

Clownfish metapopulation persistence draft

Introduction

Metapopulation dynamics and persistence depend on the demographic rates at each
3 patch and the connectivity among patches (e.g. Hastings and Botsford, 2006) OTHER
CITATIONS, maybe Hanski?. Many marine species exist in metapopulations, con-
sisting of patch populations connected through dispersal (though differing from one
6 definition of metapopulation in that individual patches are unlikely to go extinct)
(Kritzer and Sale, 2006). Assessing demographic parameters and levels of connectiv-
ity has been particularly challenging for marine species, where much of the mortality
9 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)(CITATONS, maybe Botsford et al. 2009, Roughgarden check others,
12 Cowen and Sponagule). A need to understand metapopulations for conservation and
management, such as siting marine protected areas (CITATONS), however, has led
to a large body of theory describing how marine metapopulations might persist.

15 For any population to persist, individuals must on average replace themselves

during their lifetimes. In non-spatially structured populations, we use criteria such as the average number of recruiting offspring contributed by each individual during
18 its life (called R_0 when the population is age-structured and density-independent) or the growth rate of the population (such as the dominant eigenvalue λ of an age-structured Leslie matrix) (Caswell, 2001; Burgess et al., 2014). To assess replacement,
21 metrics must take into account the demographic processes across the whole life cycle, including how likely individuals are to survive to the next age or stage, their expected fecundity at each stage, and the survival of any offspring produced to recruitment.

24 In a spatially-structured population, persistence still requires replacement but in addition to assessing whether the reproductive output and survival of a population is sufficient, we must also consider how the offspring are distributed across space.
27 The spread of offspring is often described using dispersal kernels, probability density functions that give the relative number of settlers with increasing distance from the origin patch (e.g. Bode et al., 2018). Connectivity can also be described using a connectivity matrix, where entries give the probability of dispersing from one patch to
30 another, either found by discretizing the dispersal kernel or through direct estimates of pairwise exchange among patches (CITATION). A long-held paradigm suggested
33 that marine larvae were well-mixed and dispersed far on ocean currents (Roughgarden et al., 1988), suggesting widespread connectivity. With the ability to estimate connectivity through natural tags such as otolith microchemistry or genetics and the
36 realization that larvae can alter their dispersal through behavior (e.g. Morgan et al., 2009), the paradigm is shifting and local persistence of marine populations is seeming more possible.

39 When we consider both the demographic processes within patches and the con-
nectivity among them, a metapopulation can persist in two ways: 1) at least one
patch can achieve replacement in isolation, or 2) patches receive enough recruit-
42 ment to achieve replacement through loops of connectivity with other patches in the
metapopulation (Hastings and Botsford, 2006; Burgess et al., 2014). In the first case
(termed self-persistence), enough of the reproductive output produced at a patch is
45 retained at the patch for the patch, and therefore the metapopulation as a whole, to
persist. In the second (network persistence), closed loops of connectivity among at
least some of the patches - where individuals from one patch settle at another and
48 eventually send offspring back to the first in a future generation - provide the patch
with enough recruitment to persist in the network. Though it has been challeng-
ing to estimate the parameters necessary to understand how actual metapopulations
51 persist, a large work of theory developed to guide marine protected area helps pre-
dict when each type of persistence is likely to occur (i.e. large patches relative to the
mean dispersal distance are likely to be self-persistent Botsford et al., 2001).

54 New ways of identifying individuals and determining their origins, such as otolith
microchemistry and genetic parentage analysis (e.g. Wang, 2004, 2014), however, are
making it increasingly possible to estimate both the demographic [ADD EXAMPLE
57 CITATIONS] and the connectivity (e.g. Hameed et al., 2016; Almany et al., 2017)
parameters necessary to assess persistence in real metapopulations. We might expect
that populations on isolated islands are the most likely to be self-persistent and
60 Salles et al. (2015) find that the population of orange clownfish (*Amphiprion percula*
at isolated Kimbe Island in Papua New Guinea can likely persist without outside

immigration. In contrast, a metapopulation of bicolor damselfish (*Stegastes partitus*)
63 across four isolated islands in the Bahamas does not appear able to persist without
outside input (Johnson et al., 2018). For populations that exist in patches along
a continuous coastline, rather than on separate islands, however, it is still an open
66 question of how patches interact and the scale of metapopulation persistence.

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

78 **Methods**

Study system

We focus on a tropical metapopulation of yellowtail clownfish (*Amphiprion clarkii*) in
81 the Philippines. Like many clownfish species, yellowtail clownfish have a mutualistic
relationship with anemones, where small colonies of fish live (Buston, 2003; Fautin

et al., 1992). Yellowtail clownfish are protandrous hermaphrodites and maintain a
84 size-structured hierarchy; within an anemone, the largest fish is the breeding female,
the next largest is the breeding male, and any smaller fish are non-breeding juveniles.
The fish on an anemone maintain a strict social and size hierarchy (Buston, 2003),
87 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 lunar month from November to May, laying clutches benthic eggs that the parents
90 protect and tend (Ochi, 1989). Larvae hatch after about six days and spend 7-10
days as pelagic larvae before returning to reef habitat to settle in an anemone (Fautin
et al., 1992).

93 Clownfish are particularly well-suited to metapopulation studies due to their lim-
ited movement as adults and clearly patchy habitat. Once fish have settled, they
tend to stay within close proximity of their anemones [XX meters, CITATION]. This
96 makes fish easier to relocate for mark-recapture studies and simplifies the exchange
between patches to only the dispersal during the larval phase. Patches, whether
considered to be the reef patch or the anemone territory of the fish, are clearly dis-
99 crete and easily delineated, which makes determining the spatial structure of the
metapopulation clear. Additionally, clear patches make it easier to assess how much
of the site has been surveyed. These simplifying characteristics in habitat and fish
102 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).

105 **Field data collection**

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

TO ADD: Figure 1: map of study sites, picture of clownfish [*(Add figure with map
114 of study sites and a picture of a clownfish(?). Any figure summarizing the data? How many fish captured, sequenced, etc? Could go in the appendix?)*]

Since 2012, members of the team have sampled fish and habitat at most of the
117 sites annually. During sampling, divers using SCUBA and tethered to GPS readers swim the extent of each site. Divers visit each anemone inhabited by yellowtail clownfish, tagging the anemone to be able to track anemones through time. At each
120 anemone, the divers attempt to catch all of the yellowtail clownfish 3.5cm and larger, taking a non-lethal tail fin-clip from each for use in genetic analysis, measuring the fork length, and noting the tail color (as an indicator of life stage). Starting in
123 the 2015 field season, fish 6.0cm and larger are 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.

