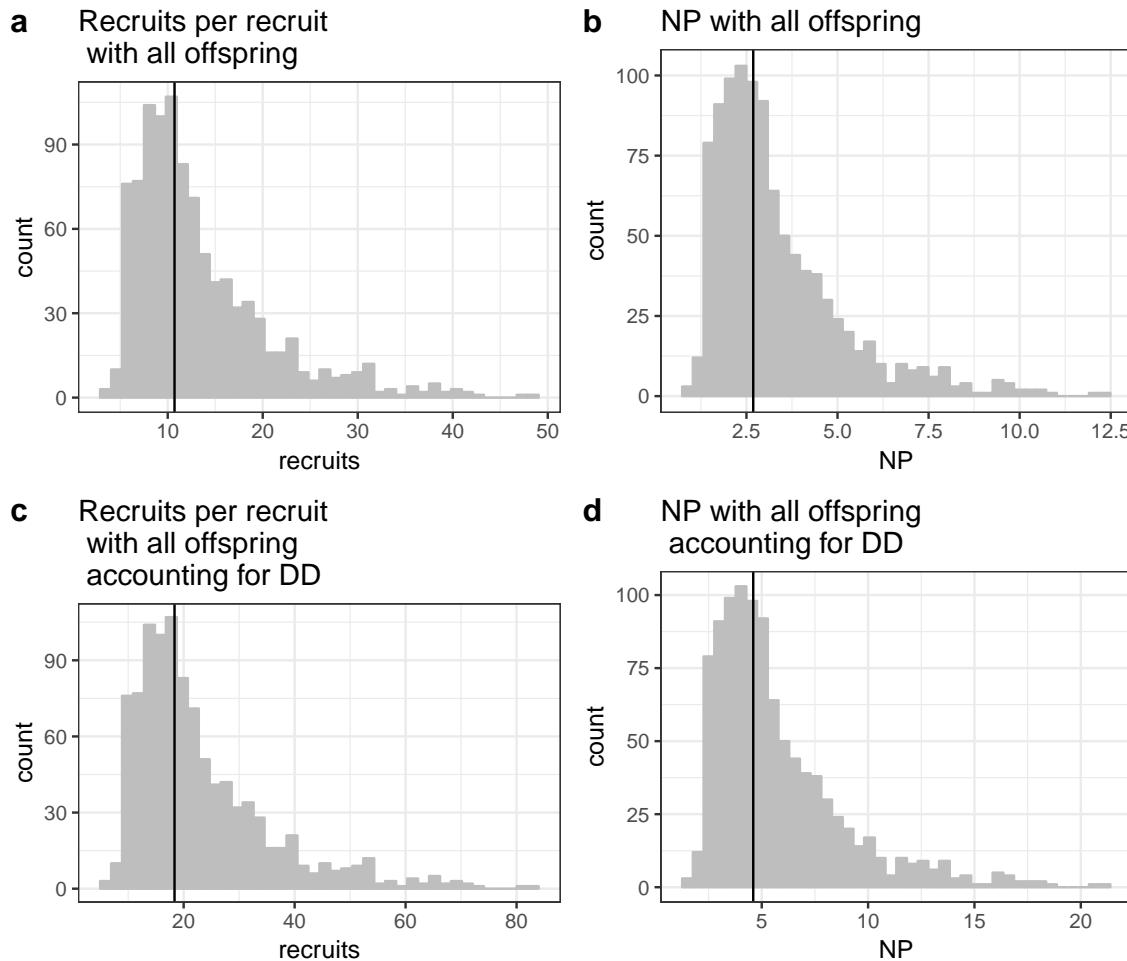


Figure B.1: a) Recruits per recruit when we consider all arriving recruits to have originated from our sites. b) Range of values of NP considering all arriving recruits to be offspring from our sites, with the best estimate in a black solid line.

