

# Integrating larval connectivity with local demography reveals regional dynamics of a marine metapopulation

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**Abstract.** Many ocean species exist within what are called marine metapopulations: networks of otherwise isolated local populations connected by the exchange of larval offspring. In order to manage these species as effectively as possible (e.g., by designing and implementing effective networks of marine protected areas), we must know how many offspring are produced within each local population (i.e., local demography), and where those offspring disperse (i.e., larval connectivity). Although there is much interest in estimating connectivity in the relatively simple sense of identifying the locations of spawning parents and their settling offspring, true measures of demographic connectivity that account for among-site variation in offspring production have been lacking. We combined detailed studies of local reproductive output and larval dispersal of a coral reef fish to quantify demographic connectivity within a regional metapopulation that included four widely spaced islands in the Bahamas. We present a new method for estimating demographic connectivity when the levels of dispersal among populations are inferred by the collection of genetically “tagged” offspring. We estimated that 13.3% of recruits returned to natal islands, on average (95% CI = 1.1–50.3%), that local retention was high on one of the islands (41%, 95% CI = 6.0–97.0%), and that larval connectivity was appreciable, even between islands 129 km apart (mean = 1.6%, 95% CI = 0.20–8.8%). Our results emphasize the importance of properly integrating measurements of production with measurements of connectivity. Had we not accounted for among-site variation in offspring production, our estimates of connectivity would have been inaccurate by a factor as much as 6.5. At a generational timescale, lifetime offspring production varied substantially (a fivefold difference among islands) and the importance of each island to long-term metapopulation growth was dictated by both larval production and connectivity. At the scale of our study (local populations inhabiting 5-ha reefs), the regional metapopulation could not grow without external input. However, an exploratory analysis simulating a network of four marine protected areas suggested that reserves of >65 ha each would ensure persistence of this network. Thus, integrating studies of larval connectivity and local demography hold promise for both managing and conserving marine metapopulations effectively.

**Key words:** conditional connectivity; dispersal; growth; larvae; marine reserves; parentage analysis; reproduction; self-recruitment; survival.

## INTRODUCTION

Many marine species have a complex life cycle in which a larval stage capable of long-distance dispersal is followed by an adult stage that is much more sedentary. One consequence of such a life cycle is that multiple populations that are otherwise demographically isolated can be connected by the periodic exchange of larvae, thus creating networks of local populations that form a “marine metapopulation” (Kritzer and Sale 2006). Understanding the long-term dynamics and persistence of marine metapopulations requires that we understand the degree to which individuals tend to replace themselves: by the retention of dispersive offspring to their natal population and the survival of those offspring to maturity and/or by the dispersal of offspring to other populations within the network and the subsequent

production of descendants (e.g., grand offspring) that return to the focal population (Armsworth 2002, Hastings and Botsford 2006, Burgess et al. 2014). Two key aspects of this process are *demographic connectivity* (the proportion of offspring produced at one local population that recruit to another) and *lifetime offspring production* (the number of offspring expected to be produced by a typical recruit). It has been difficult to obtain empirical data on both of these parameters, though scientists have made progress toward understanding metapopulation dynamics by simulating either production or connectivity (e.g., Figueira 2009, Watson et al. 2011a). Empirical studies that measure both production and connectivity simultaneously would be particularly valuable for guiding management and conservation strategies, as such studies would provide managers with information required to design marine reserves that specifically enhance population persistence of focal species, an essential objective in many management and conservation plans (Palumbi 2003, Botsford and Hastings 2006, Kaplan et al. 2006, Burgess et al. 2014).

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The long-term growth of any population depends on whether a typical individual produces enough surviving offspring to replace itself over its lifetime. However, in a network of populations characterizing a metapopulation, replacement can occur both by the retention of offspring to the local population and by the return of descendants that were produced at other populations (e.g., grand offspring, great-grand offspring, etc.; Hastings and Botsford 2006). Regional growth within such a network of local populations can be evaluated by multiplying the demographic connectivity matrix (i.e., the proportion of offspring produced at a given population that survive and recruit to each population within the network) by lifetime offspring production (which includes post-settlement survivorship and reproduction once mature, i.e., local demography). The resultant matrix (called the *realized connectivity matrix*; Burgess et al. 2014) describes the average exchange of individuals among the local populations within a generation. If the largest real eigenvalue of the realized connectivity matrix is  $>1$ , then the network of populations will grow in the long term, and likely persist (Hastings and Botsford 2006).

There are several important applications of these theoretical concepts to empirical settings. The first is to ask whether a particular network of populations is likely to grow on its own or whether immigration from outside the network is required to sustain the regional metapopulation (e.g., Salles et al. 2015). A second application is to examine the degree to which metapopulation growth depends on contributions from each local population within the network. Finally, one can ask how large the local populations within a particular metapopulation would have to be in order for the network to maintain positive growth on its own. Such an analysis would provide a broad-stroke assessment of metapopulation dynamics, yet one that has direct relevance for designing effective networks of marine protected areas (MPAs; e.g., Botsford et al. 2009, Moffitt et al. 2011). MPA design has typically focused on protecting a combination of desired habitats and species, and although persistence is a goal of MPA design, few MPA networks explicitly consider conditions for long-term demographic persistence (Williams et al. 2005, Botsford and Hastings 2006).