126 **Processing genetic samples**

[Add in brief overview of genetic methods, with citations to papers with relevant methods and to Katrina’s connectivity paper]

129 **Estimating inputs from empirical data**

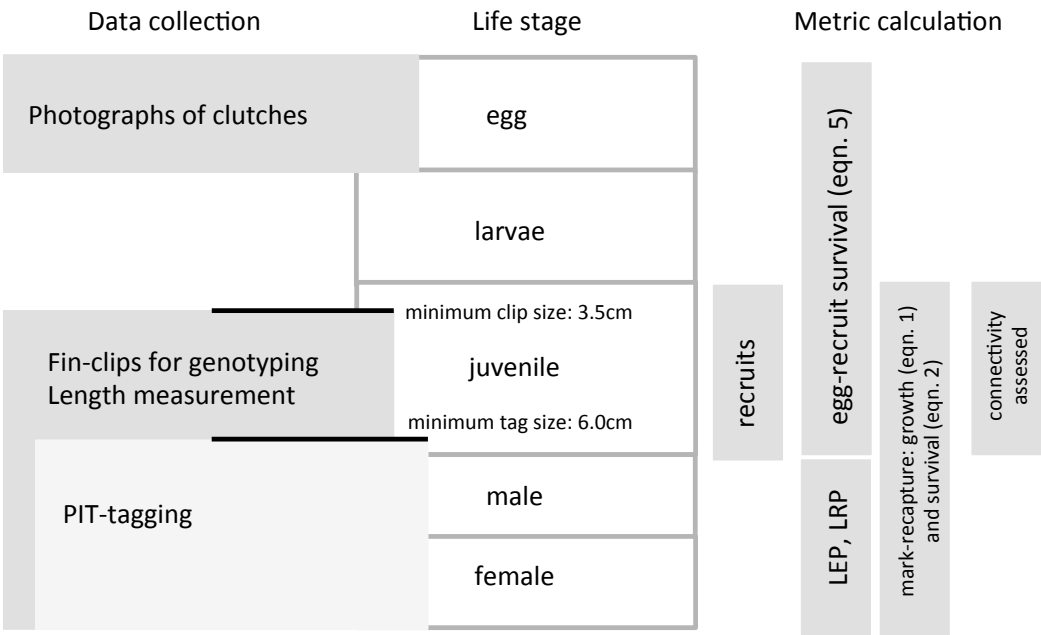


Figure 1: Here, we show the data collected for fish at each life stage (life stage boxes are not scaled by length of stage) and how the empirical data fit into the metric calculations.

Growth and survival: mark-recapture analyses

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

135 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
138 asymptotic size across the population and K controls the rate of growth:

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

We see from eqn. 1 that we would expect the first length L_t and the second length
 L_{t+1} to be related linearly (Hart and Chute, 2009). From the slope $m = e^{(-K)}$ and
141 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 .
144 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, and repeat this
process 1000 times to generate a distribution (Fig. 3b, B.1d).

147 We use the full set of fish encountered multiple times to estimate annual survival
 ϕ and probability of recapture p_r using the mark-recapture program MARK imple-

mented in R (Laake, 2013). We consider several models with year, size, and site
 150 effects on the probability of survival and year and size effects on the probability of
 recapturing a fish on a log-odds scale (see full list in Table A1. For fish that are not
 recaptured at a particular time point, we estimate their size using our growth model
 153 (eqn. 1) and the size recorded or estimated in the previous year. Because fish are
 not well-mixed at our sites and instead stay quite close to their home anemones, we
 need to swim near an anemone to have a reasonable chance of capturing the fish on
 156 it. Therefore, we also consider a distance effect on recapture probability; we use the
 GPS tracks of divers to estimate the shortest distance a diver got to the anemone for
 each tagged fish in each sample year and include it as a factor in some of the models.

159 The best-fit model using model selection with AICc has an effect of fish size on
 survival and additive effects of fish size and shortest distance to anemone on the
 probability of recapture:

$$\log\left(\frac{\phi}{1-\phi}\right) = b_{\phi} + b_a \text{size} \quad (2)$$

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

162 **Fecundity**

We use a size-dependent fecundity relationship, determined using photos of egg
 clutches and females (Yawdoszyn et al. in prep), where the number of eggs per
 165 clutch (E_c) is exponentially related to the length of the female (L) with slope β_{fem_i} ,

intercept b , and effect β_e dependent on if the eggs are old enough to have visible eyes:

$$\ln(E_c) = \beta_l \ln(L) + b_e[\text{eyed}] + b. \quad (4)$$

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

We only consider reproductive effort once the fish has reached the female stage. Though the size at which a fish transitions to become a breeding female L_f will
 171 depend on the size hierarchy in each particular colony [CITATION], we use the average size recaptured fish were first observed as female for the best estimate.

Lifetime egg production

174 We use an integral projection model (IPM) (e.g. Rees et al., 2014) to estimate the total number of eggs produced by one individual (lifetime egg production: LEP), starting at the recruit stage, when individuals have settled and survived to a size we
 177 can sample.

In an IPM, the state of the population at time t is described by the distribution of the population over a continuous trait z , for which we use size: $n(z, t)$. The total
 180 number of individuals in the population at time t is the integral of the size distribution over size from the lower size bound L to the upper size bound U : $\int_L^U n(z, t) dz$. The population is projected forward with probability density functions, called the kernel,
 183 that describe the survival, growth, and reproductive output of existing individuals into the next time step.

We initialize the IPM with one recruit-sized individual $\text{size}_{\text{recruit}}$: $n(t = 0) =$

186 $n(\text{size}_{\text{recruit}}, 0)$, then use a kernel with the size-dependent survival and growth func-
 tions described above to project forward for 100 time steps. This gives us the size
 distribution at each time step, which represents the probability that the individual
 189 has survived and grown into each of the possible size categories. The probability
 that the individual is still alive and of any size decreases as the time steps progress;
 by using a large number of steps, we are able to avoid arbitrarily setting a maximum
 192 age and instead let the probabilities become essentially zero.

We then multiply each size-distribution vector v_z in the matrix by the size-
 dependent fecundity function described above (eqn. 4) to get the total number of
 195 eggs produced at each time step. To get the total number of of eggs one individual is
 likely to produce in its lifetime, we then sum across all time steps in the individual's
 potential life.

$$\text{LEP} = \sum_{t=0}^{t=100} \sum_{z=L}^{z=U} v_z, t f_z. \quad (5)$$

198 **Survival from egg to recruit**

We estimate survival from egg to recruit S_e using the number of recruited offspring
 we can match back to genotyped parents as surviving individuals from genetically
 201 "tagged" eggs in a method similar to that in Johnson et al. (2018). We estimate
 the number of eggs produced by genotyped parent fish by multiplying the number of
 genotyped parents N_g by the expected lifetime egg production of a parent fish LEP_p ,
 204 using LEP calculated starting with an individual of 6cm. We make the assumption
 that all recruited offspring originating from the genotyped parents end up in one of

the sites we sample and estimate the total number of offspring that survive to recruit
207 R_t by dividing the number of offspring matches we find R_m by the proportion of our
site habitat we sample P_h and the probability of capturing a fish if we sample an
anemone P_c (see B.4 for details on P_h and P_c). Our estimated survival from egg
210 to recruit is the number of tagged recruits divided by the number of tagged eggs
produced:

$$S_e = \frac{\frac{R_m}{P_h P_c}}{N_g \text{LEP}_p}. \quad (6)$$

Defining recruit and census stage

213 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 its same life stage (Burgess et al., 2014). We
216 define recruit to be a juvenile individual that has settled on the reef the previous year;
lifetime egg production assesses how many offspring an individual recruit is likely to
produce in its lifetime from that point forward and egg-recruit survival gives us
219 the fraction of those eggs that will survive to reach the recruit stage. In theory, it
should not matter exactly how we define recruit so long we use that definition in our
calculations of both egg-recruit survival and LEP. In our system it is straightforward
222 to calculate LEP from any point but it is not possible to change our estimate of egg-
recruit survival to allow different definitions of recruit: we do not have enough tagged
recruits to reliably estimate survival to different recruit sizes. Instead, we choose the

225 mean size of offspring matched in the parentage study as our best estimate of the
size of a recruit ($\text{size}_{\text{recruit}}$) and test sensitivity to different sizes within the range of
sizes that the recruit stage covers (Table 1).

