

Clownfish metapopulation persistence draft

Allison G. Dedrick^{a,*}

Katrina A. Catalano^a

Michelle R. Stuart^a

J. Wilson White^b

Humberto Montes, Jr.^c

Malin Pinsky^a

a. Department of Ecology Evolution and Natural Resources, Rutgers University, 14 College Farm Road, New Brunswick, NJ 08901;

b. Oregon State University

c. Visayas State University

* Corresponding author; e-mail: agdedrick@gmail.com

(Author order not yet determined)

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
9 and persistence depend on connectivity among patches and the demographic rates at each patch (e.g. Hastings and Botsford, 2006a; Hanski, 1998). Assessing levels of connectivity and demographic parameters has been particularly challenging for
12 marine species, where much of the mortality and movement happens at larval and juvenile stages when individuals are hard to track and have the potential to travel long distances with ocean currents (e.g. Kritzer and Sale, 2006; Cowen and Sponaugle, 2009; Roughgarden et al., 1988). A need to understand metapopulations for
15 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
18 how marine 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
21 marine populations are, in addition to assessing whether the reproductive output
24 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, 2006a; 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 and shell microchemistry and genetic parentage analysis (e.g. Wang, 2004, 2014) are

making it increasingly possible to estimate both the demographic (e.g. Carson et al.,
51 Hameed et al., 2016) and the dispersal (e.g. Almany et al., 2017; D'Aloia et al.,
2013) parameters necessary to assess persistence in real metapopulations. We might
expect that populations on isolated islands are the most likely to be self-persistent,
54 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*
57 *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
60 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.

63 The number of studies estimating demographic rates and connectivity in marine
metapopulations is growing (e.g. Salles et al., 2015; Johnson et al., 2018; Garavelli
et al., 2018), but most use data from one or a few years. Longer data sets enable
66 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
69 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
72 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

Persistence theory and metrics

For a population to persist, individuals must be able to replace themselves on average at low abundance (e.g. Hastings and Botsford, 2006a; Botsford et al., 2009). In non-spatially structured populations, we use criteria such as the average number of recruiting offspring each individual produces during its life (called R_0 when the population is age-structured and density-independent) or the growth rate of the population (such as the dominant eigenvalue λ of an age-structured Leslie matrix) (Caswell, 2001; Burgess et al., 2014). For spatially-structured populations, we must also consider the spatial spread of offspring, often represented through a dispersal kernel or connectivity matrix (e.g. Cowen, 2006; Buston et al., 2011; Hogan et al.,

2011; DALoia et al., 2015)).

We consider three primary metrics to assess whether and how the population is
96 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
99 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
102 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

105 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
108 of those eggs that will survive to become recruits (egg-recruit survival: S_e) (Fig. 2
Metrics):

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

If $\text{LRP} \geq 1$, the population has the possibility for replacement; individuals produce
111 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 pro-

₁₁₄ duced by our individuals, regardless of where they settle, which requires combination
 with the dispersal kernel to understand persistence, and for recruits that settle only
 at our sites, LRP_{local} , which implicitly includes dispersal. If $LRP_{local} \geq 1$, our group
₁₁₇ of sites is able to persist locally.

Self-persistence

A patch is able to persist in isolation (self-persistent) if individuals produce enough
₁₂₀ 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
 LEP to represent offspring produced and local retention (LR) - the number of surviv-
₁₂₃ ing 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 criteria
 for self-persistence: $LEP \times LR \geq 1$. We modify this to include egg-recruit survival in
₁₂₆ the offspring term, using LRP in place of LEP , to assess whether a particular patch
 i is self-persistent:

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

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

A patch is self-persistent if $SP \geq 1$. If at least one patch is self-persistent, the
₁₂₉ metapopulation as a whole is persistent as well (Hastings and Botsford, 2006a;
 Burgess et al., 2014).

Realized connectivity matrix and network persistence

¹³² 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 create a realized connectivity matrix C by multiplying the dispersal probabilities by ¹³⁵ 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 do). The diagonal entries of C , where the origin and destination are the same site, ¹³⁸ are the values of self-persistence we calculate above.

¹⁴¹ 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, 2006a; White et al., 2010; Burgess et al., 2014).

Defining recruit and census stage

¹⁴⁴ 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 define a recruit to be a juvenile individual that has settled on the reef within the ¹⁴⁷ previous year, which also encompasses the size we are first able to sample (3.5-6.0 cm for parentage studies) (Fig. 2, Life stage). In theory, it does not matter how we define recruit as long as we use that definition in our calculations of both egg-recruit ¹⁵⁰ 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 sizes. Instead, we choose the mean size of offspring matched in
153 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 covers (3.5-6 cm, Table A1).

156 **Study system**

We focus on a tropical metapopulation of yellowtail clownfish (*Ampiprion clarkii*, Fig. 3c) on the west coast of Leyte island facing the Camotes Sea in the Philippines (Fig. 159 3a). Like many clownfish species, yellowtail clownfish have a mutualistic relationship with anemones, where small colonies of fish live (Buston, 2003b; Fautin et al., 1992). Yellowtail clownfish are protandrous hermaphrodites and maintain a size-structured hierarchy; within an anemone, the largest fish is the breeding female, the next largest is the breeding male, and any smaller fish are non-breeding juveniles. The fish on 162 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 tropical patch reef habitat of the Philippines, yellowtail clownfish spawn once per 165 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 settle in an anemone (Fautin et al., 1992).

171 Clownfish are particularly well-suited to metapopulation studies due to their limited movement as adults and clearly patchy habitat. Once fish have settled, they tend to stay within close proximity of their anemones (XX meters, Stuart et al., in

¹⁷⁴ prep). This makes fish easier to relocate for mark-recapture studies and simplifies
the exchange between patches to only the dispersal during the larval phase. Patches,
whether considered to be the reef patch or the anemone territory of the fish, are
¹⁷⁷ clearly discrete and easily delineated (Fig. 3a, b), which makes determining the spa-
tial structure of the metapopulation clear. Additionally, clear patches make it easier
to assess how much of the site has been surveyed. These simplifying characteristics in
¹⁸⁰ habitat and fish behavior make clownfish and other similarly territory-based reef fish
useful model systems for studies of metapopulation dynamics and persistence (e.g.
Buston and DAloia, 2013; Salles et al., 2015; Johnson et al., 2018). Our focal species
¹⁸³ of yellowtail clownfish tends to behave more like larger reef fishes, with territories
that can extend beyond single anemones (Hattori and Yanagisawa, 1991; Ochi, 1989)
and strong enough swimming skills that movement between patch reefs is possible
¹⁸⁶ though unusual (seen XX times at our sites, Stuart et al., in prep), than the smaller
clownfish *A. percula* commonly used in previous metapopulation studies (e.g. Buston
et al., 2011; Salles et al., 2015).

¹⁸⁹ **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. 3a). The sites consist of rocky patches of coral
¹⁹² reef and are separated by sand flats (Fig. 3b). 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
¹⁹⁵ exceed that range. On the north edge, the sites are isolated from nearby habitat

with no substantial reef habitat for at least 20 km.

Since 2012, we have sampled fish and habitat at most of the sites annually (Table 198 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, tagging the anemone to track it through time. At each anemone, the divers attempted 201 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 204 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 and genotyped 207 2772 fish and PIT-tagged 1929 fish across all years and sites combined, marking 3413 individual fish.

Parentage analysis and dispersal kernel

210 We genotyped 2772 fish from our tissue samples and used single nucleotide polymorphisms to identify parent-offspring matches with the software program COLONY2 213 (Wang, 2012) (details on genotyping and parentage analysis in Catalano et al., in prep).

Using the method described in (Bode et al., 2018), we fit a distance-based dispersal kernel (Catalano et al., in prep), where the relative dispersal is a function of 216 distance d as measured in kilometers and parameters θ and $z = e^{kd}$, 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 3413 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

²⁴⁶

249 this process 1000 times to generate a distribution.

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 ($R_m = 62$) 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 ($N_g = 1719$) 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 of
³⁰⁶ habitat in our sites we sampled over time ($P_h = 0.41$, details in A.1), the probability

of capturing a fish if we sampled its anemone ($P_c = 0.56$, see A.2 for details), and the proportion of the total dispersal kernel area from each our of sites covered within
309 our sampling region ($P_d = 0.57$, 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
312 region ($P_s = 0.20$, details in A.2.0.1) 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 (745) and the probability of success on each trial is the assignment rate of offspring from the parentage analysis
321 (0.079) (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 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 and
327 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 clown-

fish, with anemones already occupied by *A. clarkii* settlers essentially unavailable as
 330 habitat. We attempt to account for this density-dependent mortality by multiplying-
 ing 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
 333 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
 339 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 (Fig. 1). In our very simple look at whether abundance seems to be increasing or decreasing, eleven sites had a positive slope over time and five had a negative
³⁴⁸ slope (Fig. 1q). For the two largest sites, with a mean estimated number of females of between 150-200, one has a positive slope (Wangag, Fig. 1b) and one has a negative slope (Sitio Baybayon, Fig. 1p) and the next two largest sites are also split (Palanas,
³⁵¹ Fig. 1a and Haina, Fig. 1o). Overall, there is not a clear directional change in abundance across the sites we sample over our sampling period.

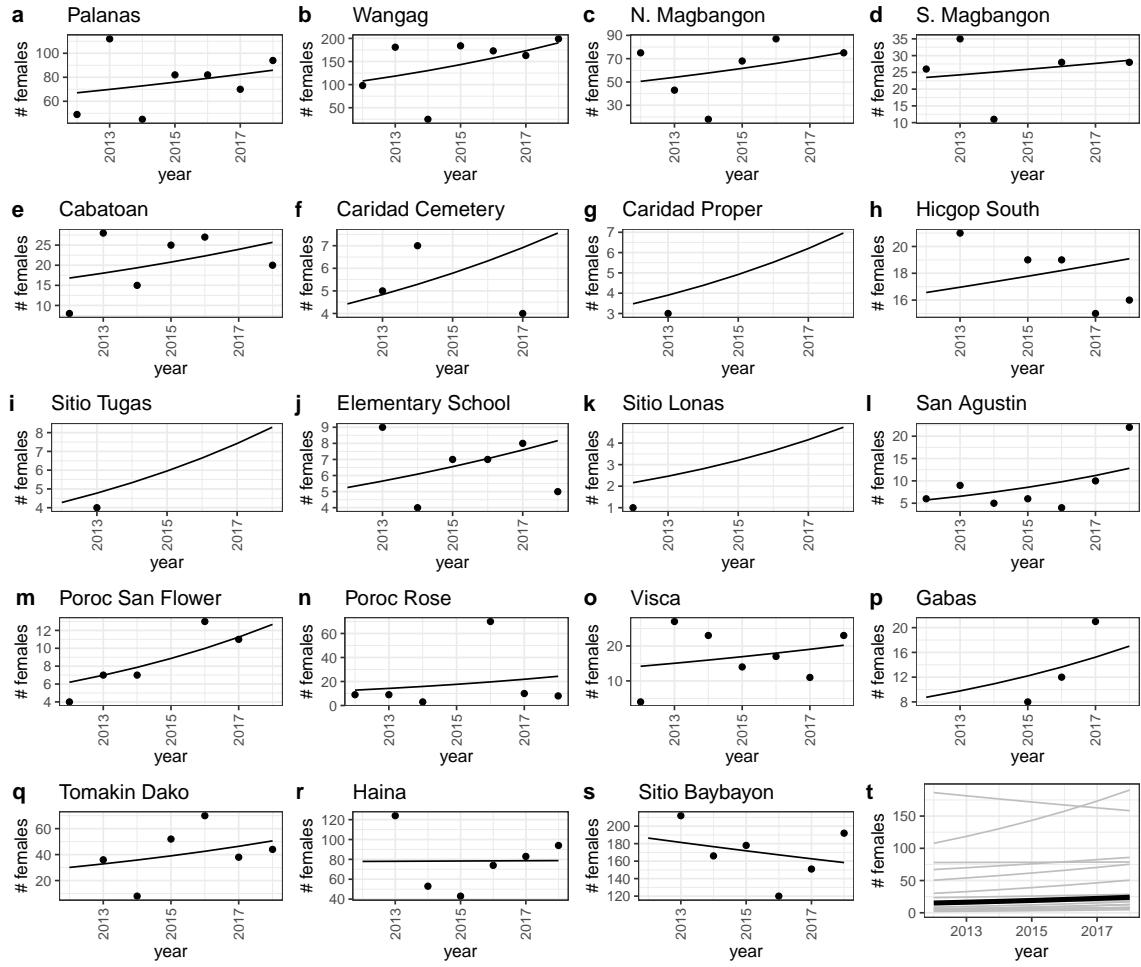


Figure 1: The estimated number of females at each site over the sampling years for sites sampled in at least three years. The total number of females at each site was estimated by scaling up the number of females captured at each site in each year by the proportion of habitat sampled at that site that 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 $L_\infty = 10.71\text{cm}$ (range of estimates 10.50 - 10.90 cm) and $K = 0.864$ (range

354

of estimates 0.785 - 0.944) for the von Bertalanffy growth curve parameters (eqn. 5, 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 $b_a = 0.169 \pm 0.028$ SE and intercept $b_\phi = -1.83 \pm 0.231$ SE (eqn. 11). 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.4).