B.2 Sensitivity to parameters

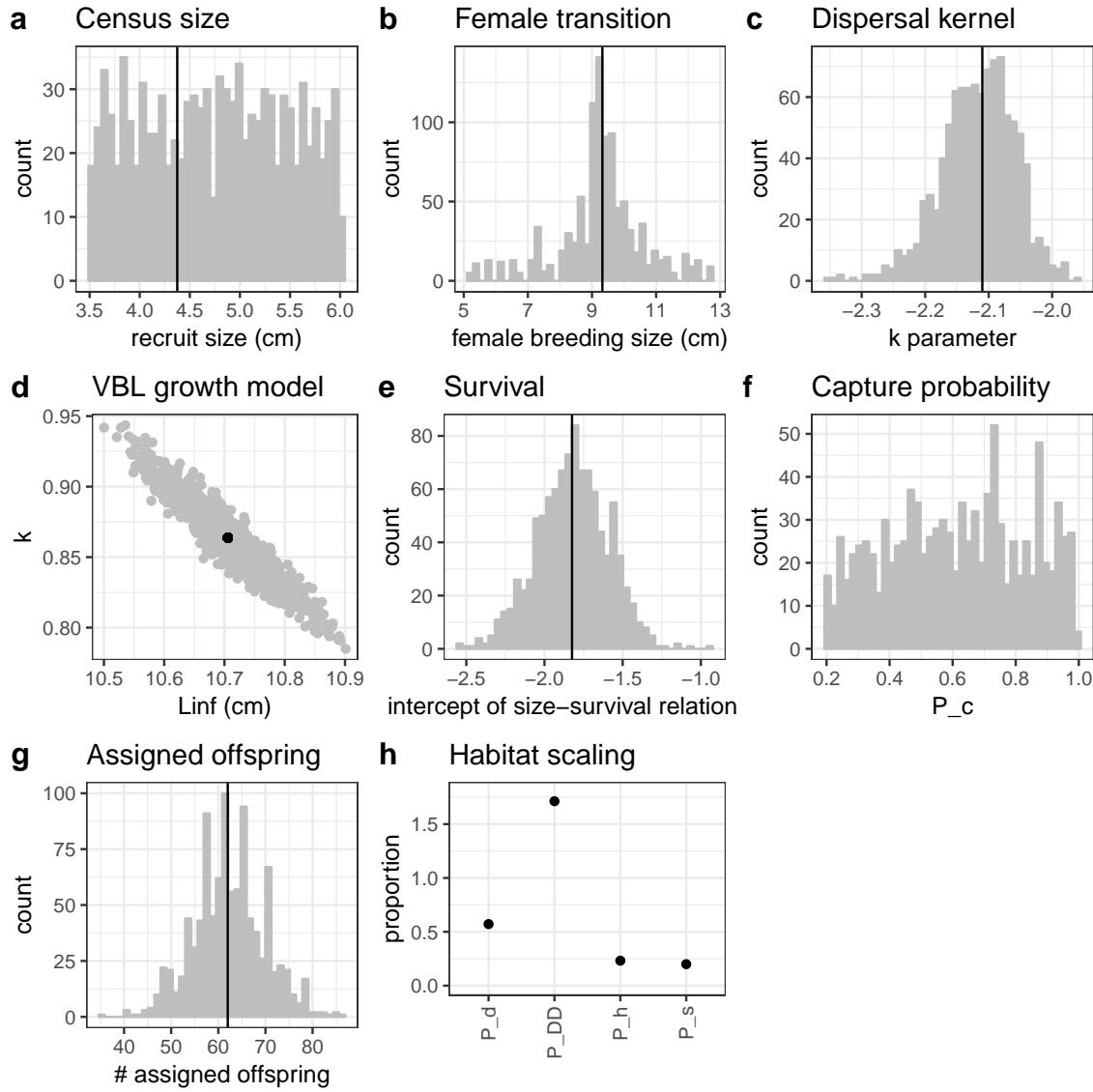


Figure B.2: Range of parameter inputs for uncertainty runs with all uncertainty included: a) $\text{size}_{\text{recruit}}$, the census size at which fish are considered to have recruited after egg-recruit survival occurs; b) L_f , the size at which fish transition from male to female and their reproductive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

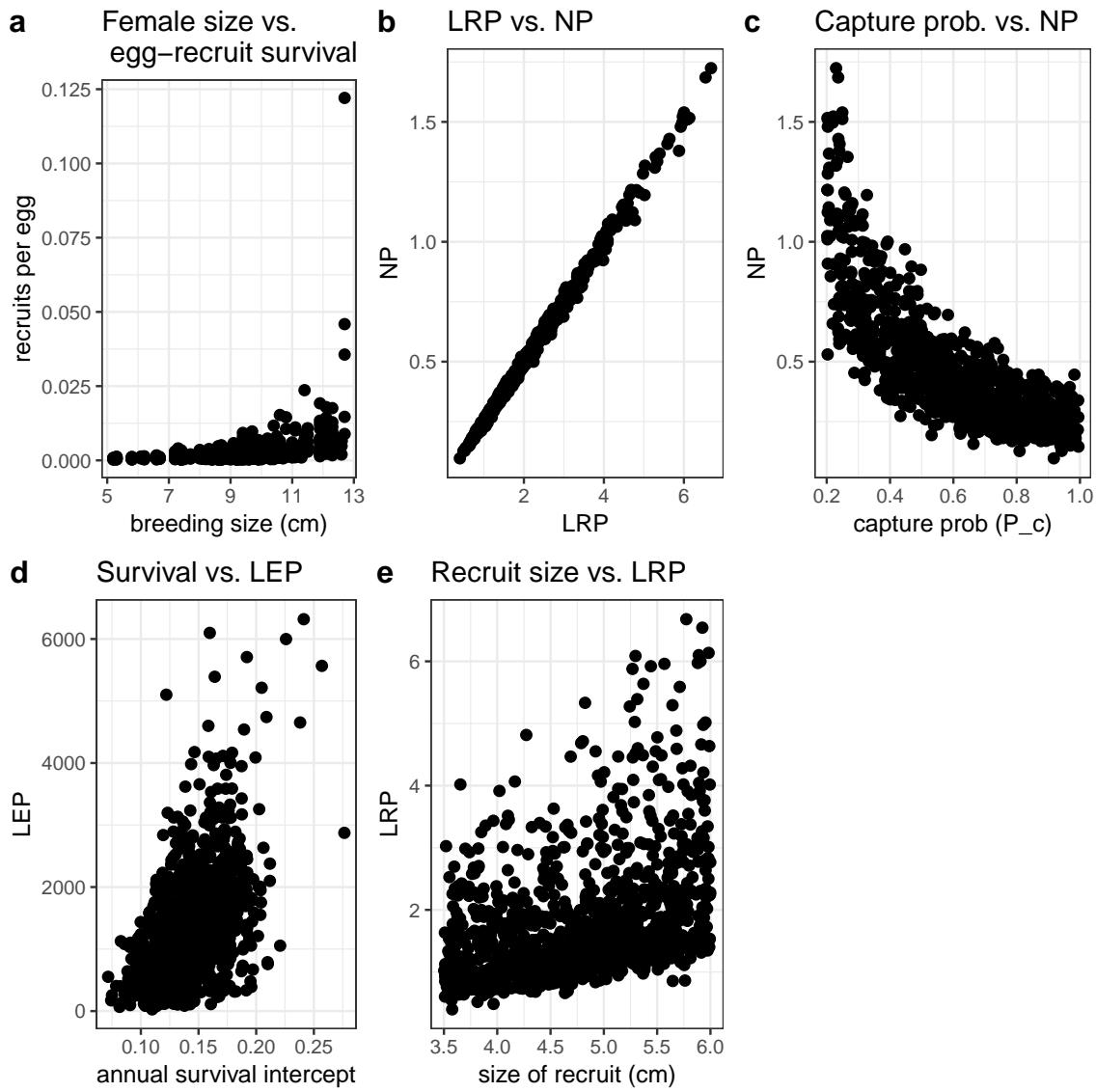


Figure B.3: Relationships among parameters and metrics. a) We only count reproductive effort by fish in the female stage so the higher the transition size to breeding female, the fewer eggs parents are considered to produce, which increases the estimated egg-recruit survival. b) LRP strongly affects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

B.3 Effects of different types of uncertainty on metrics

⁶⁷² B.3.0.1 Lifetime egg production (LEP)

Annual survival post-recruitment provides drives most of the uncertainty in LEP, as lower survivals keep fish from reaching and staying at large breeding sizes, with ⁶⁷⁵ 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 where its reproduction is counted in LEP.