228 **Probability of dispersal**

We use a distance-based dispersal kernel, estimated in other work using parent-offspring matches from our genetic data (Catalano et al. in prep) using the method
231 described in Bode et al. (2018). The relative dispersal is a function of distance d as
measured in kilometers and parameters θ and k_d , which control the shape and scale
of the kernel:

$$p(d) = e^k e^{-(e^k d)^\theta}. \quad (7)$$

234 We use a fat-tailed dispersal kernel with shape parameters $\theta = 0.5$ and scale parameter $k_d = -1.36$ (Fig. 3a, estimate done in Catalano et al. *in prep*).

The dispersal kernel is estimated using fish that have already recruited to a
237 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 larvae will
travel a particular distance. To find the probability of fish dispersing among our
240 sites, we calculate the distance between the middle of each site to the closest and
farthest edge of each other site, then use the distances as upper and lower bounds
when integrating eqn. 7, which we do numerically. For example, the probability of
243 dispersal from site A to B, where d_1 is the distance from the middle of A to the
closest edge of B and d_2 is the distance from the middle of A to the far edge of B, is:

$$p_{A,B}(d) = \int_{d_1}^{d_2} e^k e^{-(e^k d)^\theta} dd. \quad (8)$$

Persistence metrics

For a metapopulation to persist, at least one patch needs to achieve replacement, where the number of individuals entering the population balances those lost to mortality or emmigration (Burgess et al., 2014). In our focal system, adults do not move among patches so we do not need to consider emmigration and only need to assess whether fish produce enough offspring that survive to recruitment to be able to replace themselves and where those offspring travel within the metapopulation. We consider three primary metrics to assess whether and how the population is persistent: 1) lifetime production of recruits, to assess whether the population has enough surviving offspring to achieve replacement 2) self-persistence, to assess whether any individual patches would be able to persist in isolation without any input from other patches, and 3) network persistence, to assess whether the metapopulation is persistent as a connected unit. We explain each metric below in detail.

Lifetime production of recruits

To assess whether individuals at our focal patches produce enough offspring that survive to become recruits themselves, we find the estimated number of recruits an individual recruit will produce over its lifetime (lifetime recruit production: LRP) by multiplying LEP by the estimated survival from egg to recruit S_e :

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

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

267 **Self-persistence**

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

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

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

276 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).

279 **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. 7 over the distance between each set of sites. We
282 then 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). The diagonal entries of C , where the origin and destination are the
285 same sites, are the values of self-persistence we calculate above.

Network persistence requires that the largest real eigenvalue of the realized connectivity matrix be λ_C be greater than 1: $\text{NP} = \lambda_C > 1$ (e.g. Hastings and Botsford,
288 2006; White et al., 2010; Burgess et al., 2014).

Incorporating uncertainty

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

294 **Results**

Estimated abundance of females at each site over time is relatively constant [*add some sort of actual analysis here*] (Fig. 2, suggesting that our sample populations
297 are persistent.

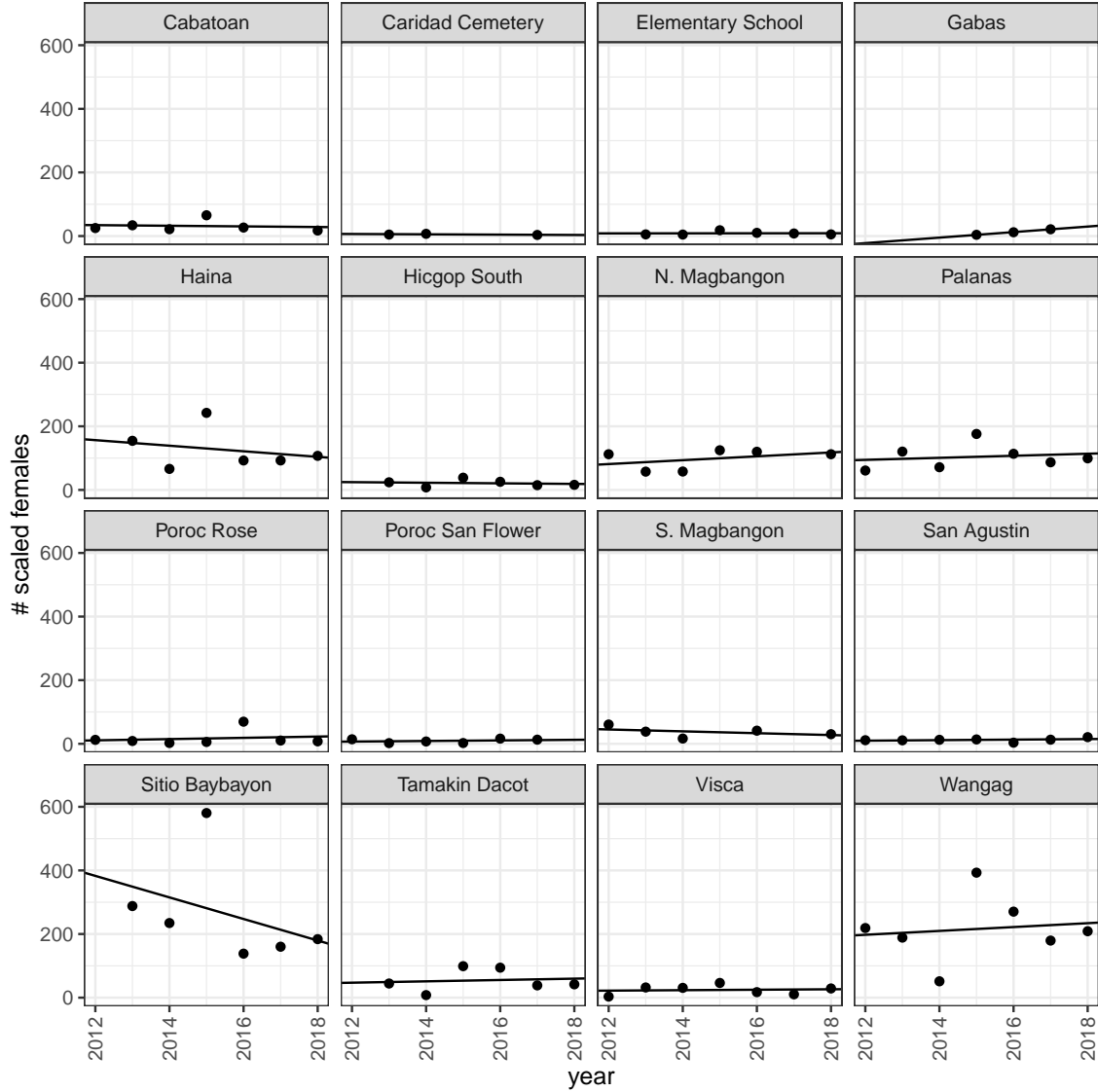


Figure 2: The estimated number of females at each site over the sampling years. The total number of females at each site was estimated by taking the number of females (fish ≥ 5 cm with the yellow pointed tail indicating female) captured at each site in each year and scaling up by the proportion of habitat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

Using tagged and genotyped mark-recaptures, we estimate growth parameters XX (Fig. 3b) and survival parameters XX (Fig. 3c). [Put rest of actual parameter
 300 estimates here].