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

Using our best estimates for growth, survival, and fecundity, we calculate a value for LEP of 1061, ranging from 39 to 10345 when we consider uncertainty in the inputs (Fig. 5b). Adult survival has the most effect on the value of LEP (Fig. B.6), with higher values of LEP the higher annual survival of adults.

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 (APPENDIX FIG!). When we compensate for density-dependence 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 dispersal probability, rather than in S_e . Uncertainty in the size of transition to breeding female L_f has the largest effect on egg-recruit survival (Fig.

³⁷⁵ B.8); 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.

³⁷⁸ 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 we compensate for density-dependence, we estimate a value of 1.42 for LRP, with a ³⁸¹ 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 before considering dispersal. This mean that individuals at our sites produce enough ³⁸⁴ 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 and drive persistence.

³⁸⁷ We also estimate replacement for recruits from our sites returning to our sites, LRP_{local} , which implicitly includes dispersal mortality, to be 0.09 (ranging from 0.03 to 0.44 when we include uncertainty) or 0.16 (0.05 to 0.76) when we compensate for ³⁹⁰ 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 sites do not persist as an independent network. When we calculate LRP_{local} using all ³⁹³ arriving recruits to our sites, however, rather than just those originating there, the best estimates are > 1 whether or not we compensate for density dependence (2.06, 1.22, respectively), suggesting that there is recruit-recruit replacement at our sites ³⁹⁶ when we include immigrant recruits.

We do not find any sites with $SP > 1$, whether we compensate for density-

dependence or not (Fig. 6a), indicating that no site could persist in isolation. Given
399 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 val-
ues of self-persistence at Haina (SP = 0.079, 0.13 when compensating for density-
402 dependence) and Wangag (SP = 0.048, 0.082 when compensating for density-dependence),
our two widest sites.

For network persistence, our best estimate of the dominant eigenvalue of the
405 realized connectivity matrix λ_c is 0.21 with a range of 0.07 - 0.92 (Fig. 6), or 0.36
with a range 0.12 - 1.58 when we compensate for density-dependence (Fig. 6). Our
sites are likely not network persistent, as our best estimates and most of the values we
408 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 among the sites in the northern part of
411 our sample area, from Palanas to Caridad Cemetery, and at the southern part of our
sample area from Tomakin Dako to Sitio Baybayon (Fig. 6b, d), where the largest
sites are.

414 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. With our
site configuration and dispersal kernel estimate, we would need a value of LRP of
417 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), to have a best estimate of
420 $\lambda_c = 1$ and network persistence.

Discussion

We do not see strong evidence for persistence in our metric estimates. We see no
423 evidence for self-persistence where an individual site could persist alone and weak
evidence for network persistence; it is possible at the upper end of our range of esti-
mates with uncertainty but not suggested by most of the range or our best estimates
426 (Fig. 6). The abundances through time at our sites do not show a clear directional
change, however, suggesting that the population at our sites is relatively constant
but relies on input of recruits from outside sites to persist. The portion of coastline
429 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
432 higher. With our estimated connectivity, 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 3-5 times higher than our best estimates, without and with
435 density-dependence compensation. Our best estimate of LRP when we com-
pensate for density-dependence is greater than one, so higher connectivity and retention
of offspring among our sites could lead to network persistence, but almost all sur-
438 viving offspring would need to be retained. At our best estimate without density-
dependence compensation, however, LRP is less than one - the average recruit only
produces 0.83 of a surviving recruit of the same stage - so no amount of increased
441 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
444 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 reef sites such as Cuatro Islas have higher quality
447 habitat and could be contributing recruits to our sites.

We do not find clear evidence for network persistence for our sites despite esti-
mates of the mean dispersal distance of *A. clarkii* from previous genetic work (11
450 km, Pinsky et al., 2010) and from our samples (8.25 km, with 95% confidence in-
terval 7.41 to 9.36, Catalano et al., in prep) that are well within the 30 km span of
our sites. Though the width of our sampling region is more than twice the mean
453 dispersal distance, which Lockwood et al. (2002) find sufficient for persistence of an
isolated reserve, their estimate assumes continuous habitat within the reserve and
our region is only about 20% habitat. For a habitat configuration more similar to
456 our system, habitat patches (reserves) spaced on a coastline with non-habitat in be-
tween, they find that either 40% of the coastline needs to be preserved or a minimum
patch size must be 1.25 times the mean dispersal distance to ensure persistence. Our
459 largest site, Haina, is only about 0.8 km wide, about 10 times less than the mean
dispersal distance, so it is possible we do not have enough habitat in our region for
network persistence, exacerbated by our 4 largest sites being at the edges of our
462 area and sending half of their recruits away from our sites. Our low, and possibly
below-replacement, estimate for LRP also suggests that lack of persistence in these
sites is not due to excessive dispersal out of the area but due to low production and
465 survival of offspring. The reef health and habitat quality in our sites is generally

low, due anthropogenic effects such as pollution and silt from a nearby gravel mine, and habitat disturbance due to storms. Our sites are in an area that was hit in 2013
468 by Typhoon Haiyan, one of the strongest typhoons ever to make landfall, which de-
stroyed 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
471 surviving recruits in our sites (seen in other populations with low habitat quality,
e.g. Hayashi et al., 2019) necessitating subsidization by outside populations.

We see considerable uncertainty in our estimate of persistence metrics depending
474 on the particular input values we use (Figs. 5, B.9). Our highest estimate for LRP is
about 24 times more than our lowest estimate and our highest NP estimate is about
22 larger than our lowest, spanning the range between network persistence for our set
477 of sites to far from it. Measuring demographic and dispersal parameters in the field
is challenging; in the face of limited and imperfect data, characterizing uncertainty
and propagating it from our estimates of demographic and dispersal inputs through
480 to our estimates of persistence metrics is important to contextualize our results. In
our study, uncertainty in egg-recruit survival (a commonly challenging parameter
to estimate, e.g. Johnson et al., 2018; Hameed et al., 2016), partially driven by
483 uncertainty in how likely we are to capture recruits during sampling (Figs. B.8,
??), has a large effect on whether or not we think our populations are persistent.
For a marine metapopulation, our system is relatively uncomplicated and yet still
486 hard in which to concretely ascertain persistence. As we accumulate more empirical
assessments of metapopulations to compare to our expectations from theory and
models, we will have to think carefully about how to handle uncertainty as we move

⁴⁸⁹ to tackling larger and more complicated systems.

Persistence criteria, such as those detailed in Hastings and Botsford (2006a) and Burgess et al. (2014), ask whether a population at low abundance can grow and recover rather than going extinct. Density-dependence is often ignored at low abundances (e.g. Caswell, 2001; Hastings and Botsford, 2006b) 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*, 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 (e.g. Buston and Elith, 2011). In other species of clownfish, individuals on the same anemone maintain strict size spacing, restricting their food intake and growth to avoid encroaching on the position of another fish and being attacked or evicted (seen in *A. percula*, Buston, 2003a,b). This suggests that while fish are in the pre-reproductive queue, density-dependence may lower growth rates compared to the growth of fish alone on an anemone, as would be the case in a population at low abundance. We attempt to account for the primary effect of density-dependence on our estimate of egg-recruit survival but other estimates, particularly growth and survival, would also likely be higher in the absence of density-dependence and increase LRP.

Our estimates of persistence metrics suggest that it is possible but not likely that the region of sites we sample persist as a network without outside input, despite covering an area more than twice the estimated mean dispersal distance for our focal

species. Our estimate of LRP near the threshold of one required for replacement
513 (slightly < 1 when we do not compensate for density-dependence, slightly > 1 when
we do), suggests that dispersal is not likely the primary reason our sites do not persist
as a network. If density-dependence is strongly present in our data such that our
516 compensated estimate is the best, then our sites could persist if there were no losses
to dispersal. Otherwise, our sites do not produce enough offspring for replacement
regardless of dispersal patterns, possibly due to worsening habitat quality. This is
519 a reminder that dispersal is only part of the persistence story for metapopulations;
even areas that seem large enough to contain a persistent network based on dispersal
distance will not be able to persist in isolation if they have low production and
522 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 likely enables our
sites to persist.

525 **Figures**

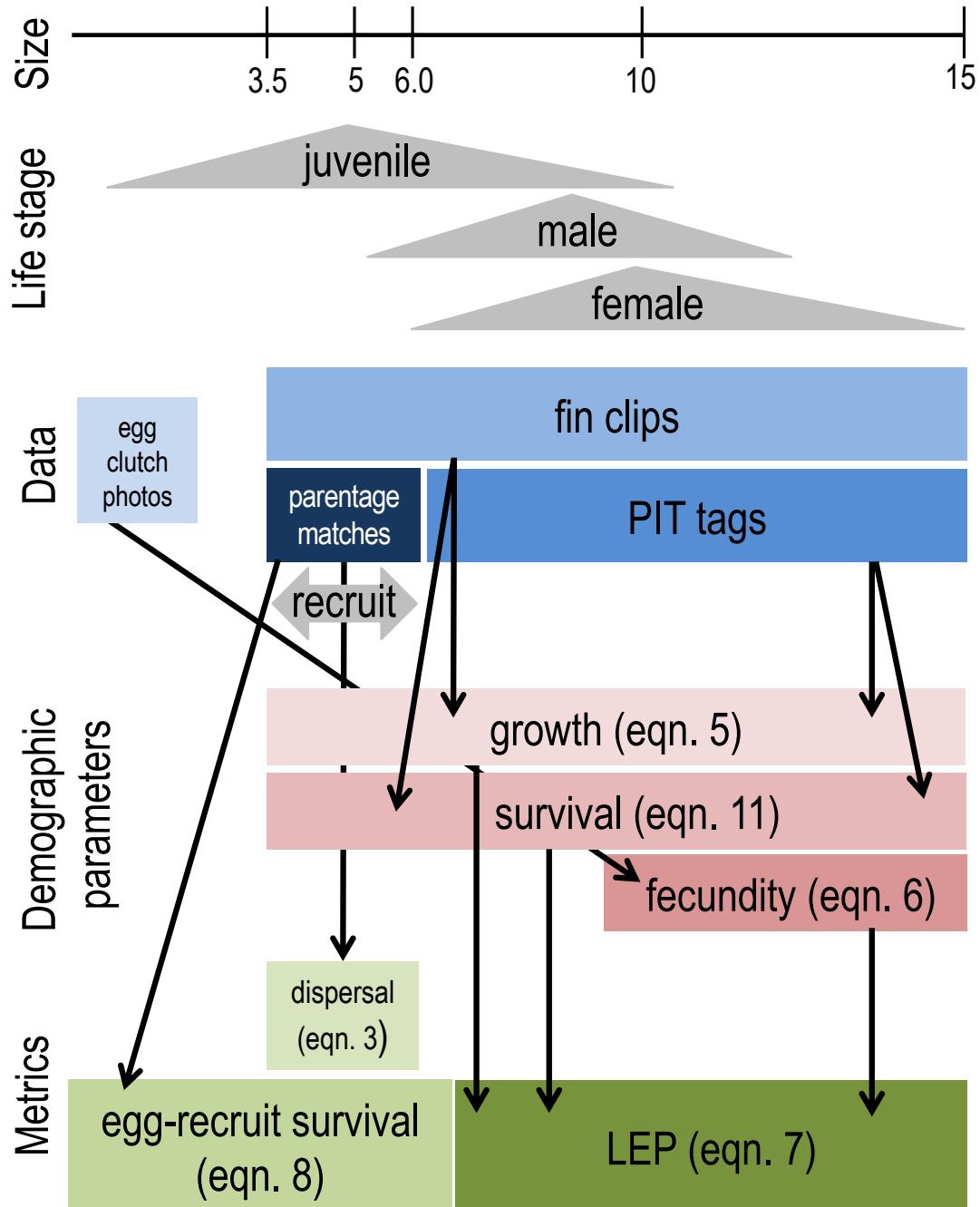


Figure 2: Here, we show the data collected²⁹ for fish at each life stage (life stage boxes are not scaled by length of stage) and how the empirical data fit into our parameter and metric calculations.