Uncertainty in LEP

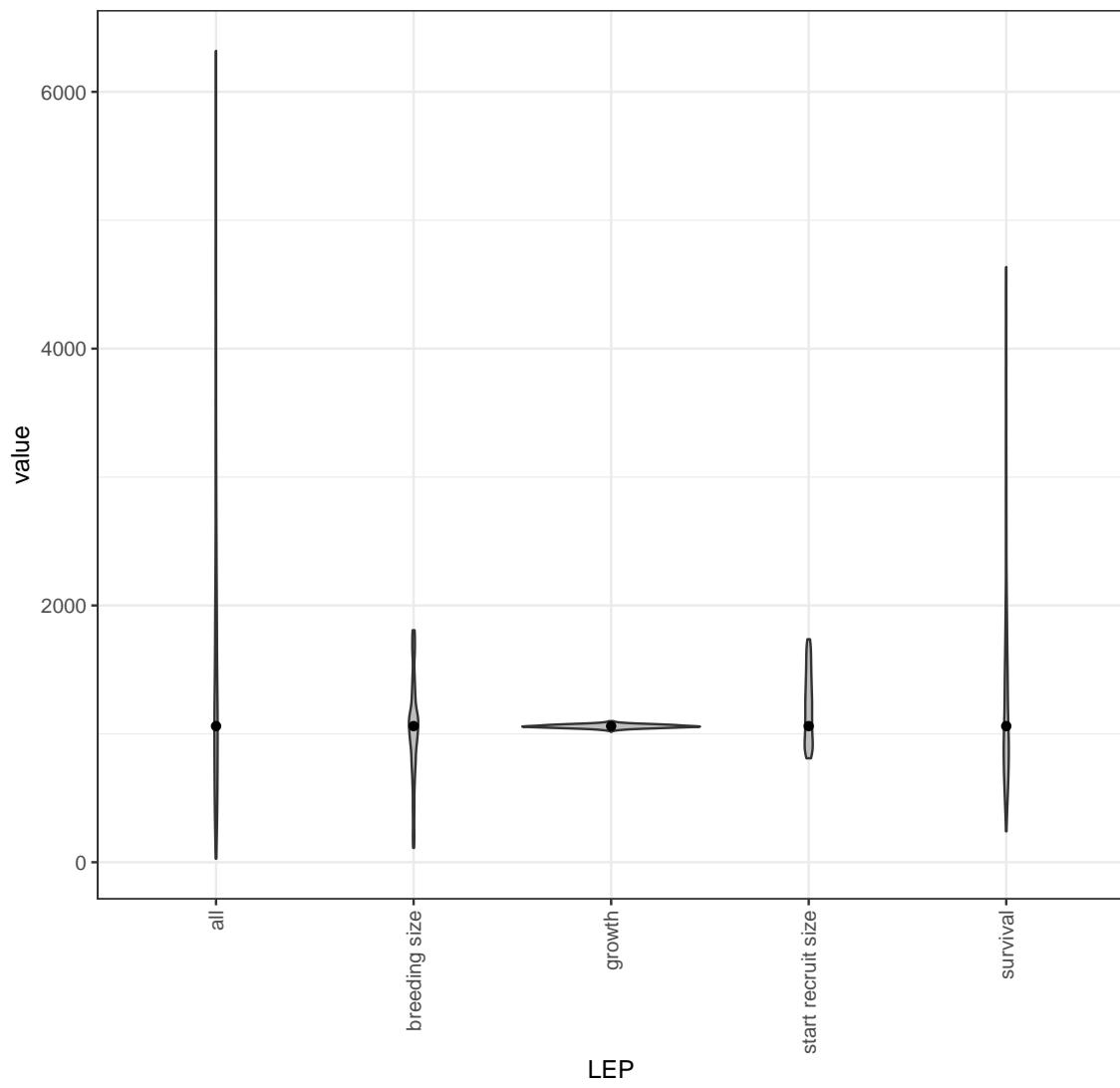


Figure B.4: The contribution of different sources of uncertainty in LEP.

⁶⁷⁸ **B.3.0.2 Lifetime recruit production (LRP)**

Most of the uncertainty in LRP comes from uncertainty in the size of a recruit. This is an artifact of our sampling, where we are unable to estimate egg-recruit survival
⁶⁸¹ 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 egg-recruit survival, as it should in an ideal situation.