[Not sure where to put this, or if it should exist, but seems like it might be helpful - not fully filled out yet:]

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)
size _{recruit}	size (cm) of recruited offspring	mean of size of offspring in parentage analysis = 4.4cm	3.5 - 6.0cm	

S_e	egg-recruit survival			
E_c	eggs per clutch	depends on female size (eqn. 4)		relationship from Yawdoszyn et al. (in prep)
b_e	coefficient for eyed eggs	-0.608		Yawdoszyn et al. (in prep)
b_l	slope 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	

Table 1:

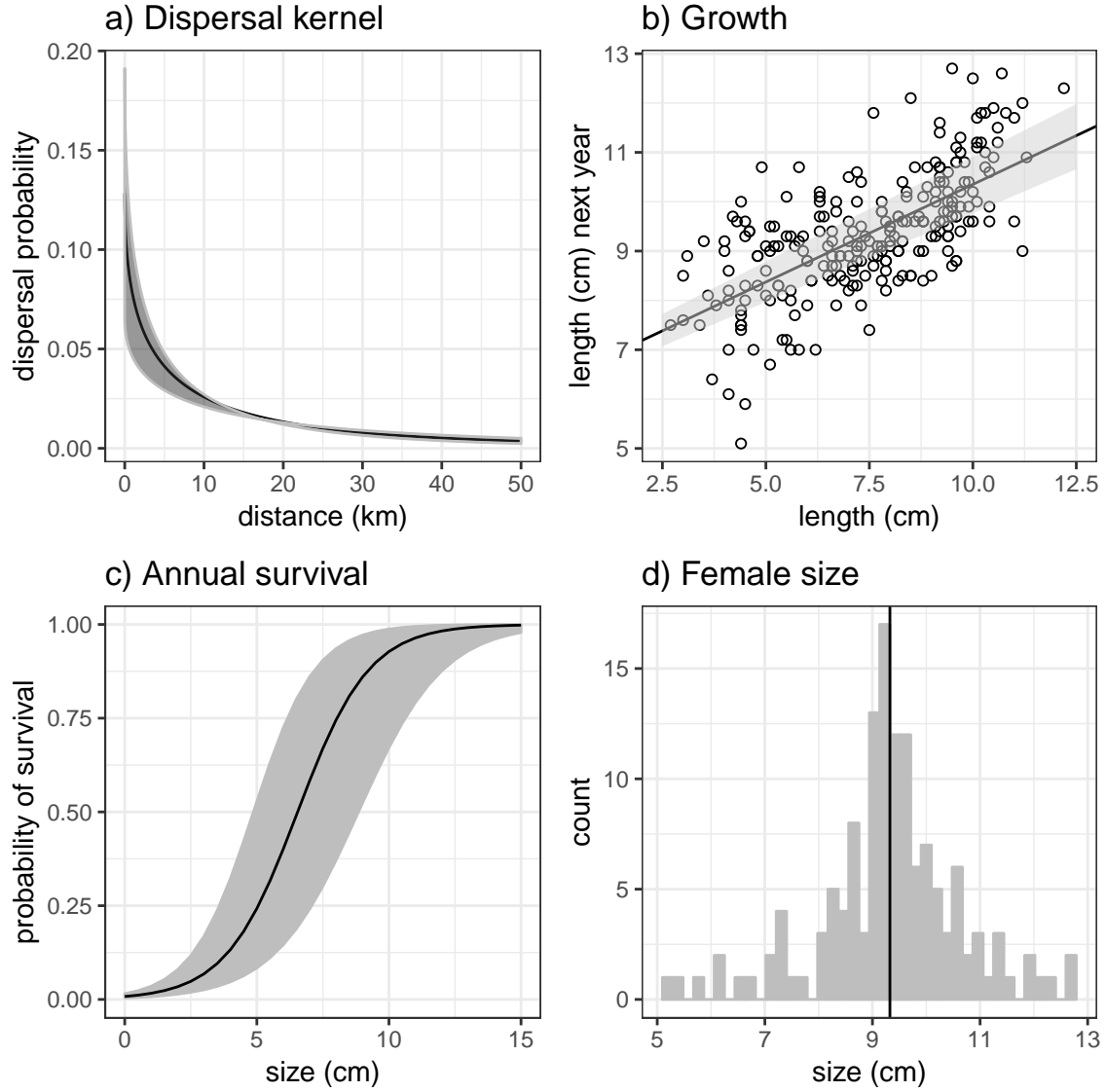


Figure 3: Best estimates (solid black line) and range (gray) for dispersal, growth, survival, and size at female transition parameters.

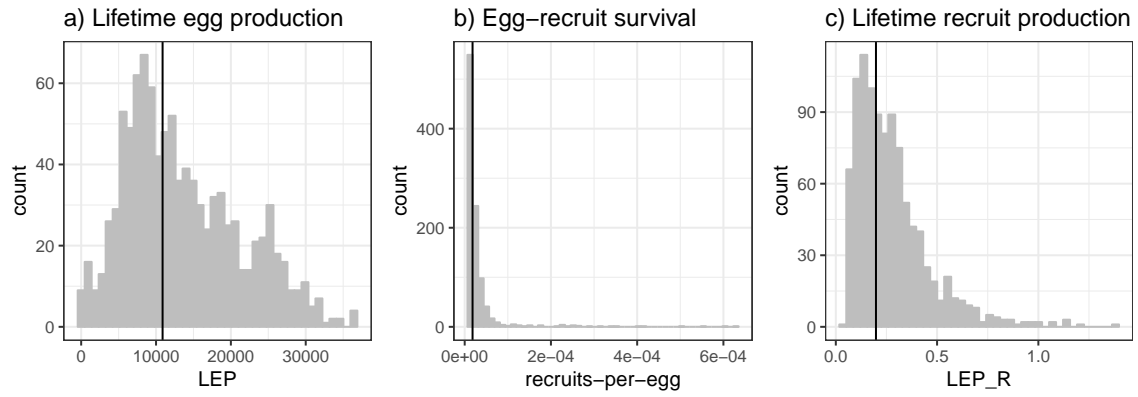


Figure 4: Metrics with best estimate (using recruit size of mean of offspring size) and uncertainty. WRITE A CAPTION!