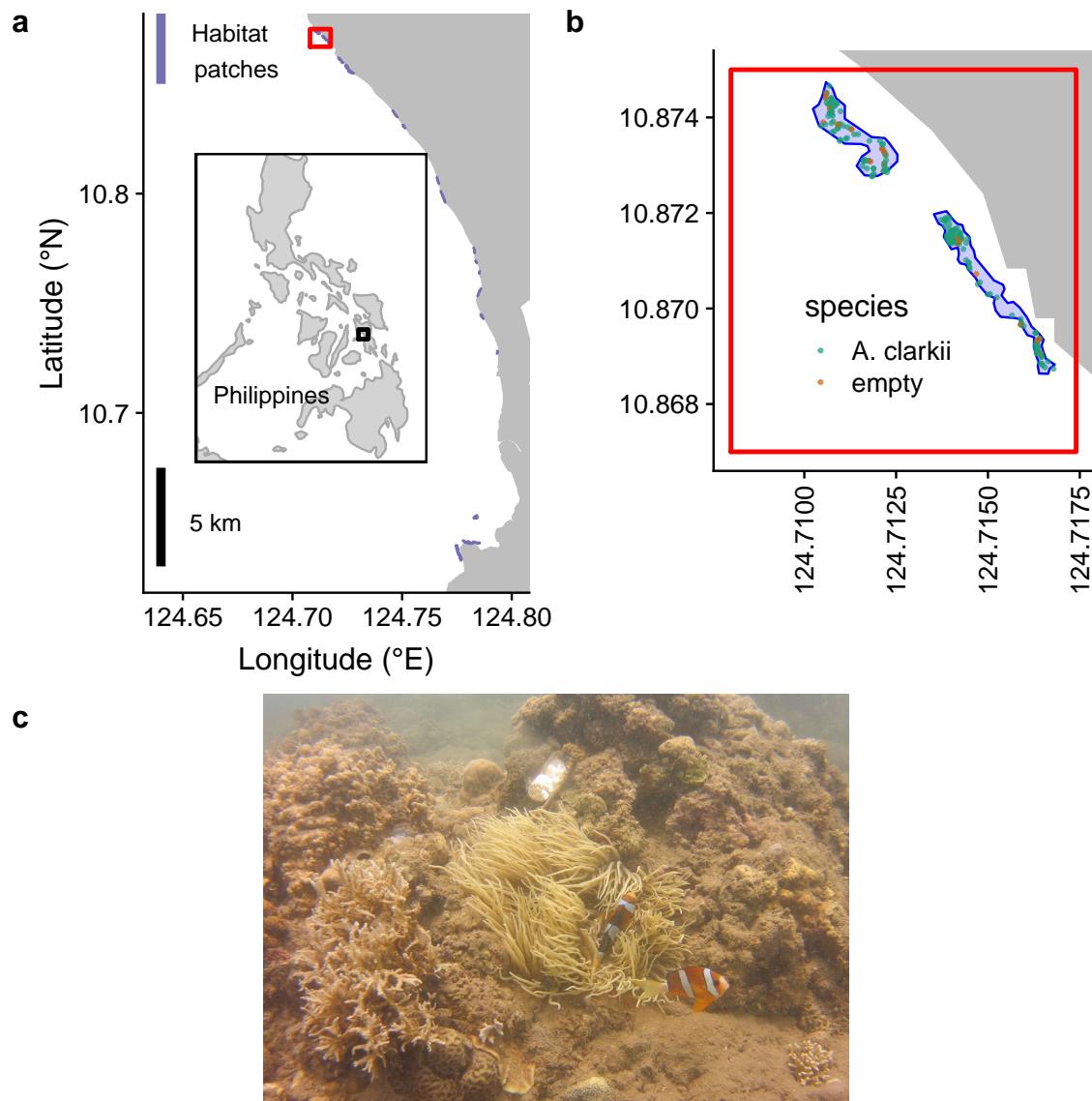


Figure 3: a) Map of the sites along the coast of Leyte in the Philippines. b) Zoomed-in map of the two northern-most sites, Palanas and Wangag, to show anemone arrangement, with anemones occupied by *A. clarkii* (green) or unoccupied by clownfish (orange). c) An example anemone occupied by *A. clarkii* in a typical habitat at the sites. The metal anemone tag is visible just above the anemone on the rock.

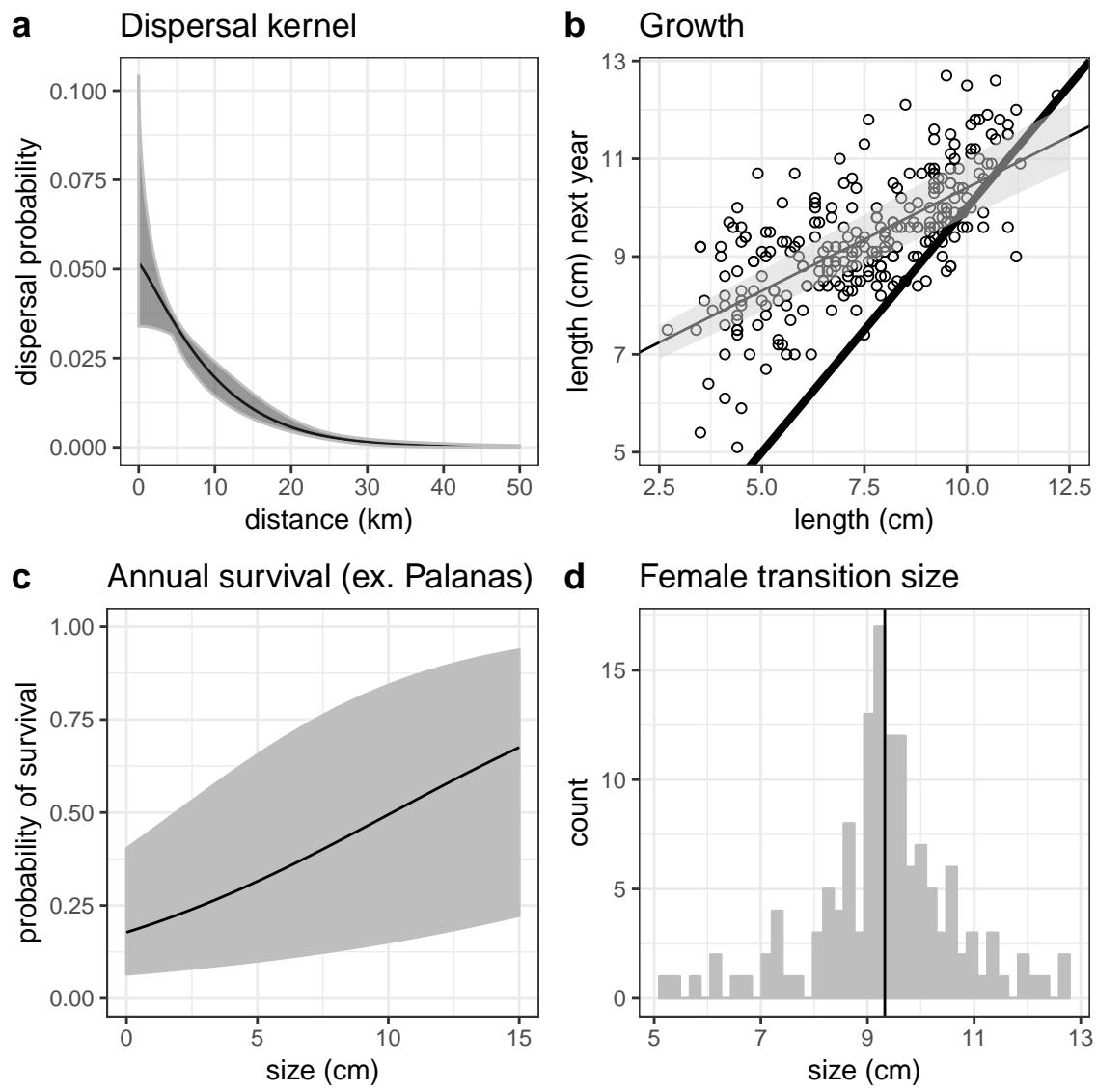


Figure 4: Best estimates (solid black line) and range included for uncertainty (gray) for dispersal (a), growth, including the 1:1 line in thick black (b), post-recruit survival at Palanas as an example site (c), and size at female transition (d) parameters.

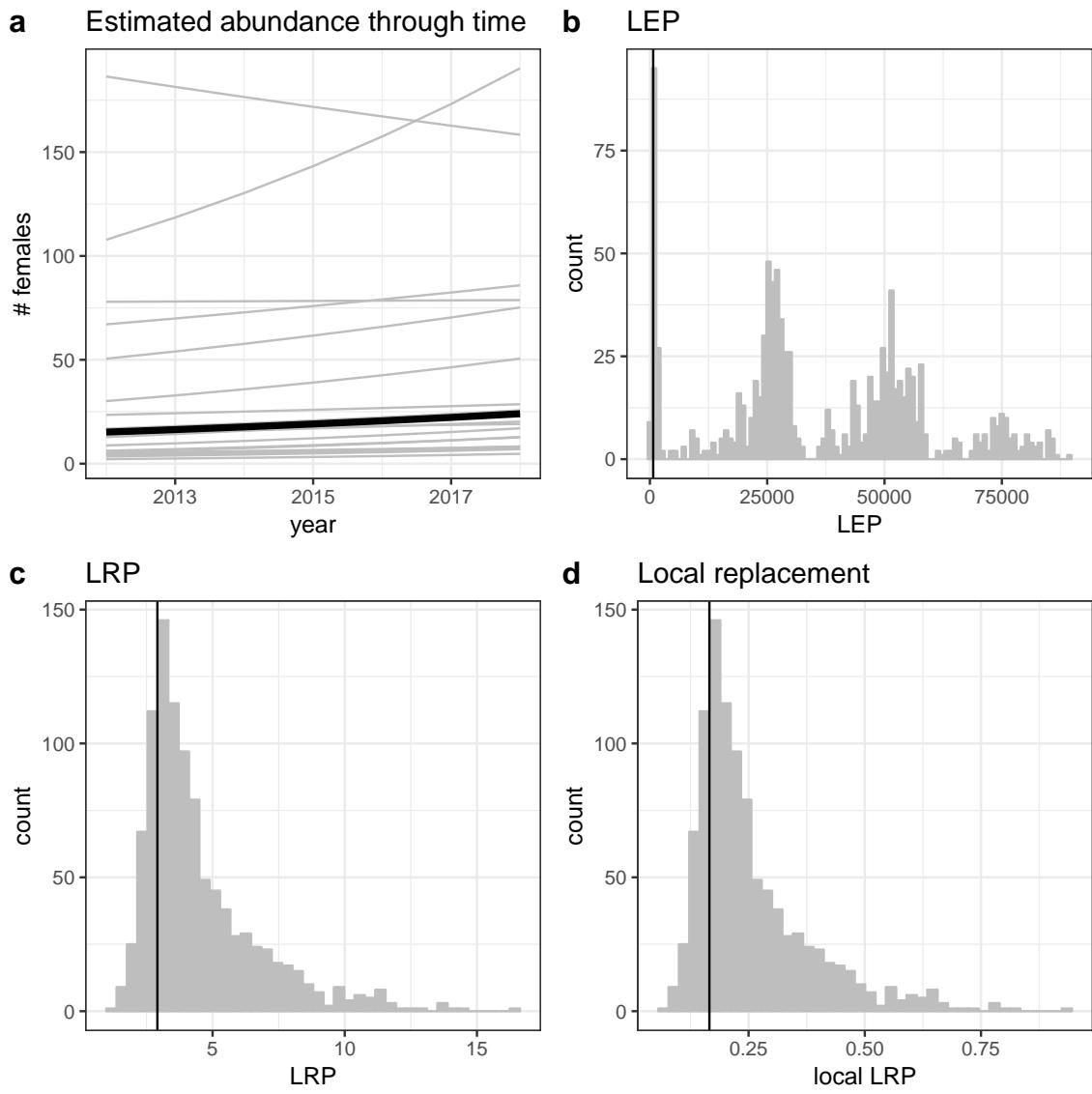


Figure 5: Estimates of a) estimated abundance of females at each site (grey lines) and for an average site (black line) b) average LEP across sites, c) LRP, and d) LRP_{local} , showing the best estimate (black solid line) and range of estimates considering uncertainty in the inputs. The estimates in c-d include our attempt to remove density-dependence in the early life stages. We only consider density-dependence in egg-recruit survival so LEP (a) estimates are the same in both cases.