Uncertainty in LRP

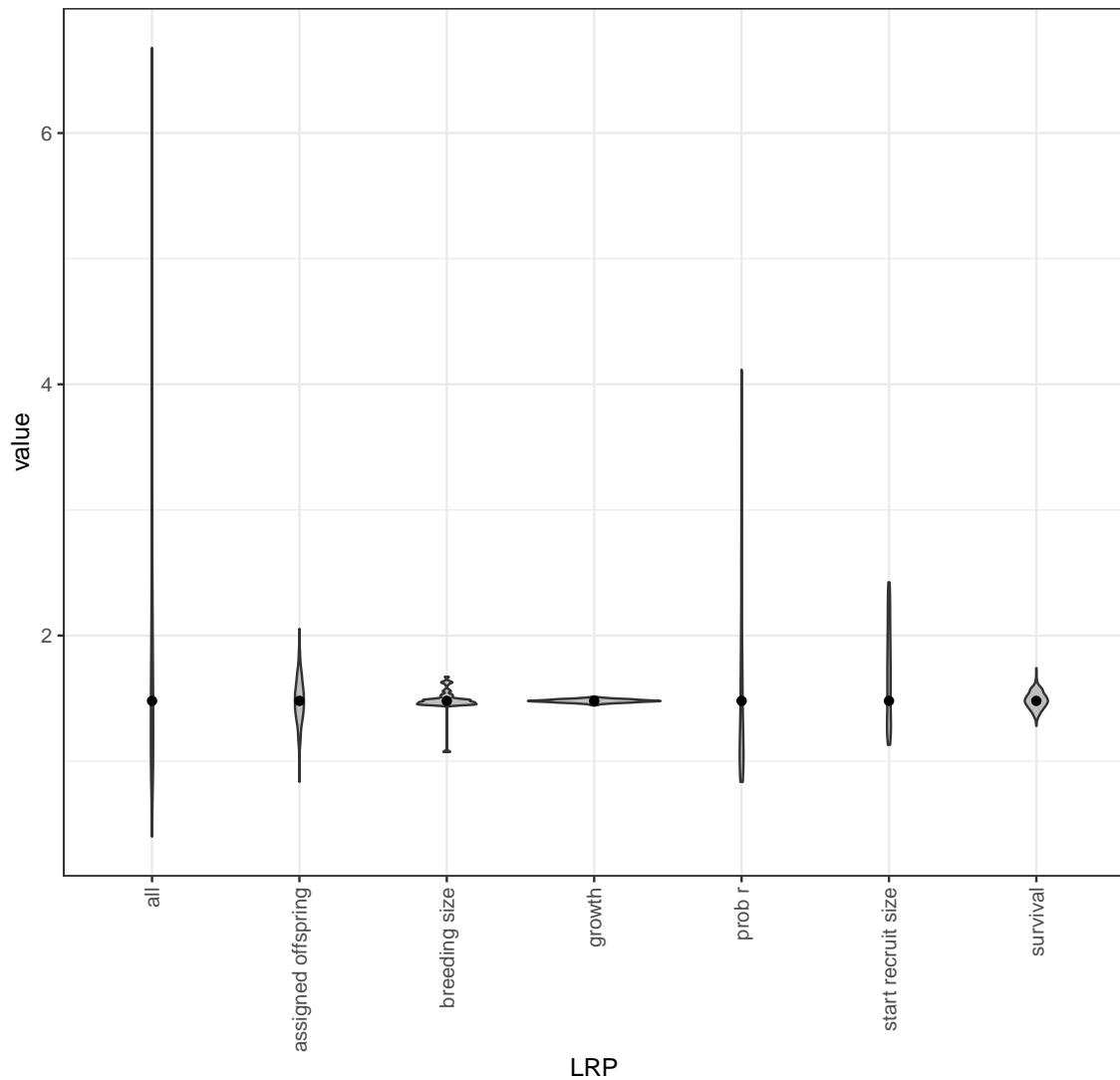


Figure B.5: The contribution of different sources of uncertainty in LRP.

Uncertainty in LRP accounting for DD

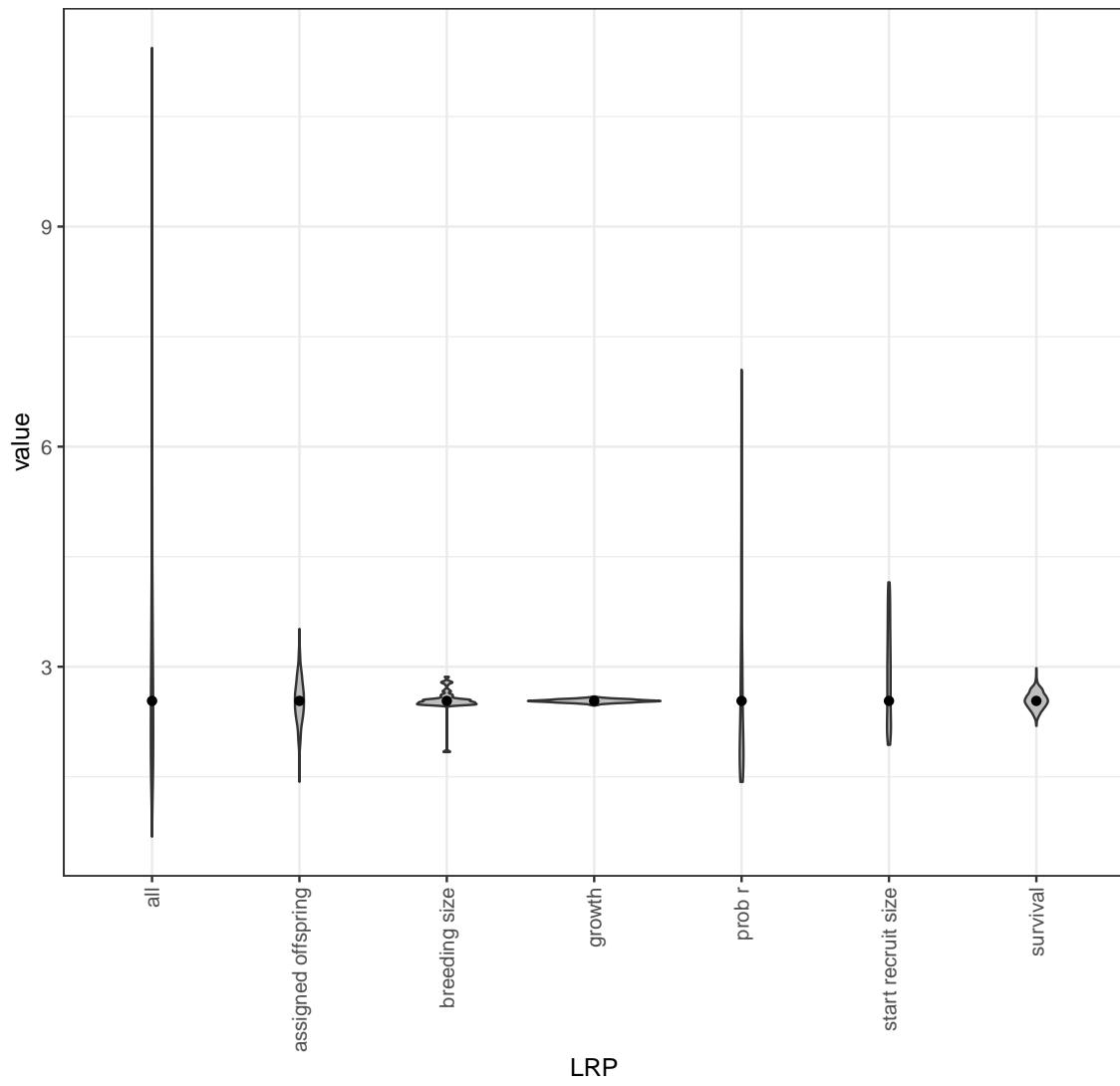


Figure B.6: The contribution of different sources of uncertainty in LRP, when we account for density-dependence in egg-recruit survival.