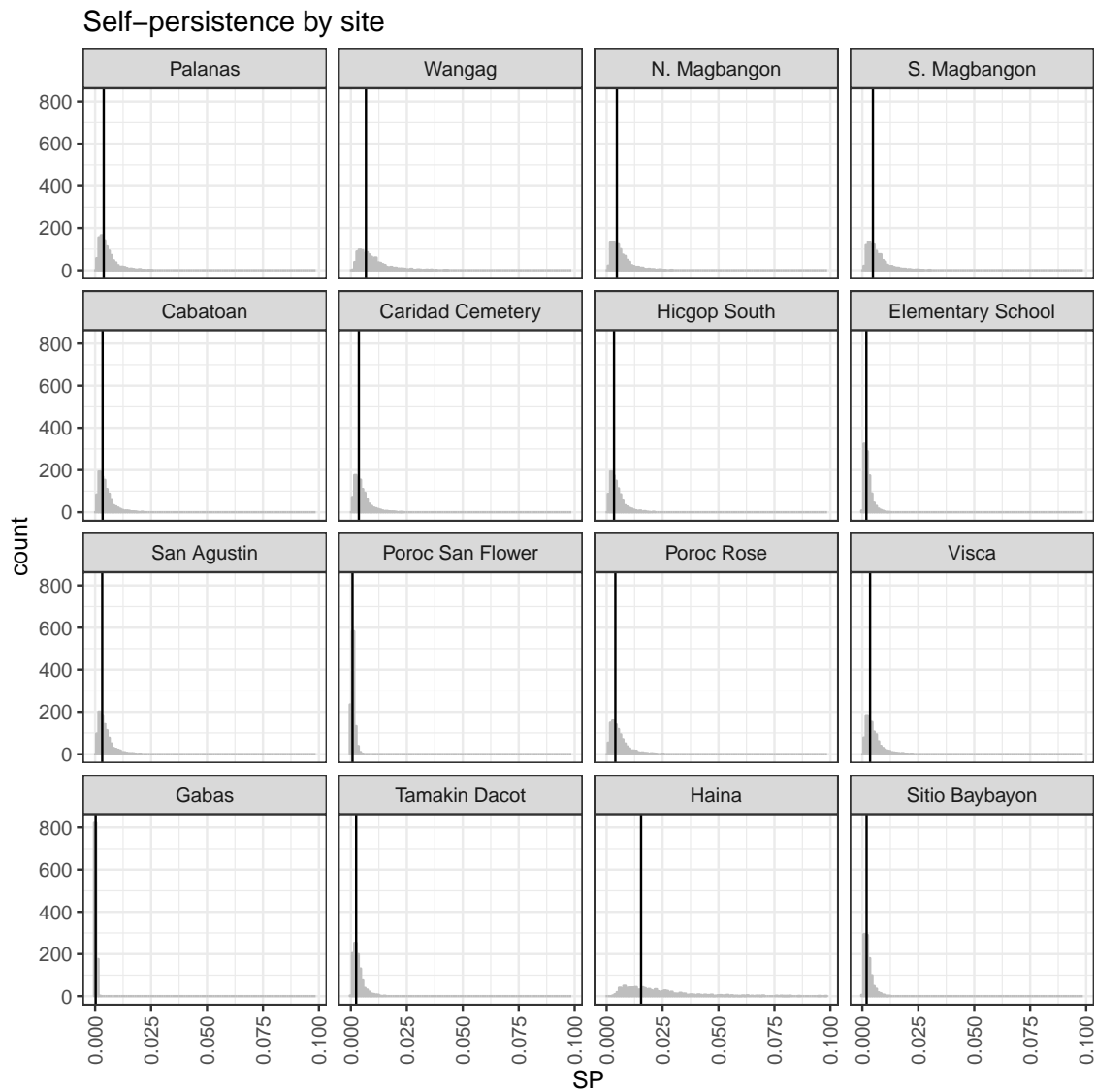


Figure 5: Metrics with best estimate (using recruit size of mean of offspring size) and uncertainty. WRITE A CAPTION!

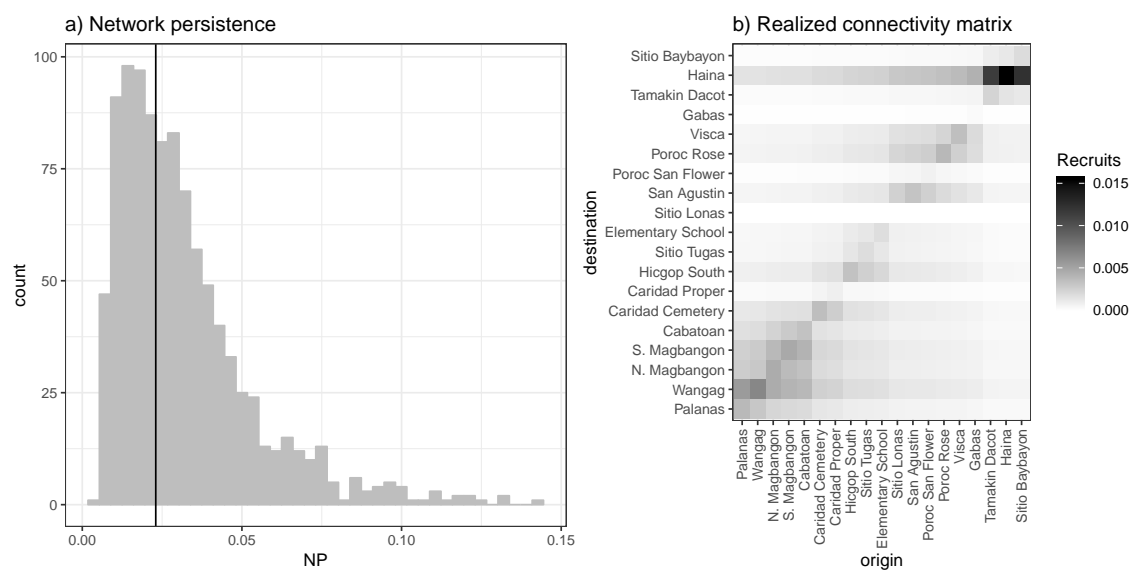


Figure 6: Metrics with best estimate (using recruit size of mean of offspring size) and uncertainty. WRITE A CAPTION!

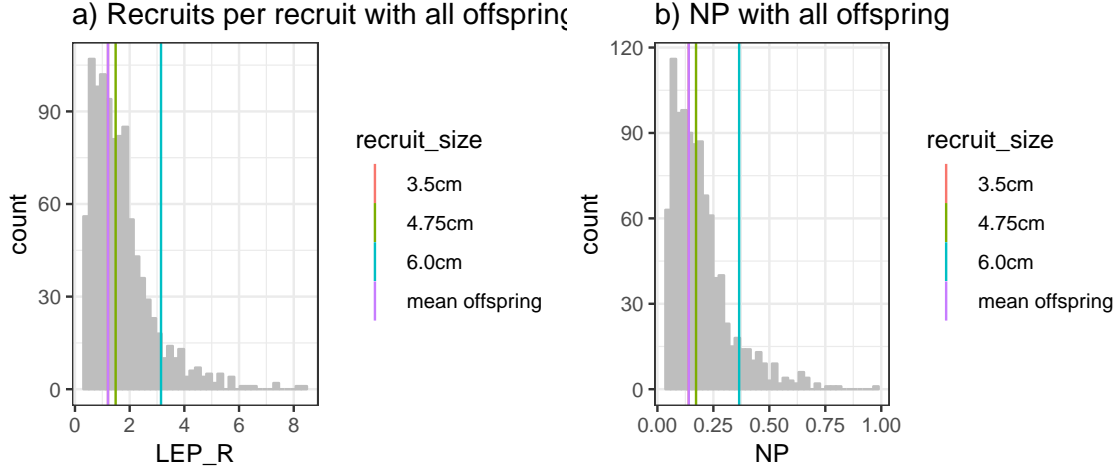


Figure 7: Range of parameter inputs for uncertainty runs with all uncertainty included. Census size is the size at fish are considered to have recruited, such that egg-recruit survival ends. Female transition is the size at which fish transition from male to female and their reproductive output is included in the estimate of lifetime egg production (LEP). FINISH LISTING PARAMS!

Discussion

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

- So we don't see persistence in our metrics, either self-persistence or network persistence but our abundances don't seem to be changing. Suggests that this is just a portion of a larger metapopulation, rather than a self-contained metapopulation. Maybe it is a sink? Persistent in terms of constant abundance but relies on outside immigration to persist.

312 • How does dispersal spread interact with scale of a self-contained metapopulation? How do we reconcile this in our system?

• 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), what we see for persistence 315 when estimate recruits/recruits instead.

More detailed discussion of our estimates, limitations, ways to move forward:

318 • Discuss density-dependence: not explicitly accounting for it, included in our egg-recruit survival estimate. But it's these metrics at low abundance, when DD isn't happening, that really matter for persistence. Egg-recruit-survival is 321 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).

• Discuss site-specific demographic rates, why we don't have them in our system, 324 the importance they play in other studies, what we might need to go about resolving them.