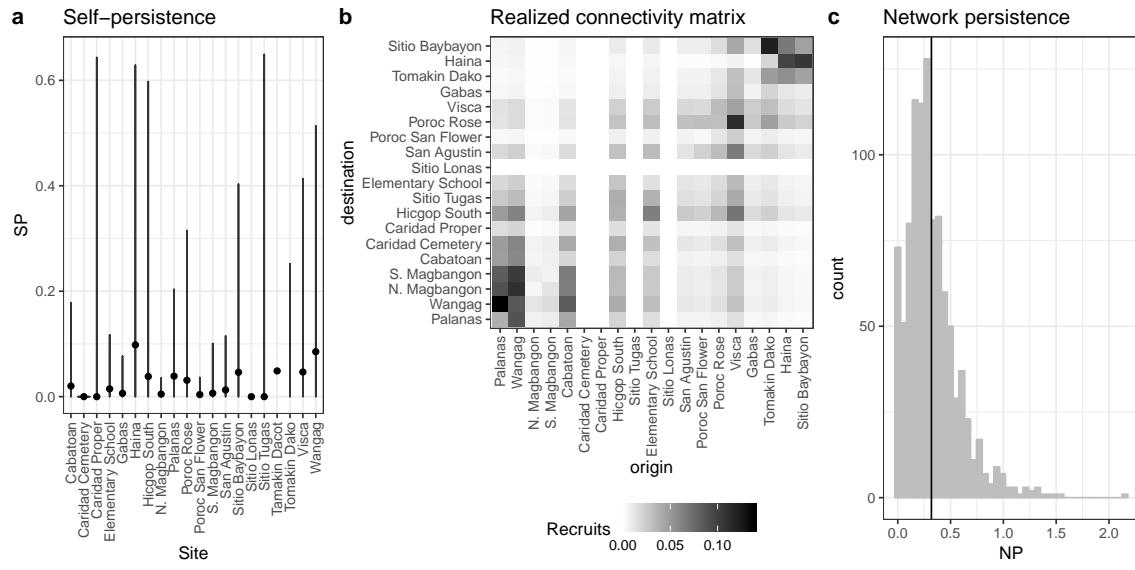


Figure 6: Values of self-persistence (a), realized connectivity among sites (b), and network persistence (c). All estimates include compensation for density-dependence in early life stages in our data. For self-persistence (a) and network persistence (c), the best estimate is shown with in black (point for (a), line for (c)) and the range of estimates considering uncertainty is shown in grey.

Appendix

Summary of parameters

Parameter	Description	Best estimate	Range in uncertainty runs	Notes
k_d	scale parameter in dispersal kernel	-2.11	-2.36 to -1.96	estimated using methods in Bode et al. (2018) in Catalano et al. (in prep)
θ	shape parameter in dispersal kernel	1	NA	estimated using methods in Bode et al. (2018) in Catalano et al. (in prep)
L_∞	average asymptotic size in von Bertalanffy growth curve	10.70 cm	10.50 to 10.90 cm	

K	growth coefficient in von Bertalanffy growth curve	0.864	0.785 to 0.944	
b_ϕ	intercept for adult survival	-1.82	± 0.231 standard error	on a log-odds scale
b_a	size effect for adult survival	0.169	± 0.028 standard error	on a log-odds scale
b_{pr}	intercept for recapture probability from mark-recapture analysis	2.10	± 0.849 standard error	on a log-odds scale, not used in persistence estimates
b_1	size effect for recapture	-0.161	± 0.088 standard error	on a log-odds scale, not used in persistence estimates
b_2	distance effect for recapture	-0.196	± 0.023 standard error	on a log-odds scale, not used in persistence estimates

size _{recruit}	size (cm) of recruited offspring	mean of size of offspring in parentage analysis = 4.37 cm	3.5 - 6.0 cm	drawn from uniform distribution across range
size _{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	1.45		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)

c_e	egg clutches per year	11.9		Holtswarth et al. (2017)
L_f	size at transition to female	9.32cm	5.2 - 12.7cm	drawn from distribution in data
P_h	proportion of sites sampled cumulatively across time	0.41		details in A.1
P_d	proportion of dispersal kernel area from each site covered by our sampling region	0.57		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	0.20		details in A.2.0.1
DD	proportion of habitat that would be available without density-dependence at settlement	1.71		
p_U	proportion of anemones unoccupied by clownfish	0.53		used to estimate DD
p_A	proportion of anemones occupied by <i>A. clarkii</i>	0.38		used to estimate DD

Table A1

528 **A Method details**

A.1 Proportion of habitat sampled

We used tagged anemones to estimate the proportion of habitat sampled at each site
531 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. 3c), 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.

540 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.

		% 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

549 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
555 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
558 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 : $P_c = \frac{m_2}{n_2}$.

561 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
564 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
567 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

⁵⁷⁰ $V_{P_c} = 0.069$, 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

⁵⁷³ 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.

⁵⁷⁶ **Scaling up recruits**

ADD SOME TEXT!

How could we have missed potential recruits originating from our sites?

- 1) Failed to catch recruit when sampling (P_c)
- 2) Did not sample all habitat areas within our sites (P_h)
- 3) Recruit dispersed outside our study region (P_d)
- 4) Recruit dispersed to non-habitat within our region (P_s)
- 5) Recruit died due to density-dependent competition with other settlers (DD)

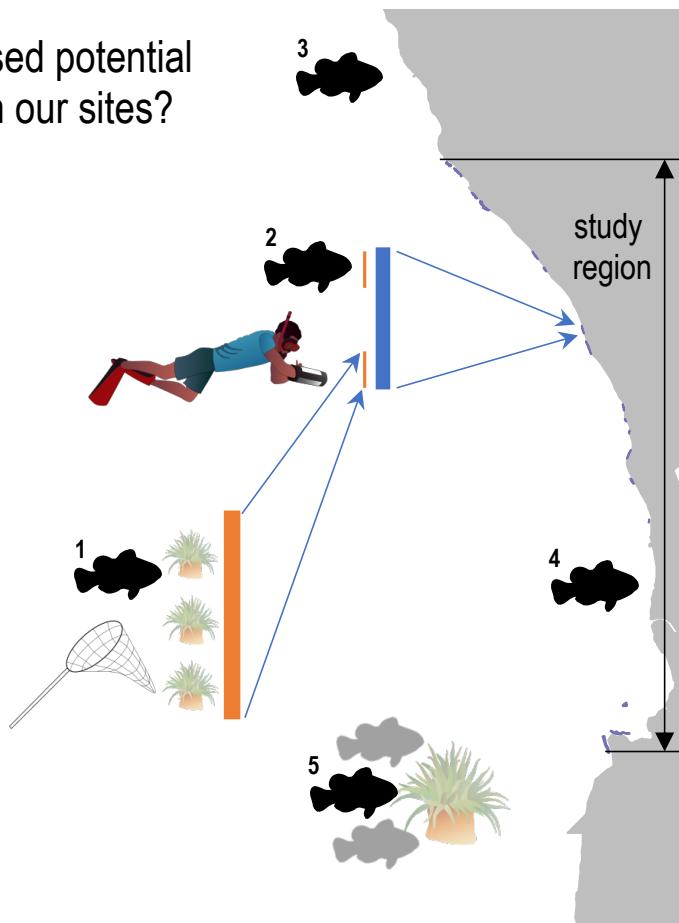


Figure A.1: Schematic of five ways we could have missed recruits while sampling and used to scale up our raw estimate of recruits from matched offspring.

Proportion of dispersal kernel area sampled

⁵⁷⁹ [Add in description of calculation and equation]

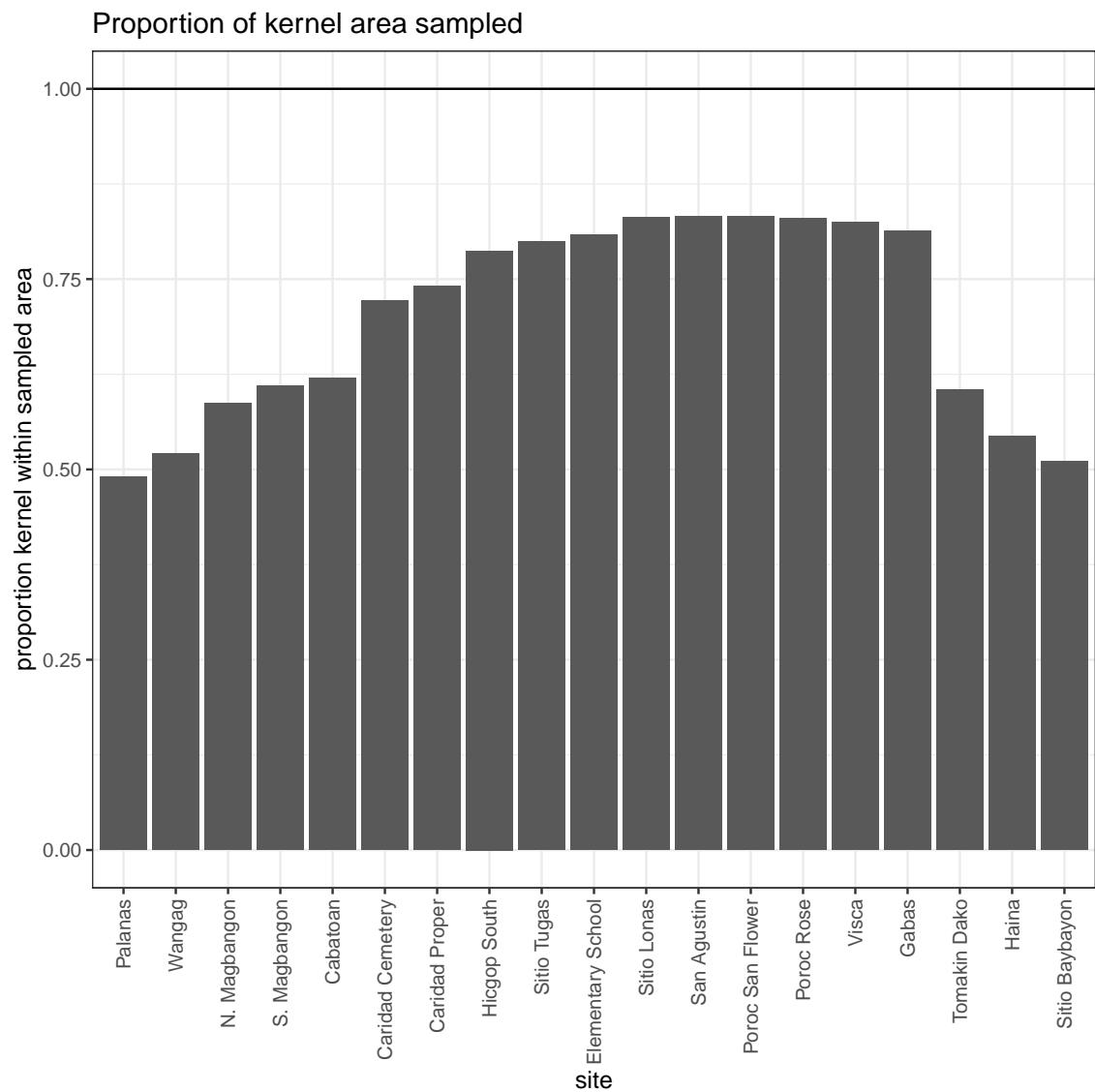


Figure A.2: Proportion of the dispersal kernel area from the center of each site covered by our sampling.

A.2.0.1 Proportion habitat in sampling area

We assume that larvae are unable to navigate to habitat if they attempt to settle
582 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
585 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
588 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 $P_s = 0.20$.