₆₈₄ **B.3.0.3 Egg-recruit survival (S_e)**

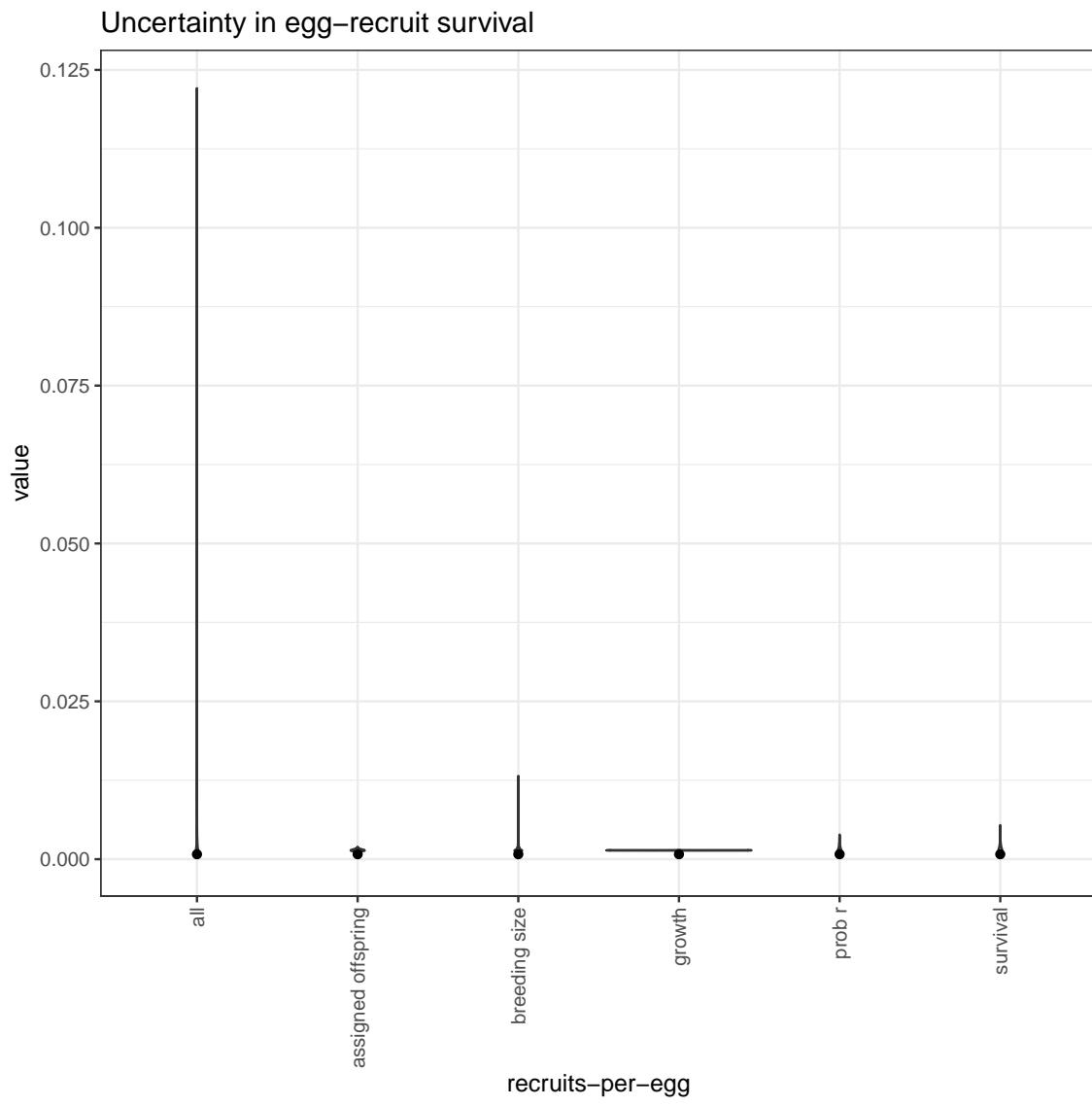


Figure B.7: The contribution of different sources of uncertainty in egg-recruit survival.