• Contextualize our parameter estimates with those from other studies (esp. survival, growth, egg-recruit survival). 327

Appendix

A Method details

³³⁰ **Proportion of habitat sampled**

Probability of capturing a fish, from recapture dives

Full set of MARK models

³³³ We consider the following set of models in MARK:

Model	Model description	AICc	dAICc
	survival size, recapture size+distance	3348.861	0
	survival size, recapture distance	3359.998	-11.1371
	survival constant, recapture distance	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 constant	3570.908	222.04690

Table A1:

B Uncertainty details

B.1 Sensitivity to parameters

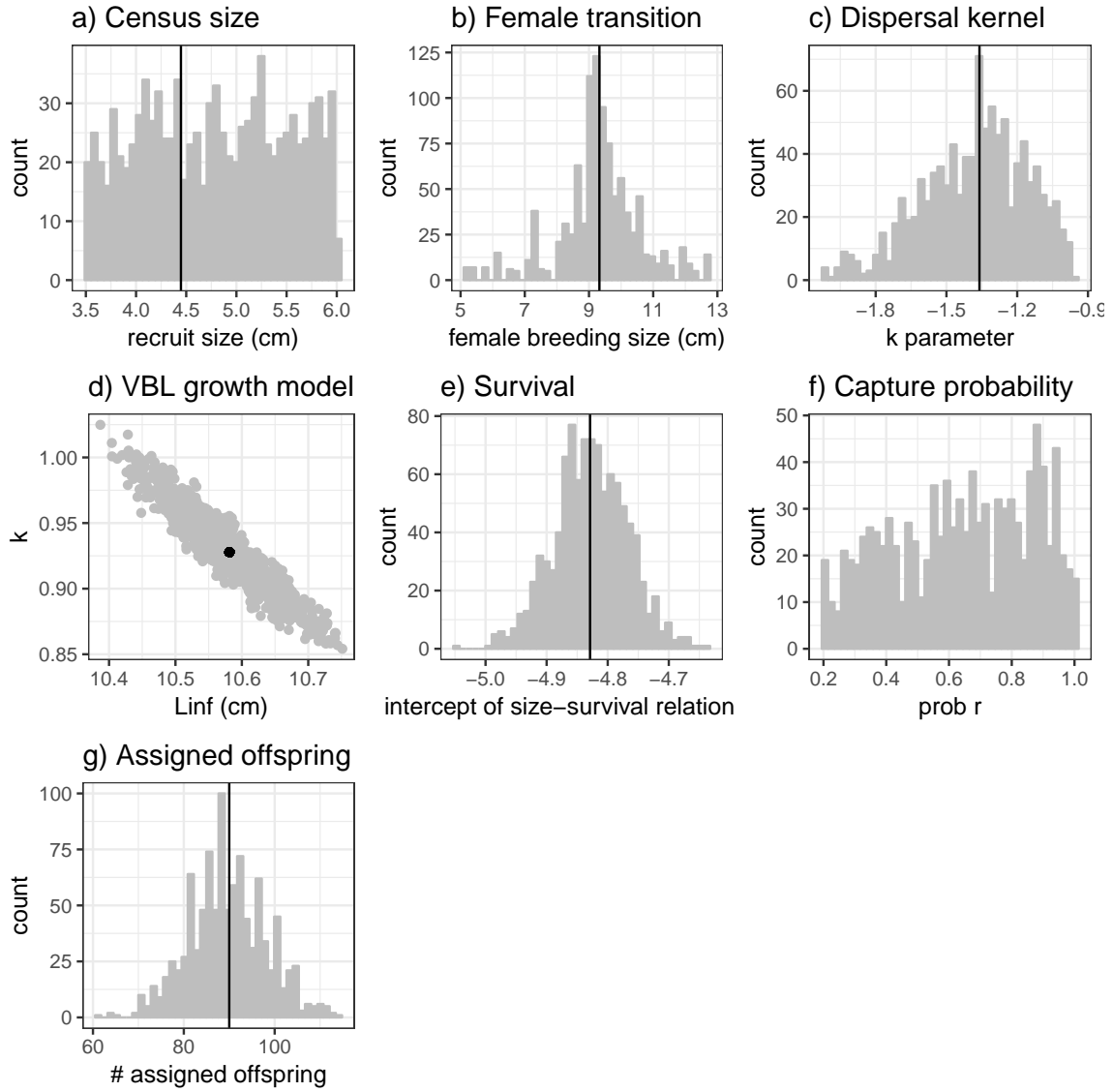


Figure B.1: Range of parameter inputs for uncertainty runs with all uncertainty included. Census size is the size at fish are considered to have recruited, such that egg-recruit survival ends. Female transition is the size at which fish transition from male to female and their reproductive output is included in the estimate of lifetime egg production (LEP). FINISH LISTING PARAMS!

B.2 Effects of different types of uncertainty on metrics

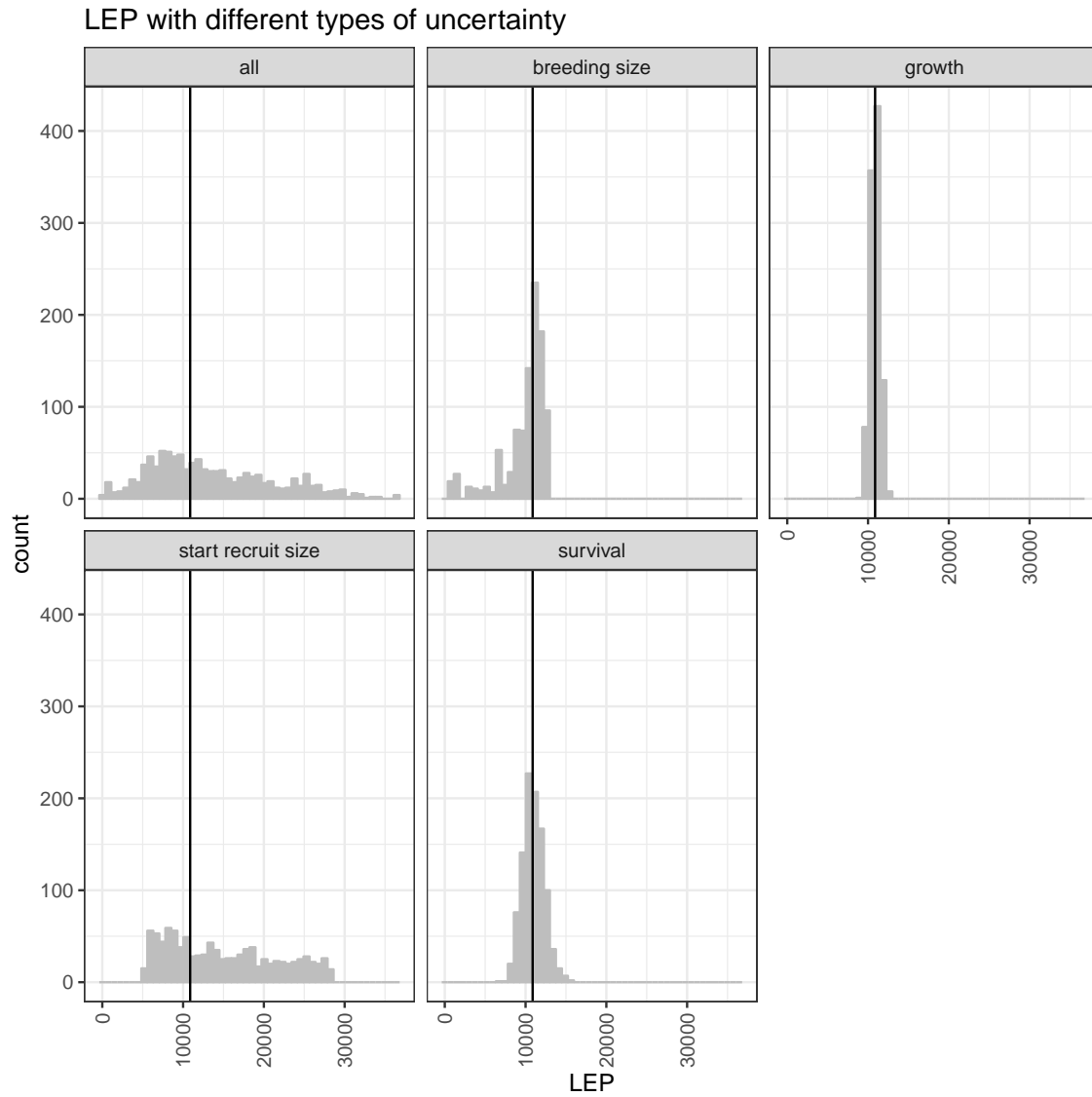


Figure B.2: WRITE A CAPTION!