Model	Model description	AICc	dAICc
$\phi \sim S, p \sim S + D$	survival size, recapture size+distance	3348.861	0
$\phi \sim S, p \sim D$	survival size, recapture distance	3359.998	-11.1371
$\phi, p \sim D$	survival constant, recapture distance	3383.175	34.3141
$\phi, p \sim S + D$	survival constant, recapture size+distance	3384.959	36.0981
$\phi \sim t, p$	survival time, recapture constant	3408.342	59.4816
$\phi \sim i, p$	survival site, recapture constant	3440.842	91.98112
$\phi \sim i, p \sim S + D$	survival site, recapture size+distance	3440.842	91.98112
$\phi, p \sim t$	survival constant, recapture time	3453.609	104.74839
$\phi \sim S, p \sim S$	survival size, recapture size	3527.710	178.84940
ϕ, p	survival constant, recapture constant	3570.908	222.04690

Table A3

A.3 Full set of MARK models

- ⁵⁹¹ We consider the following set of models in MARK for survival (ϕ) and recapture (p) probability, including effects of size (S), minimum distance from diver to anemone during surveys (D), time (t), and site (i) (Table A3):
- ⁵⁹⁴ The best model includes both site and size in survival

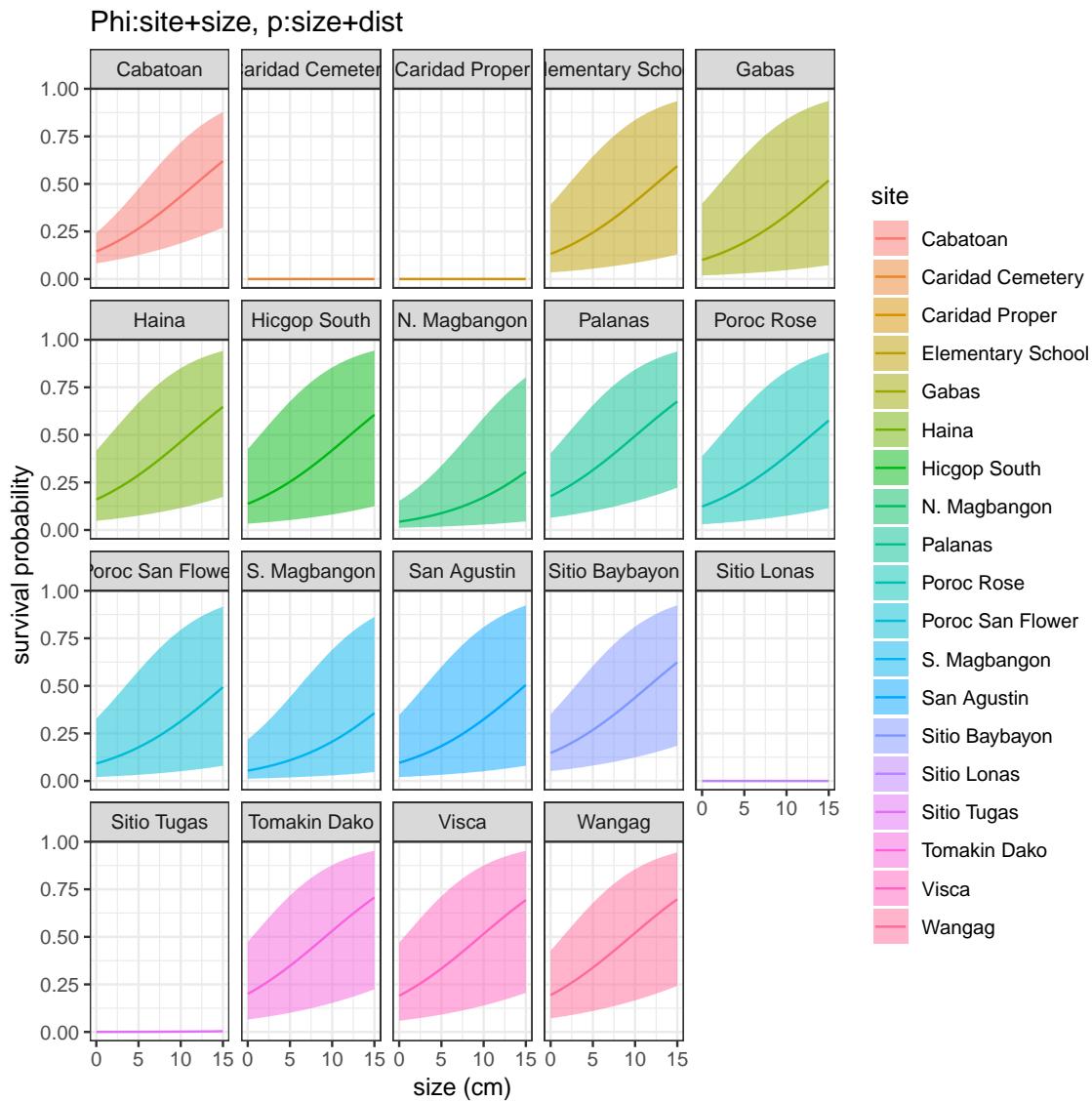


Figure A.3: Annual survival by size at each site.

A.3.0.1 Recapture model

The best model for log-odds recapture probability, accompanying the survival model
⁵⁹⁷ in eqn. 11, has a size effect ($b_1 = -1.816 \pm 0.080$ SE, Fig. A.4a) and a negative

effect of diver distance from the anemone ($b_2 = -0.171 \pm 0.021$ SE, Fig. A.4b), with intercept $b_{pr} = 17.93 \pm 0.858$ SE:

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

600 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.

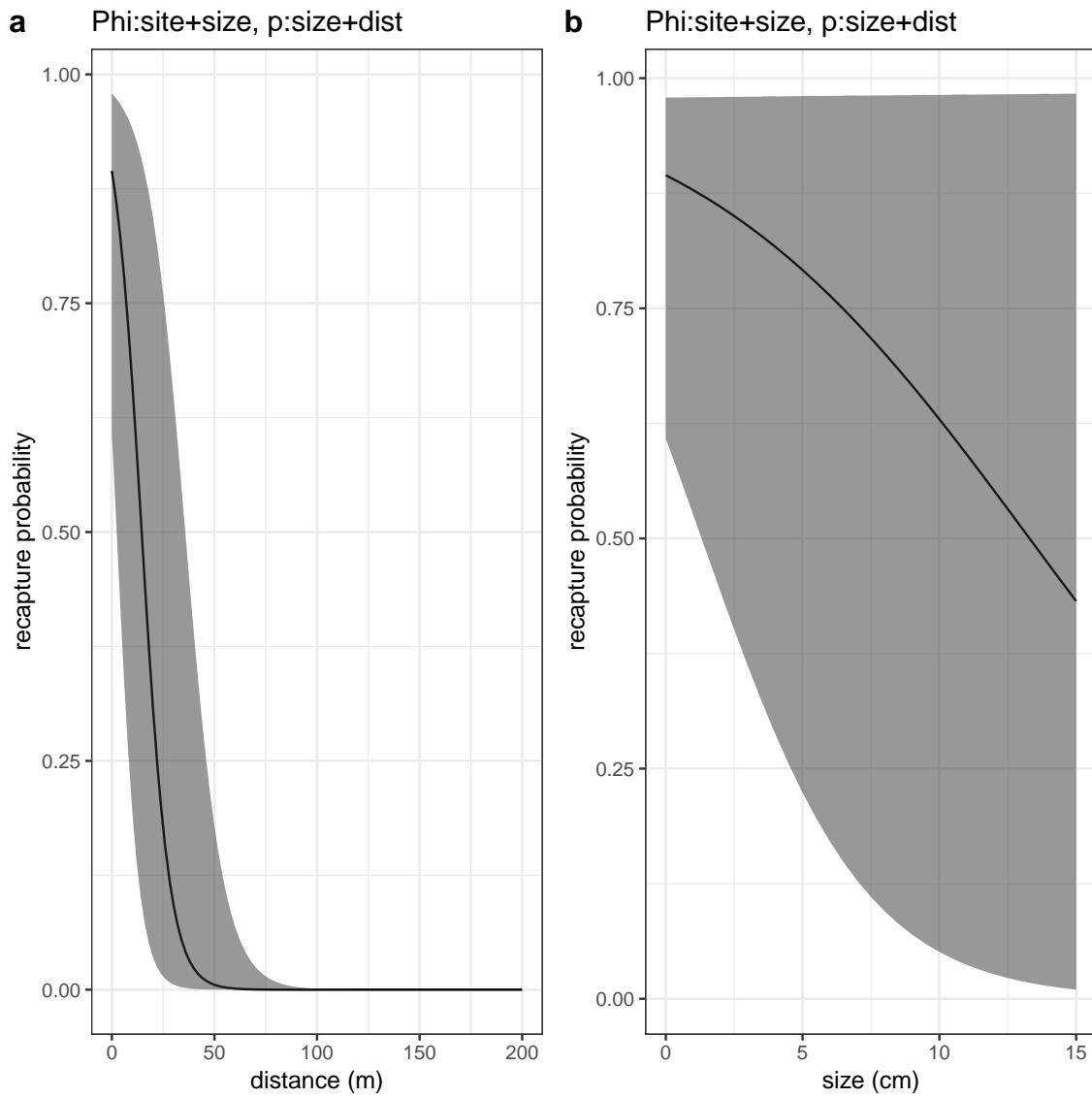


Figure A.4: Effects of a) minimum distance between divers and the anemone where the fish was first caught and b) fish size on the probability the fish will be recaptured, estimated along with survival in a mark-recapture analysis. Size has a slightly negative effect on the probability of recapture - larger fish are stronger swimmers and more likely to flee the anemone when divers approach, but with high uncertainty at larger sizes. 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 Result details and sensitivity

603 Abundance trends by site

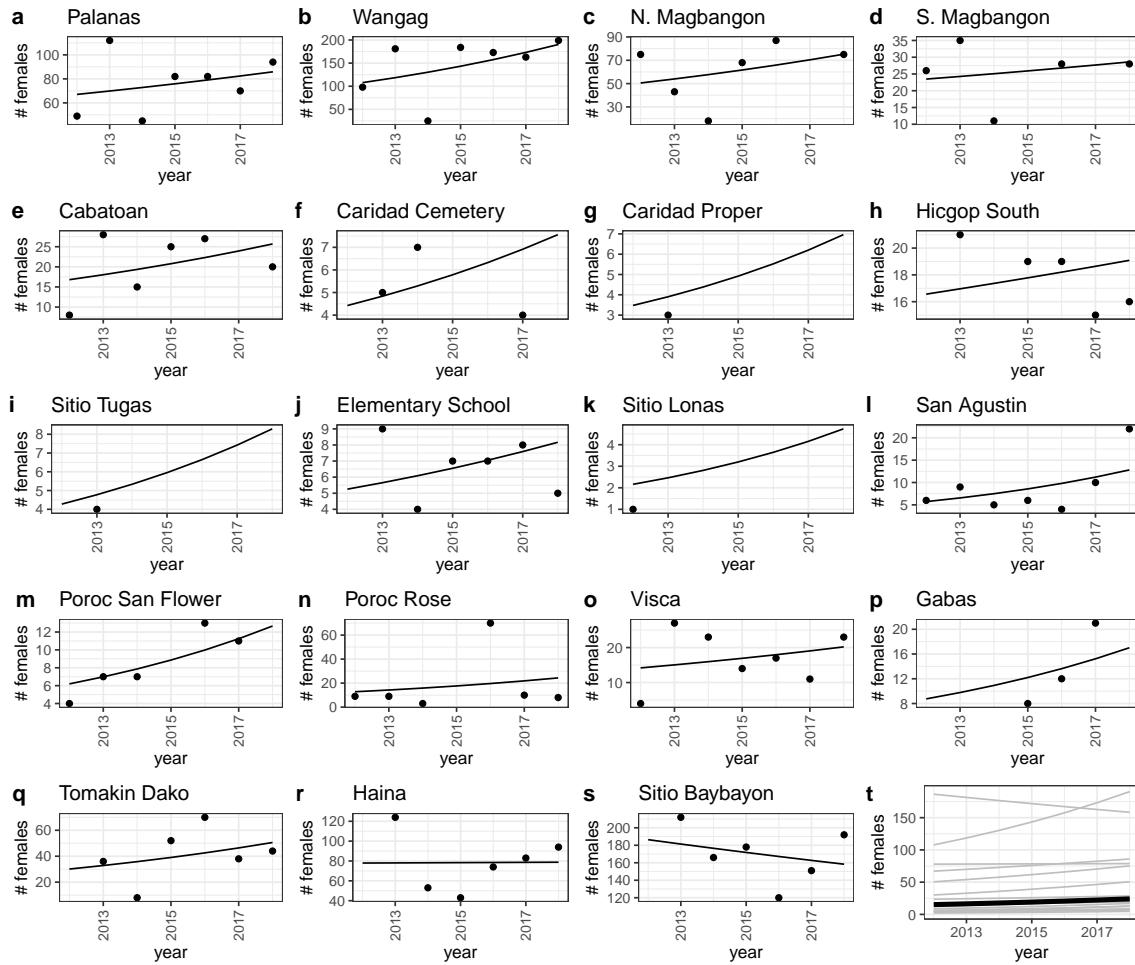


Figure B.1: Scaled estimates of females and abundance trends by site.