Uncertainty in egg–recruit survival /n accounting for DD

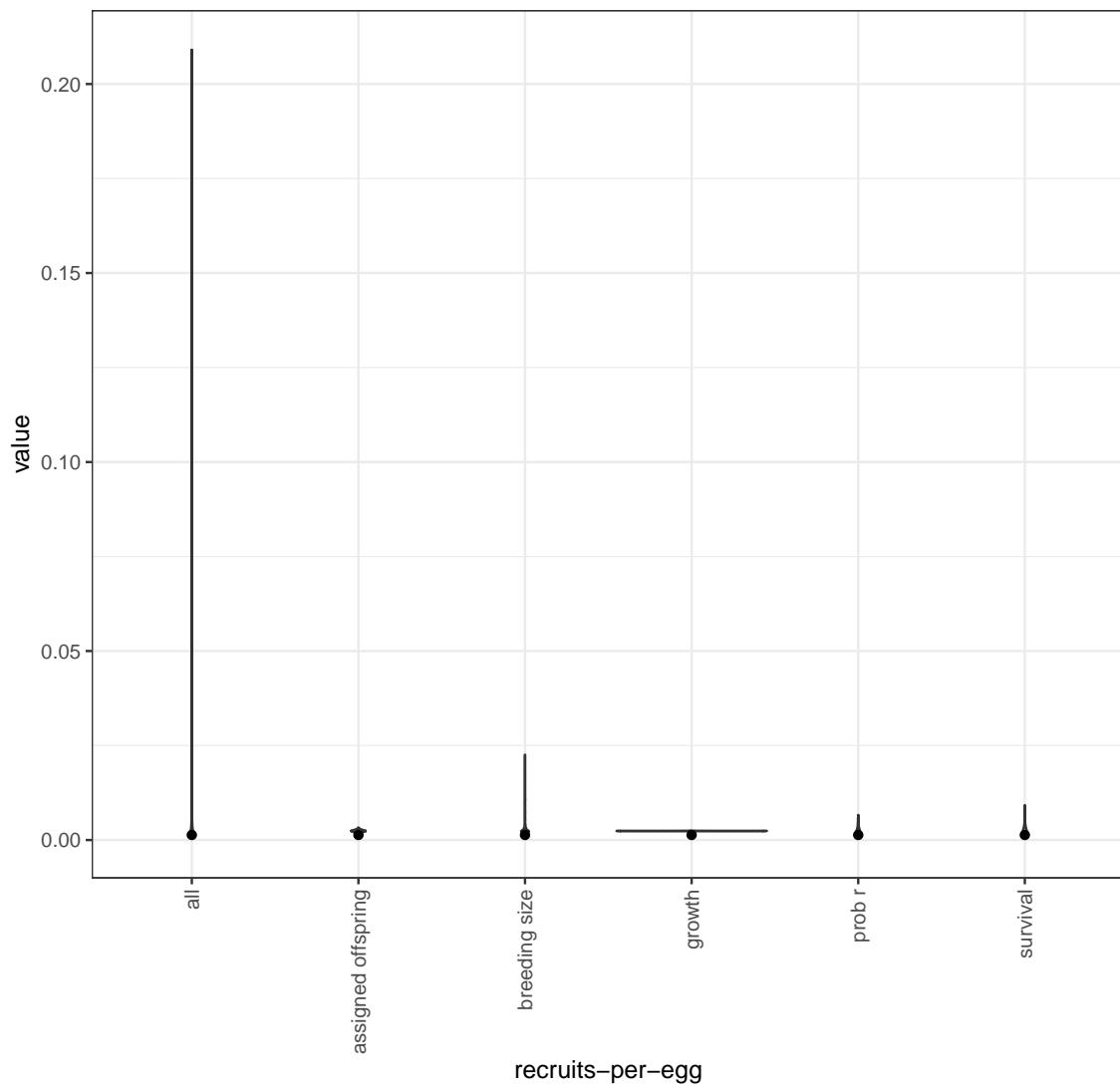


Figure B.8: The contribution of different sources of uncertainty in egg–recruit survival when we account for density-dependence in egg–recruit survival.

B.3.0.4 Network persistence (NP)