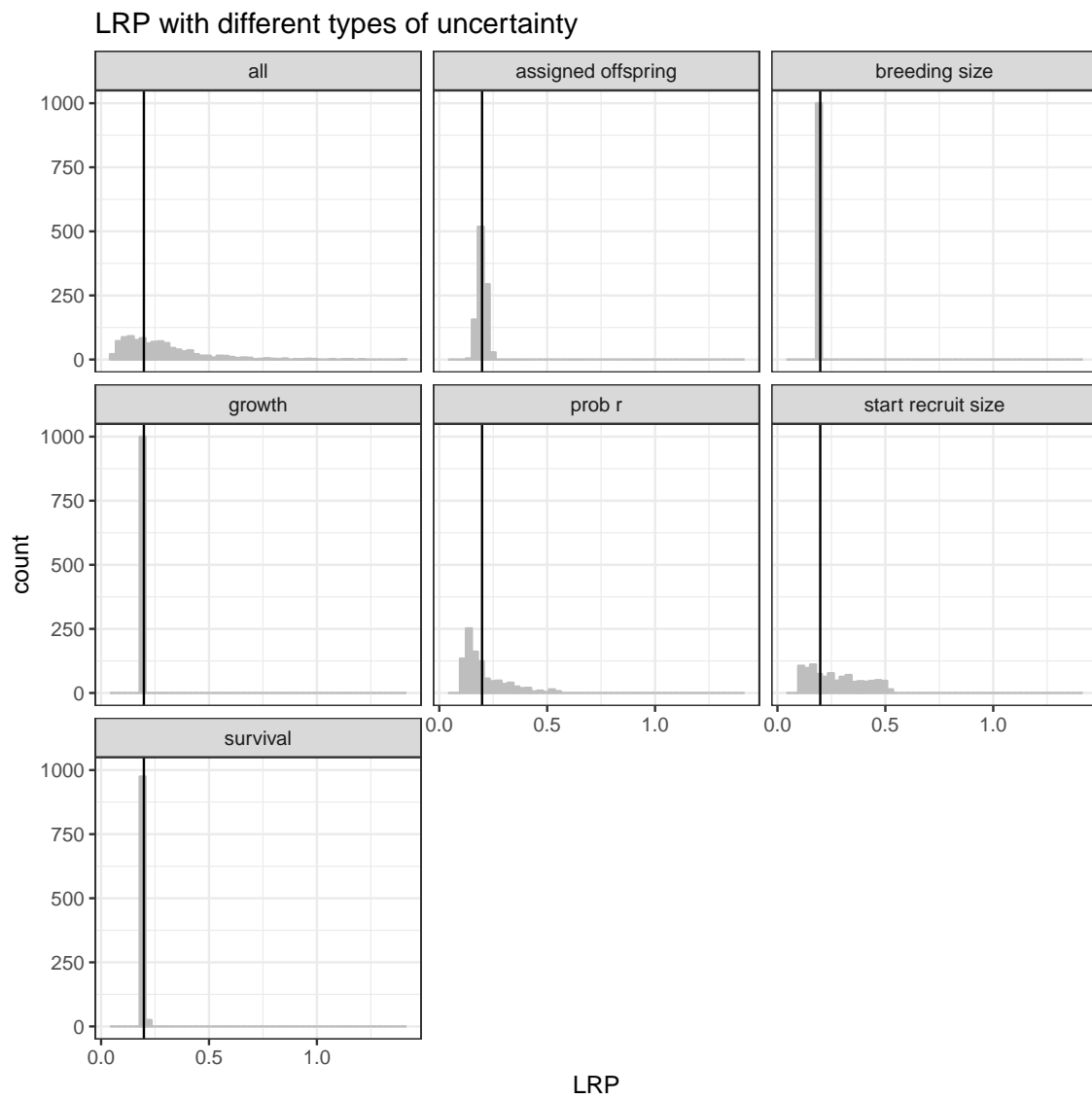


Figure B.3: WRITE A CAPTION!

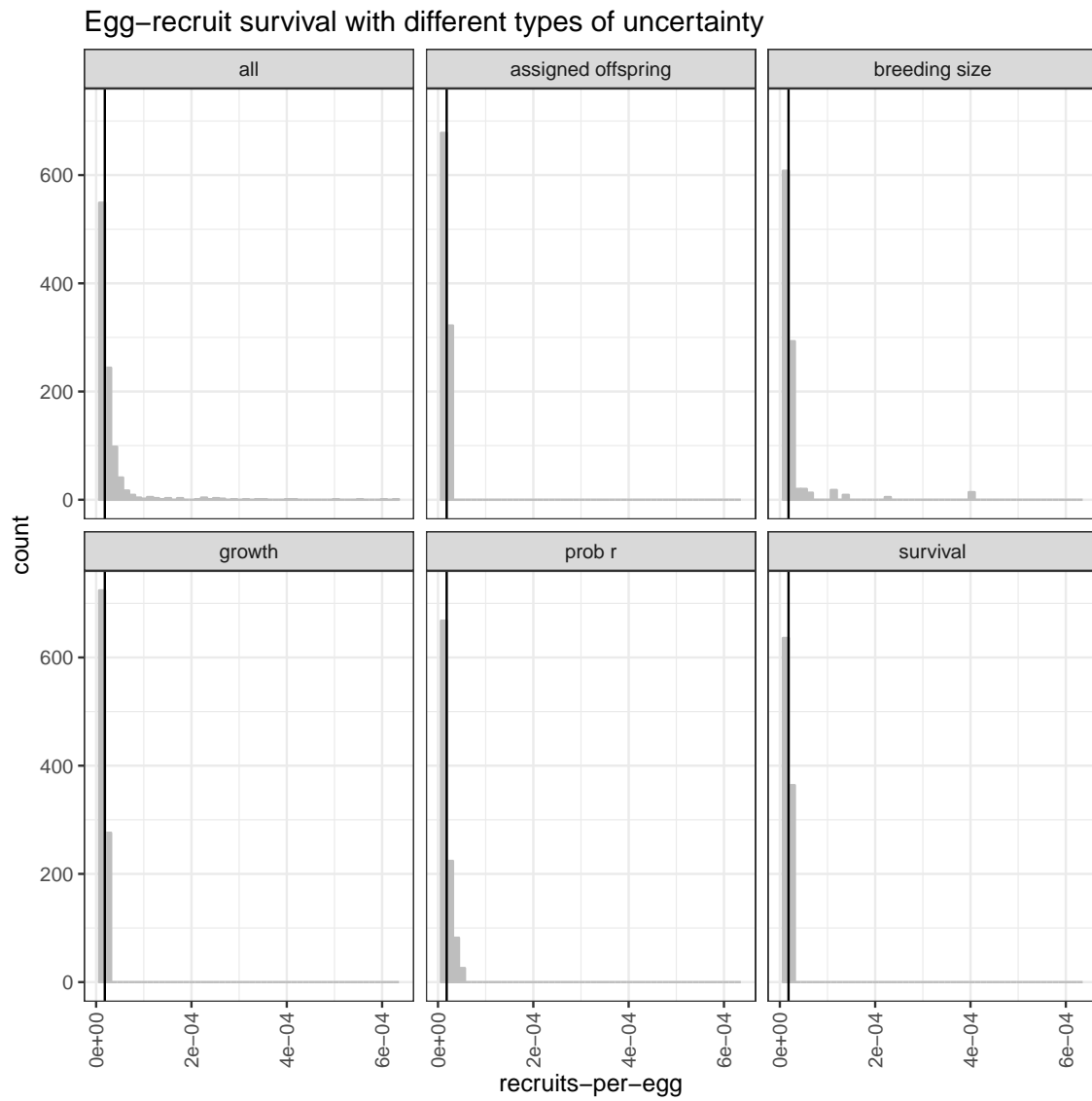


Figure B.4: WRITE A CAPTION!