B.1 Sensitivity to parameters

EXPLAIN THAT THESE ARE THE REST OF THE PARAMETERS, NOT SHOWN

606 IN THE MAIN TEXT

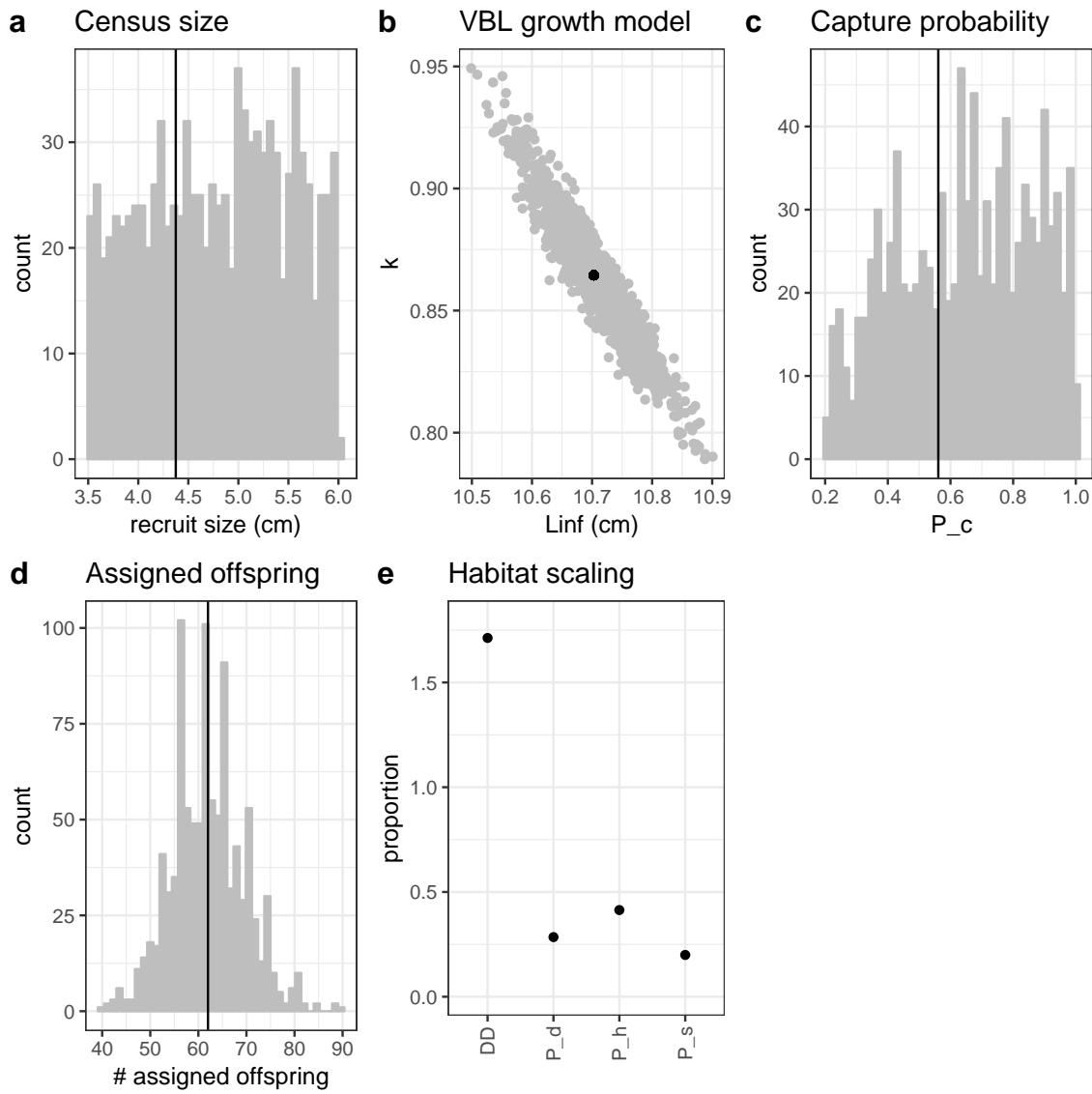


Figure B.2: Range of parameter inputs for uncertainty runs with all uncertainty included, where the black line or point is the value used for the best estimate: a) $\text{size}_{\text{recruit}}$, the census size at which fish are considered to have recruited after egg-recruit survival occurs; b) the parameters L_{∞} and K of the von Bertalanffy growth model; c) P_c , the probability of capturing a fish; d) number of offspring assigned back to parents in the parentage analysis; e) factors that scale the number of estimated recruits from our site based on density-dependence in settler success (DD), proportion of the dispersal kernel captured by our sampling region (P_d), the cumulative proportion of our sites we sampled over time (P_h), and the proportion of our sampling area that is habitat (P_s).

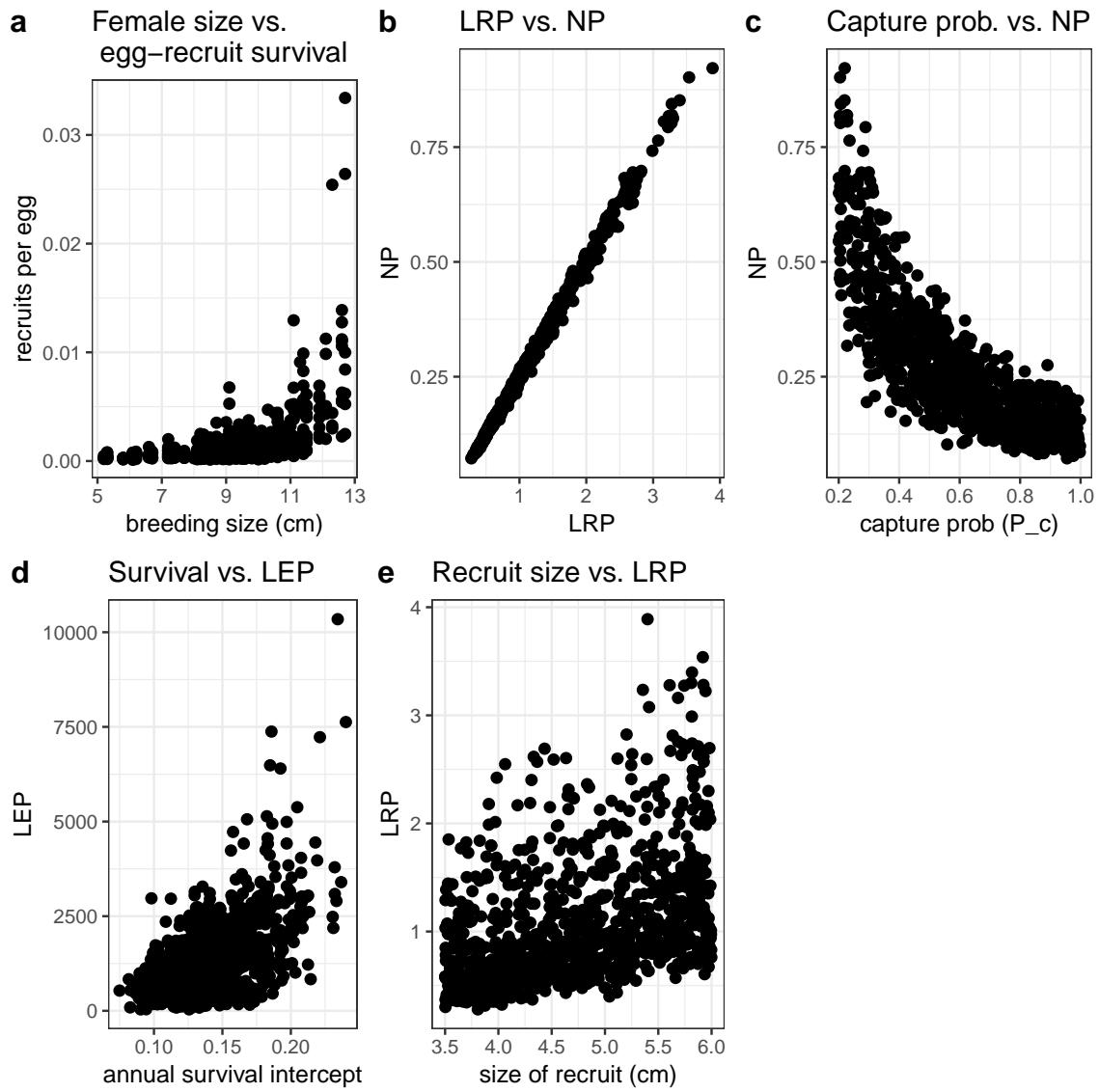


Figure B.3: Relationships among parameters and metrics. a) We only count reproductive effort by fish in the female stage so the higher the transition size to breeding female, the fewer eggs parents are considered to produce, which increases the estimated egg-recruit survival. b) LRP strongly affects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

Compensating for density dependence

TALK ABOUT HOW DENSITY DEPENDENCE AFFECTS OUR RESULTS, CITE

609 SECTION OR EQUATION WHERE WE COMPENSATE FOR IT

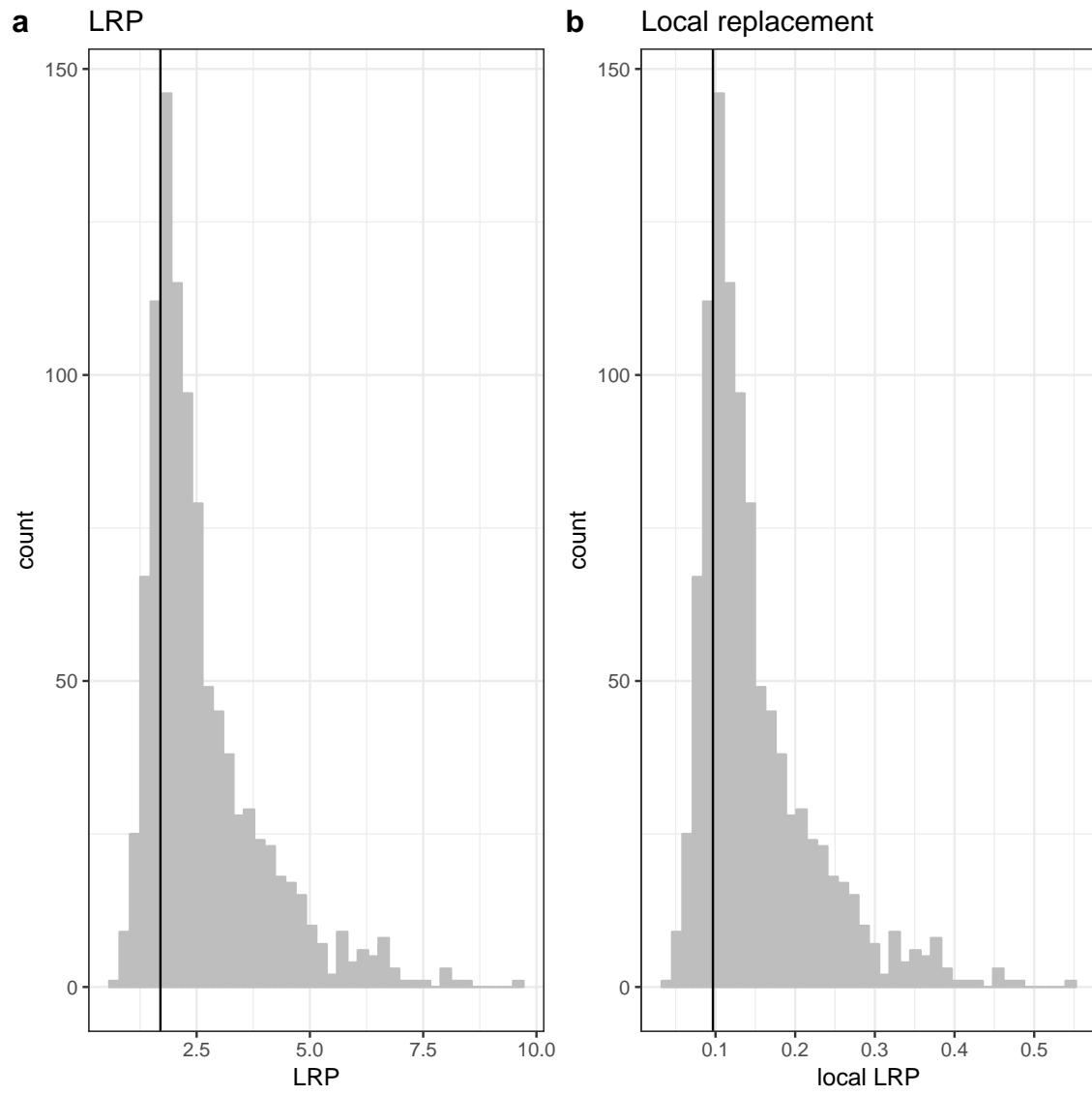


Figure B.4: Estimates of a) LRP, and b) local replacement without compensating for density dependence in early life stages in our data, showing the best estimate (black solid line) and range of estimates considering uncertainty in the inputs. These estimates compare to those in 5c,d, where we attempt to compensate for additional mortality in early life due to density dependence.