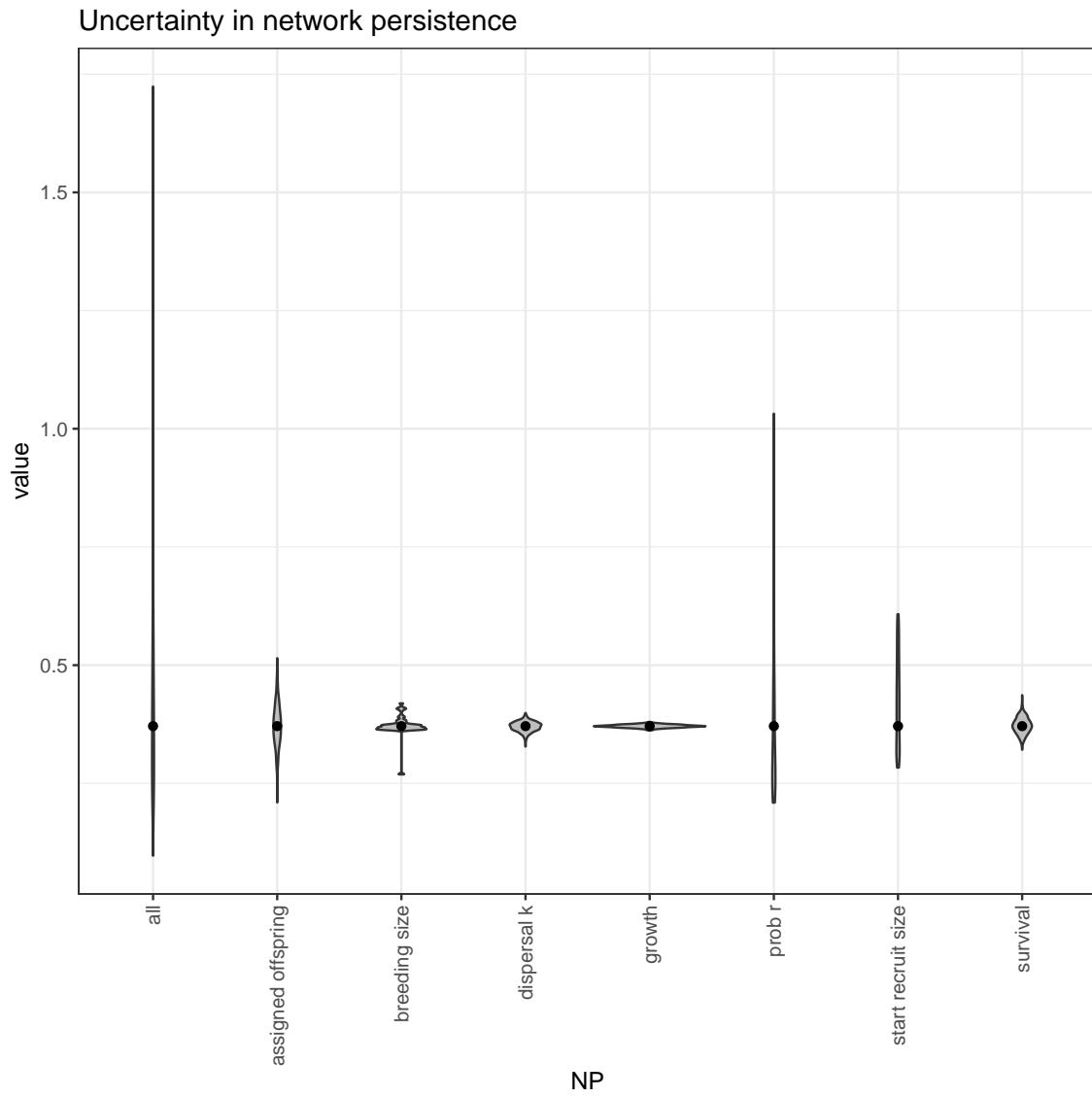


Figure B.9: The contribution of different sources of uncertainty in NP.

Uncertainty in network persistence /n accounting for DD

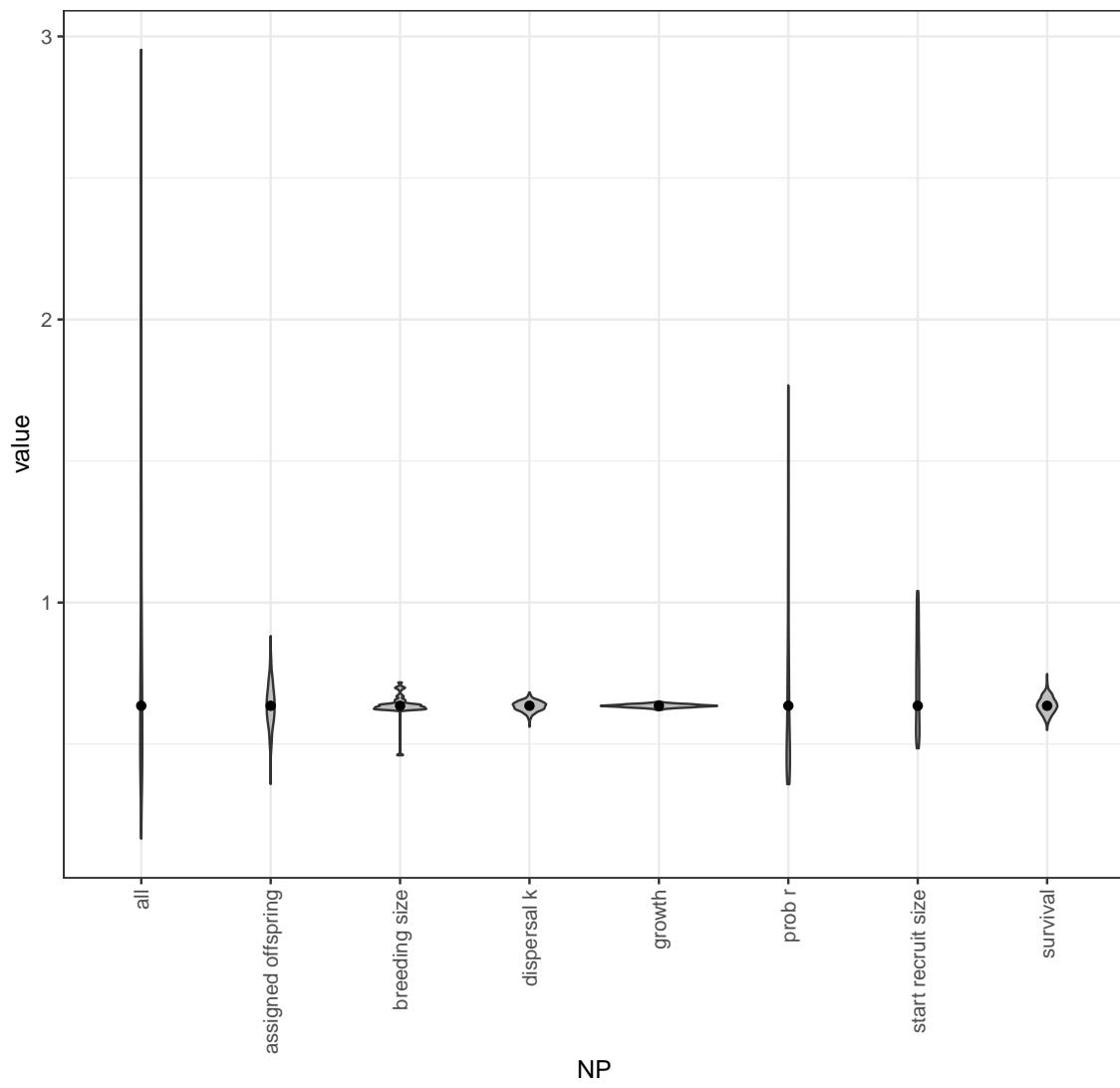


Figure B.10: The contribution of different sources of uncertainty in NP when we account for density-dependence in egg-recruit survival.

References

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

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

⁷⁰⁸ Peter M Buston, Geoffrey P Jones, Serge Planes, and Simon R Thorrold. Probability of successful larval dispersal declines fivefold over 1 km in a coral reef fish. *Proceedings of the Royal Society of London B: Biological Sciences*, page rspb20112041,
⁷¹¹ 2011.

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

⁷¹⁴ Katrina A Catalano, Allison G Dedrick, Michelle Stuart, Jonathan Purtiz, Humberto Montes, Jr., and Malin Pinsky. Interannual variability of genetic connectivity in a coral reef fish *Amphiprion clarkii*. in prep.

⁷¹⁷ Robert K. Cowen and Su Sponaugle. Larval Dispersal and Marine Population Connectivity. *Annual Review of Marine Science*, 1(1):443–466, January 2009. ISSN 1941-1405, 1941-0611. doi: 10.1146/annurev.marine.010908.163757. URL <http://www.annualreviews.org/doi/abs/10.1146/annurev.marine.010908.163757>.