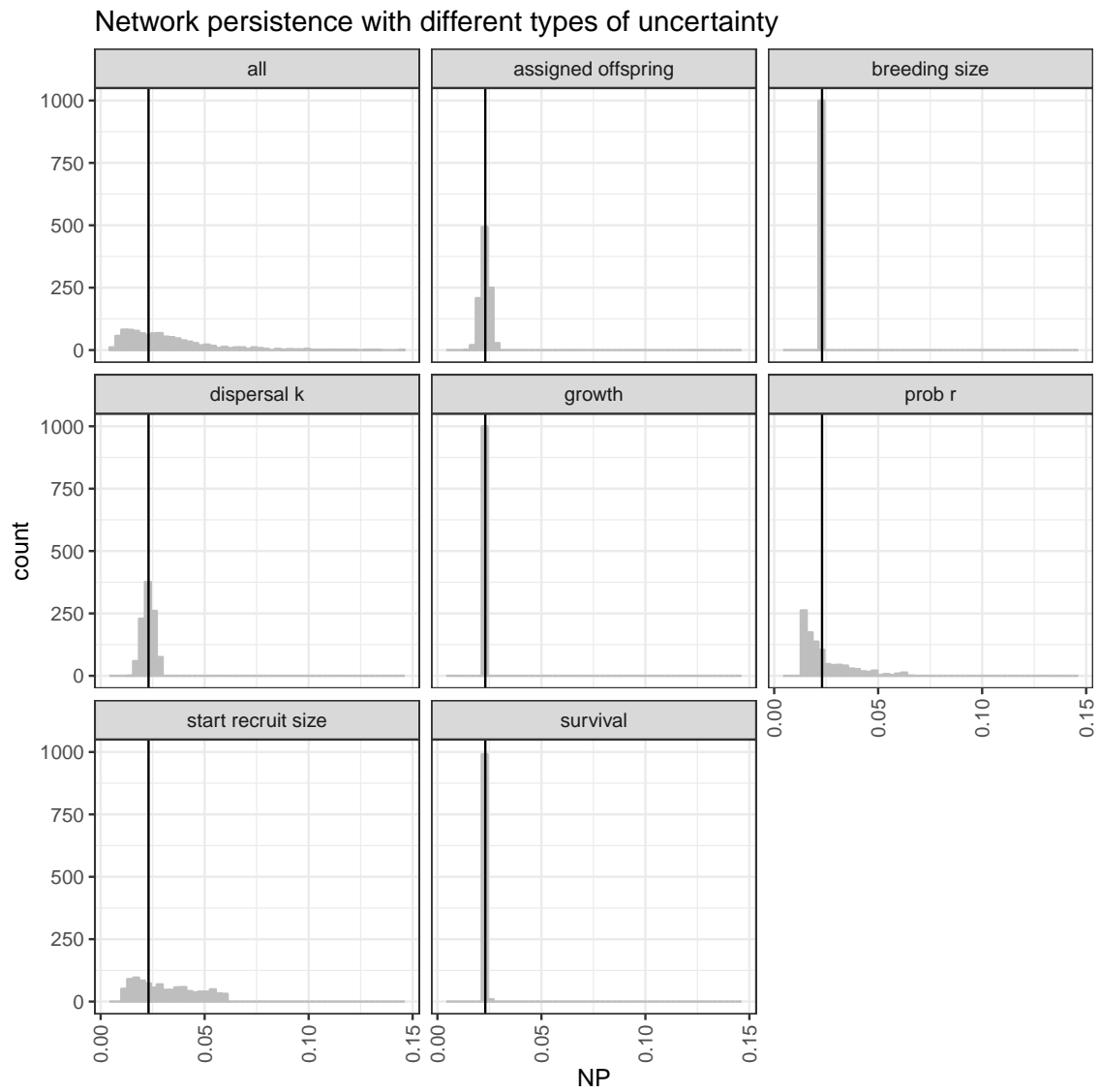


Figure B.5: WRITE A CAPTION!

References

- Glenn R Almany, Serge Planes, Simon R Thorrold, Michael L Berumen, Michael
339 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.
- 342 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.
- 345 Louis W. Botsford, Alan Hastings, and Steven D. Gaines. Dependence of sustainabil-
ity on the configuration of marine reserves and larval dispersal distance. *Ecology
Letters*, 4:144–150, 2001.
- 348 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
351 quantify population persistence to improve marine protected-area design. *Ecolog-
ical Applications*, 24(2):257–270, 2014.
- Peter Buston. Social hierarchies: size and growth modification in clownfish. *Nature*,
354 424(6945):145–146, 2003.
- Peter M Buston and Cassidy C DAloia. Marine ecology: reaping the benefits of local
dispersal. *Current Biology*, 23(9):R351–R353, 2013.

- 357 Hal Caswell. *Matrix population models: construction, analysis, and interpretation*.
Sinauer Associates Inc., Sunderland, Massachusetts, 2nd edition, 2001.
- Augustus J. Fabens. Properties and fitting of the von bertalanffy growth curve.
360 *Growth*, 29:265–289, 1965.
- Daphne Gail Fautin, Gerald R Allen, Gerald Robert Allen, Australia Naturalist,
Gerald Robert Allen, and Australie Naturaliste. Field guide to anemonefishes and
363 their host sea anemones. 1992.
- 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
366 connectivity along 700 km of wave-swept open coast. *Proceedings of the Royal
Society B: Biological Sciences*, 283(1833):20160370, 2016.
- Deborah R Hart and Antonie S Chute. Estimating von bertalanffy growth parameters
369 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.
- 372 Alan Hastings and Louis W. Botsford. Persistence of spatial populations depends on
returning home. *Proceedings of the National Academy of Sciences*, 103:6067–6072,
2006.
- 375 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,
378 2017.
- Darren W Johnson, Mark R Christie, Timothy J Pusack, Christopher D Stallings,
and Mark A Hixon. Integrating larval connectivity with local demography reveals
381 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.
- 384 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/](http://www.afsc.noaa.gov/Publications/ProcRpt/PR2013-01.pdf)
387 [Publications/ProcRpt/PR2013-01.pdf](http://www.afsc.noaa.gov/Publications/ProcRpt/PR2013-01.pdf).
- Steven G. Morgan, Jennifer L. Fisher, Seth H. Miller, Skyli T. McAfee, and John L.
Largier. Nearshore larval retention in a region of strong upwelling and recruit-
390 ment limitation. *Ecology*, 90(12):3489–3502, December 2009. ISSN 0012-9658.
doi: 10.1890/08-1550.1. URL [http://www.esajournals.org/doi/abs/10.1890/](http://www.esajournals.org/doi/abs/10.1890/08-1550.1)
08-1550.1.
- 393 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.
- 396 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.
- 399 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.
- J Roughgarden, S Gaines, and H Possingham. Recruitment dynamics in complex
402 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>.
- 405 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
408 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>.
411 [rspb.2015.1311](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.
- 414 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 ma-
417 rine reserve networks: incorporating spatial heterogeneities in larval dispersal.

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/>.

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