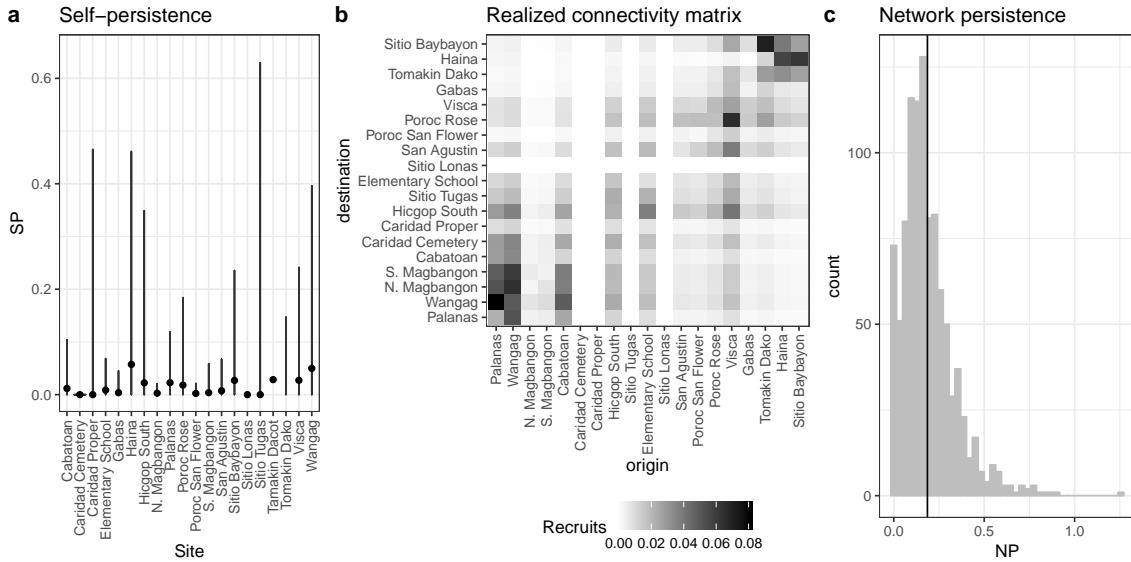


Figure B.5: Values of self-persistence (a), realized connectivity among sites (b), and network persistence (c) without compensation for density-dependence in early life stages in our data. For self-persistence (a) and network persistence (c), the best estimate is shown with in black (point for (a), line for (c)) and the range of estimates considering uncertainty is shown in grey. These estimates compare to those in 6 where we attempt to compensate for density dependence in early life stages.

B.2 Effects of different types of uncertainty on metrics

B.2.0.1 Lifetime egg production (LEP)

612 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 higher fecundity. The transition size to breeding female also drives uncertainty in
 615 LEP - the higher the transition size to female, the less time the fish has at a size where its reproduction is counted in LEP.

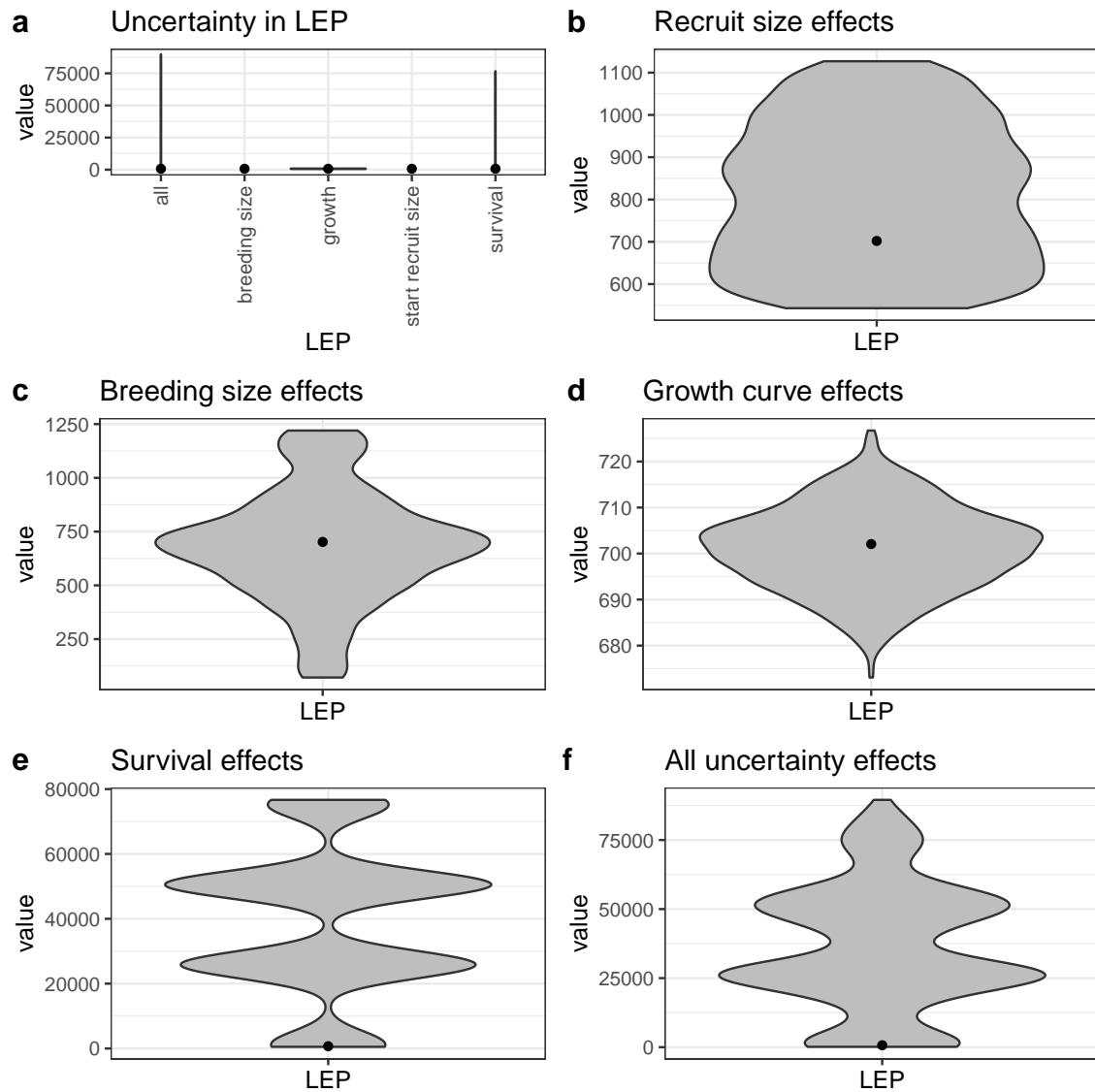


Figure B.6: The contribution of different sources of uncertainty in LEP.

B.2.0.2 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

differently to account for changes in the size of a recruit, so raising the size of a recruit
621 reduces the mortality included in LRP without increasing the mortality included in egg-recruit survival, as it should in an ideal situation.

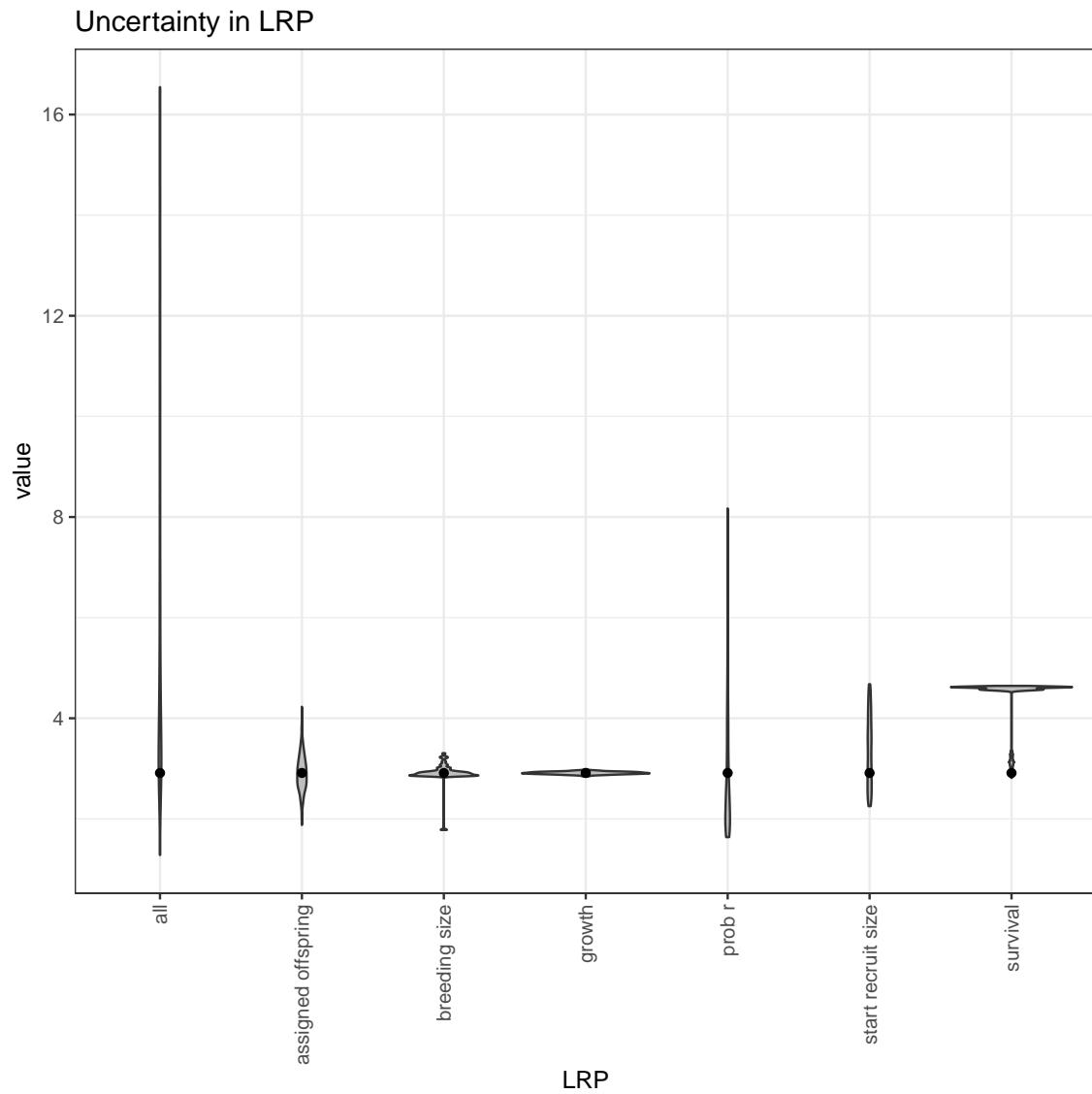


Figure B.7: The contribution of different sources of uncertainty in LRP.

B.2.0.3 Egg-recruit survival (S_e)

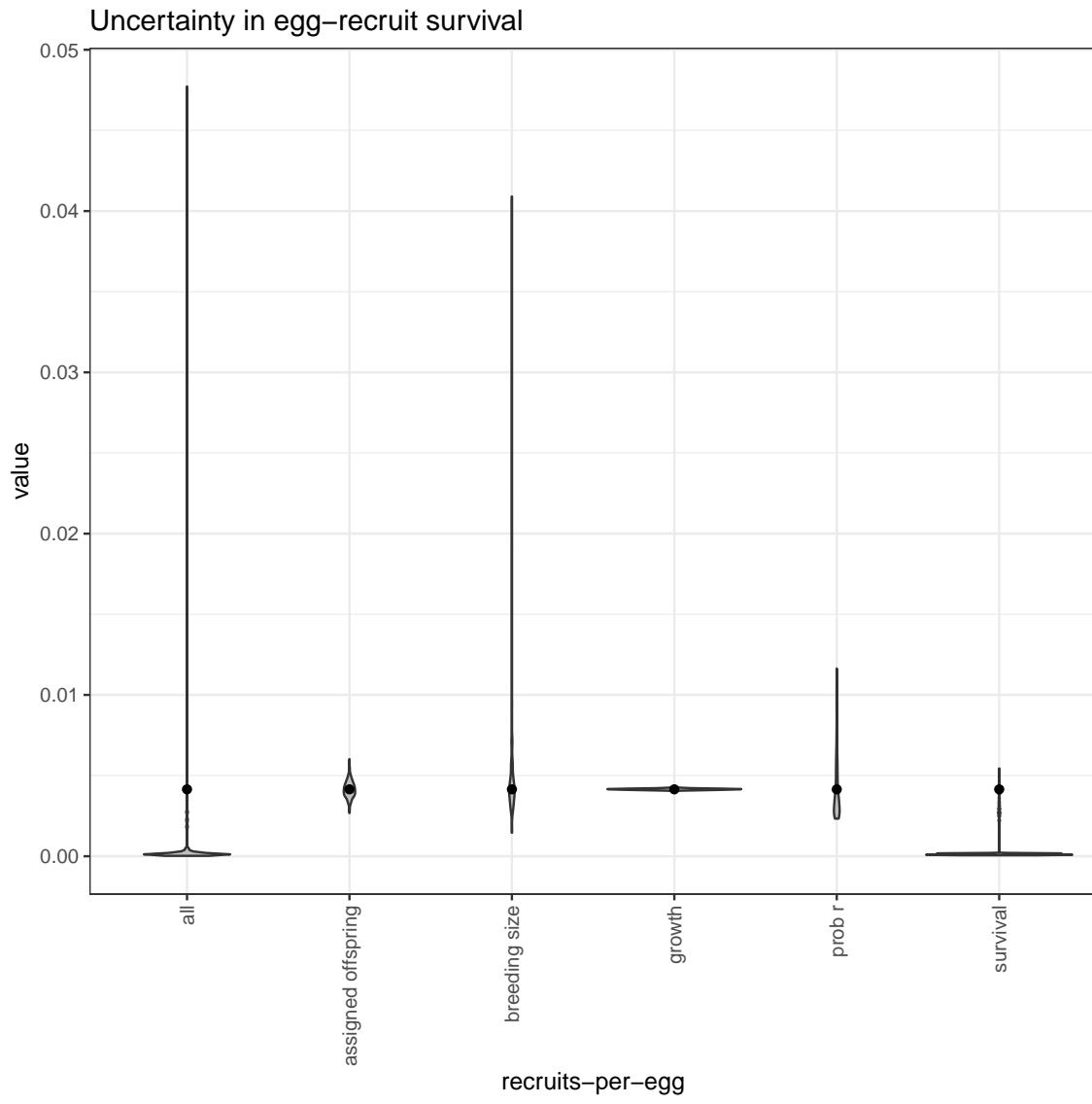


Figure B.8: The contribution of different sources of uncertainty in egg-recruit survival.