⁷²⁰ C. C. D’Aloia, S. M. Bogdanowicz, J. E. Majoris, R. G. Harrison, and P. M. Buston. Self-recruitment in a Caribbean reef fish: a method for approximating dispersal kernels accounting for seascape. *Molecular Ecology*, 22(9):2563–2572, May 2013. ISSN 09621083. doi: 10.1111/mec.12274. URL <http://doi.wiley.com/10.1111/mec.12274>.

726 Augustus J. Fabens. Properties and fitting of the von bertalanffy growth curve.
Growth, 29:265–289, 1965.

Daphne Gail Fautin, Gerald R Allen, Gerald Robert Allen, Australia Naturalist,
729 Gerald Robert Allen, and Australie Naturaliste. Field guide to anemonefishes and
their host sea anemones. 1992.

Sarah O Hameed, J Wilson White, Seth H Miller, Kerry J Nickols, and Steven G
732 Morgan. Inverse approach to estimating larval dispersal reveals limited population
connectivity along 700 km of wave-swept open coast. *Proceedings of the Royal
Society B: Biological Sciences*, 283(1833):20160370, 2016.

735 Ilkka Hanski. Metapopulation dynamics. *Nature*, 396(6706):41–49, 1998.

Deborah R Hart and Antonie S Chute. Estimating von bertalanffy growth parameters
from growth increment data using a linear mixed-effects model, with an application
738 to the sea scallop *placopecten magellanicus*. *ICES Journal of Marine Science*, 66
(10):2165–2175, 2009.

Alan Hastings and Louis W. Botsford. Persistence of spatial populations depends on
741 returning home. *Proceedings of the National Academy of Sciences*, 103:6067–6072,
2006.

Jordan N. Holtswarth, Shem B. San Jose, Humberto R. Montes Jr., James W. Morley,
744 and Malin. L Pinsky. The reproductive seasonality and fecundity of yellowtail
clownfish (*amphiprion clarkii*) off the philippines. *Bulletin of Marine Science*, 93,
2017.

⁷⁴⁷ Darren W Johnson, Mark R Christie, Timothy J Pusack, Christopher D Stallings, and Mark A Hixon. Integrating larval connectivity with local demography reveals regional dynamics of a marine metapopulation. *Ecology*, 99(6):1419–1429, 2018.

⁷⁵⁰ Jacob P Kritzer and Peter F Sale. *Marine metapopulations*. Elsevier Academic Press, 2006.

J.L. Laake. RMark: An r interface for analysis of capture-recapture data with
⁷⁵³ MARK. AFSC Processed Rep. 2013-01, Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., Seattle, WA, 2013. URL <http://www.afsc.noaa.gov/Publications/ProcRpt/PR2013-01.pdf>.

⁷⁵⁶ Haruki Ochi. Mating behavior and sex change of the anemonefish, amphiprion clarkii, in the temperate waters of southern japan. *Environmental Biology of Fishes*, 26(4):257–275, 1989.

⁷⁵⁹ Brant K Peterson, Jesse N Weber, Emily H Kay, Heidi S Fisher, and Hopi E Hoekstra. Double digest radseq: an inexpensive method for de novo snp discovery and genotyping in model and non-model species. *PloS one*, 7(5):e37135, 2012.

⁷⁶² Malin L Pinsky, Humberto R Montes Jr, and Stephen R Palumbi. Using isolation by distance and effective density to estimate dispersal scales in anemonefish. *Evolution*, 64(9):2688–2700, 2010.

⁷⁶⁵ Jonathan B Puritz, Christopher M Hollenbeck, and John R Gold. ddocent: a radseq, variant-calling pipeline designed for population genomics of non-model organisms. *PeerJ*, 2:e431, 2014.

⁷⁶⁸ Mark Rees, Dylan Z Childs, and Stephen P Ellner. Building integral projection models: a user's guide. *Journal of Animal Ecology*, 83(3):528–545, 2014.

⁷⁷¹ J Roughgarden, S Gaines, and H Possingham. Recruitment dynamics in complex life cycles. *Science*, 241(4872):1460–1466, September 1988. ISSN 0036-8075, 1095-9203. doi: 10.1126/science.11538249. URL <http://www.sciencemag.org/cgi/doi/10.1126/science.11538249>.

⁷⁷⁴ Ocane C. Salles, Jeffrey A. Maynard, Marc Joannides, Corentin M. Barbu, Pablo Saenz-Agudelo, Glenn R. Almany, Michael L. Berumen, Simon R. Thorrold, Geoffrey P. Jones, and Serge Planes. Coral reef fish populations can persist without ⁷⁷⁷ immigration. *Proceedings of the Royal Society B: Biological Sciences*, 282(1819): 20151311, November 2015. ISSN 0962-8452, 1471-2954. doi: 10.1098/rspb.2015.1311. URL <http://rspb.royalsocietypublishing.org/lookup/doi/10.1098/rspb.2015.1311>.

Jinliang Wang. Sibship reconstruction from genetic data with typing errors. *Genetics*, 166(4):1963–1979, 2004.

⁷⁸³ Jinliang Wang. Computationally efficient sibship and parentage assignment from multilocus marker data. *Genetics*, 191(1):183–194, 2012.

⁷⁸⁶ Jinliang Wang. Estimation of migration rates from marker-based parentage analysis. *Molecular ecology*, 23(13):3191–3213, 2014.

Jw White, Lw Botsford, A Hastings, and Jl Largier. Population persistence in marine reserve networks: incorporating spatial heterogeneities in larval dispersal.

⁷⁸⁹ *Marine Ecology Progress Series*, 398:49–67, January 2010. ISSN 0171-8630, 1616–
1599. doi: 10.3354/meps08327. URL <http://www.int-res.com/abstracts/meps/v398/p49-67/>.

⁷⁹² Adam Yawdoszyn. Fecundity in clownfish. in prep.