624 **B.2.0.4 Network persistence (NP)**

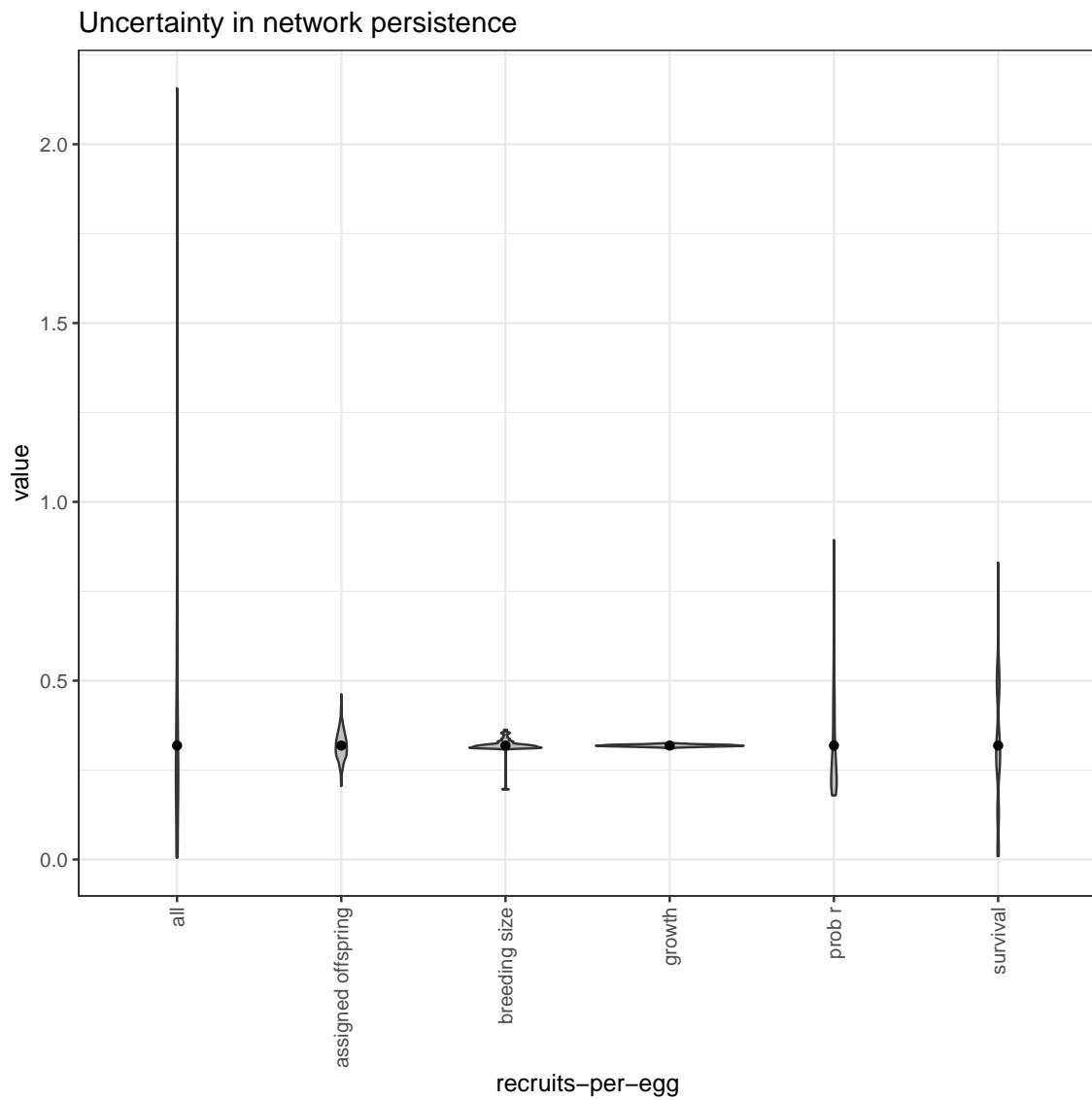


Figure B.9: The contribution of different sources of uncertainty in NP.

References

- Glenn R Almany, Serge Planes, Simon R Thorrold, Michael L Berumen, Michael
627 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.
- Michael Bode, David H Williamson, Hugo B Harrison, Nick Outram, and Geoffrey P
630 Jones. Estimating dispersal kernels using genetic parentage data. *Methods in
Ecology and Evolution*, 9(3):490–501, 2018.
- L. W. Botsford, J. W. White, M.-A. Coffroth, C. B. Paris, S. Planes, T. L.
633 Shearer, S. R. Thorrold, and G. P. Jones. Connectivity and resilience of coral
reef metapopulations in marine protected areas: matching empirical efforts to
predictive needs. *Coral Reefs*, 28(2):327–337, June 2009. ISSN 0722-4028, 1432-
636 0975. doi: 10.1007/s00338-009-0466-z. URL <http://link.springer.com/10.1007/s00338-009-0466-z>.
- 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.
- Scott C Burgess, Kerry J Nickols, Chris D Griesemer, Lewis AK Barnett, Alli-
642 son G Dedrick, Erin V Satterthwaite, Lauren Yamane, Steven G Morgan, J Wilson
White, and Louis W Botsford. Beyond connectivity: how empirical methods can

645 quantify population persistence to improve marine protected-area design. *Ecological Applications*, 24(2):257–270, 2014.

Peter Buston. Forcible eviction and prevention of recruitment in the clown anemone-
648 fish. *Behavioral Ecology*, 14(4):576–582, 2003a.

Peter Buston. Social hierarchies: size and growth modification in clownfish. *Nature*, 424(6945):145–146, 2003b.

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

Peter M Buston and Jane Elith. Determinants of reproductive success in dominant
654 pairs of clownfish: a boosted regression tree analysis. *Journal of Animal Ecology*, 80(3):528–538, 2011.

Peter M Buston, Geoffrey P Jones, Serge Planes, and Simon R Thorrold. Probability
657 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,
2011.

660 Henry S Carson, Geoffrey S Cook, Paola C López-Duarte, and Lisa A Levin. Evaluating the importance of demographic connectivity in a marine metapopulation. *Ecology*, 92(10):1972–1984, 2011.

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

- Katrina A Catalano, Allison G Dedrick, Michelle Stuart, Jonathan Purtiz, Humberto
666 Montes, Jr., and Malin Pinsky. Interannual variability of genetic connectivity in
a coral reef fish *Amphiprion clarkii*. in prep.
- R. K. Cowen. Scaling of Connectivity in Marine Populations. *Science*, 311(5760):
669 522–527, January 2006. ISSN 0036-8075, 1095-9203. doi: 10.1126/science.1122039.
URL <http://www.sciencemag.org/cgi/doi/10.1126/science.1122039>.
- Robert K. Cowen and Su Sponaugle. Larval Dispersal and Marine Population Con-
672 nectivity. *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>.
- 675 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.
678 ISSN 09621083. doi: 10.1111/mec.12274. URL <http://doi.wiley.com/10.1111/mec.12274>.
- Cassidy C DAloia, Steven M Bogdanowicz, Robin K Francis, John E Majoris,
681 Richard G Harrison, and Peter M Buston. Patterns, causes, and consequences
of marine larval dispersal. *Proceedings of the National Academy of Sciences*, 112
(45):13940–13945, 2015.
- 684 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,
687 Gerald Robert Allen, and Australie Naturaliste. Field guide to anemonefishes and
their host sea anemones. 1992.
- Lysel Garavelli, J Wilson White, Iliana Chollett, and Laurent Marcel Chérubin. Pop-
690ulation models reveal unexpected patterns of local persistence despite widespread
larval dispersal in a highly exploited species. *Conservation Letters*, 11(5):e12567,
2018.
- 693 Sarah O Hameed, J Wilson White, Seth H Miller, Kerry J Nickols, and Steven G
Morgan. Inverse approach to estimating larval dispersal reveals limited population
connectivity along 700 km of wave-swept open coast. *Proceedings of the Royal
696 Society B: Biological Sciences*, 283(1833):20160370, 2016.
- Ilkka Hanski. Metapopulation dynamics. *Nature*, 396(6706):41–49, 1998.
- Deborah R Hart and Antonie S Chute. Estimating von bertalanffy growth parameters
699 from growth increment data using a linear mixed-effects model, with an application
to the sea scallop *placopecten magellanicus*. *ICES Journal of Marine Science*, 66
(10):2165–2175, 2009.
- 702 Alan Hastings and Louis W. Botsford. Persistence of spatial populations depends on
returning home. *Proceedings of the National Academy of Sciences*, 103:6067–6072,
2006a.
- 705 Alan Hastings and Louis W. Botsford. A simple persistence condition for structured
populations. *Ecology Letters*, 9(7):846–852, July 2006b. ISSN 1461-023X, 1461-

0248. doi: 10.1111/j.1461-0248.2006.00940.x. URL <http://doi.wiley.com/10.1111/j.1461-0248.2006.00940.x>.

708

Akihisa Hattori and Yasunobu Yanagisawa. Life-history pathways in relation to gonadal sex differentiation in the anemonefish, *amphiprion clarkii*, in temperate waters of japan. *Environmental Biology of Fishes*, 31(2):139–155, 1991.

711

Kina Hayashi, Katsunori Tachihara, and James Davis Reimer. Low density populations of anemonefish with low replenishment rates on a reef edge with anthropogenic impacts. *Environmental Biology of Fishes*, 102(1):41–54, 2019.

714

J. Derek Hogan, Roger J. Thiessen, Peter F. Sale, and Daniel D. Heath. Local retention, dispersal and fluctuating connectivity among populations of a coral reef fish. *Oecologia*, 168(1):61–71, July 2011. ISSN 0029-8549, 1432-1939. doi: 10.1007/s00442-011-2058-1. URL <http://link.springer.com/10.1007/s00442-011-2058-1>.

717

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

723

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.

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

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

Dale R Lockwood, Alan Hastings, and Louis W Botsford. The effects of dispersal
patterns on marine reserves: does the tail wag the dog? *Theoretical population
735 biology*, 61(3):297–309, 2002.

Anna Metaxas and Megan Saunders. Quantifying the "Bio-" Components in Bio-
physical Models of Larval Transport in Marine Benthic Invertebrates: Advances
738 and Pitfalls. *Biological Bulletin*, 216:257–272, 2009.

Haruki Ochi. Mating behavior and sex change of the anemonefish, *amphiprion clarkii*,
in the temperate waters of southern japan. *Environmental Biology of Fishes*, 26
741 (4):257–275, 1989.

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

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.

747 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>.

750 Steven S. Rumrill. Natural mortality of marine invertebrate larvae. *Ophelia*, 32
(1-2):163–198, October 1990. ISSN 0078-5326. doi: 10.1080/00785236.1990.
753 10422030. URL <http://www.tandfonline.com/doi/abs/10.1080/00785236.1990.10422030>.

756 Ocane C. Salles, Jeffrey A. Maynard, Marc Joannides, Corentin M. Barbu, Pablo
Saenz-Agudelo, Glenn R. Almany, Michael L. Berumen, Simon R. Thorrold, Ge-
offrey P. Jones, and Serge Planes. Coral reef fish populations can persist without
immigration. *Proceedings of the Royal Society B: Biological Sciences*, 282(1819):
759 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>.

762 Michelle Stuart, Katrina Catalano, and Malin Pinsky. Home range in clownfish. in
prep.

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

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

⁷⁶⁸ Jinliang Wang. Estimation of migration rates from marker-based parentage analysis.
Molecular ecology, 23(13):3191–3213, 2014.

J Wilson White, Steven G Morgan, and Jennifer L Fisher. Planktonic larval mortality
⁷⁷¹ rates are lower than widely expected. *Ecology*, 95(12):3344–3353, 2014.

Jw White, Lw Botsford, A Hastings, and Jl Largier. Population persistence in marine reserve networks: incorporating spatial heterogeneities in larval dispersal.
⁷⁷⁴ *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/>.

⁷⁷⁷ Adam Yawdoszyn. Fecundity in clownfish. in prep.