The dynamics of a marine metapopulation will depend on larval dispersal, a process that is notoriously difficult to measure. Larvae are minuscule and have the capability to disperse long distances in a vast ocean. Fortunately, the larvae of marine species may be tracked to various degrees by artificial or natural tags. For example, natural or deliberate exposure of developing offspring to chemicals may leave a permanent signal in their bodies, allowing recruits to be identified to source populations (e.g., Jones et al. 1999, Swearer et al. 1999, Almany et al. 2007, Becker et al. 2007, Cuif et al. 2015). Similarly, one can use multi-locus genotypes to find parent-offspring pairs within samples of adults and new recruits (e.g., Jones et al. 2005, Planes et al. 2009, Saenz-Agudelo et al. 2009, Christie et al. 2010, Berumen et al. 2012, Harrison et al. 2012, Pusack et al. 2014, D'Aloia et al. 2015). Such methods are valuable because they yield definitive information about the beginning and endpoints of larval dispersal. However, because sampling parents and offspring from the field is a labor-intensive process, and because marine metapopulations can be large in

size, a potential drawback of these techniques is that information on larval connectivity may be sparse (Christie et al. 2017). Unless populations are very small, it is possible to tag only a small proportion of the population, and the number of recruits whose source population is found will naturally be quite low. Because of this fact, there is a need for analytical techniques that accommodate sparse, but nonetheless definitive information on larval connectivity.

We present a new method for estimating demographic connectivity when the levels of dispersal among populations are inferred by the collection of "tagged" offspring. Demographic connectivity, expressed as the proportion of offspring produced at population  $j$  that survived and recruited to population  $i$  (Jacobi and Jonsson 2011, Burgess et al. 2014, Lett et al. 2015), can be calculated by combining estimates of local offspring production with information gathered by the collection of recruits whose source population is known. Our approach accounts for variation in sampling effort and spatial scale, and is appropriate even when the number of tagged offspring observed within a sample is low, as it often is in natural populations (e.g., D'Aloia et al. 2013, Pusack et al. 2014, Nanninga et al. 2015). Importantly, if offspring production is known, then inferences about demographic connectivity can be made from both positive results (cases where tagged offspring are found) and negative results (cases where tagged offspring are not found). Statistical power is derived from the total number of individuals sampled and tagged, not just the number of cases where the source population of recruits is known. These features allow investigators who track larvae (by chemical and/or genetic tagging) to generate robust estimates of demographic connectivity, and to quantify uncertainty in those connectivity estimates. Such information will help to bridge the gap between empirical estimates of dispersal and analyses of metapopulation dynamics (Botsford et al. 2009, Burgess et al. 2014).

We measured local demography and larval connectivity of a common coral-reef fish, the bicolor damselfish (*Stegastes partitus*). By measuring reproductive output and larval dispersal at the same time, we estimated average demographic connectivity within a network of populations inhabiting the reefs at four islands within a semi-enclosed ocean basin. Specifically, we measured the proportion of eggs produced at each island population that recruited to other island populations. This information is essential for understanding the dynamics of metapopulations, but values of demographic connectivity may be difficult to interpret on their own. Successful recruitment depends on survival, and because survivorship throughout the early life stages may be exceedingly low for marine species, values of demographic connectivity may also be low. In such cases it will not be obvious whether demographic connectivity is low because of low survival or because few of the survivors went from point A to point B. To decouple the effects of survival and dispersal, we also estimated the proportion of surviving recruits produced at one population that were found at other populations, a property we call *conditional connectivity* because it is conditional on early life survival. This measure factors out mortality during early life stages and provides a complementary assessment of local retention and exchange among populations. We estimated lifetime offspring production and evaluated the potential for a metapopulation of four island

populations, each inhabiting 5 ha of reef, to persist on its own. Finally, we conducted an exploratory analysis to evaluate how large four marine protected areas in this network would need to be in order to ensure protection of a species whose combined patterns of lifetime reproduction and demographic connectivity (regardless of life history characteristics) are similar to our study species.

## METHODS

### *Study system and genetic sampling*

We measured reproduction and larval connectivity of bicolor damselfish at four widely separated islands lining the perimeter of Exuma Sound, Bahamas, a semi-enclosed, deep-water (~2,000 m) basin: the Exuma Cays Land and Sea Park, the island of Eleuthera, Cat Island, and Lee Stocking Island. Our study reefs at each island ranged in depth from 4 to 12 m (see Hixon et al. 2012 and Pusack et al. 2014 for detailed descriptions). Bicolor damselfish have dispersive larvae, yet juveniles and adults inhabit small home ranges (~2 m in diameter) and exhibit strong site fidelity (Myrberg 1972, Knapp and Warner 1991, Johnson 2008, Hixon et al. 2012). They live in loosely structured social groups centered on specific coral heads, and consume both passing plankton and benthos. Males defend clutches of demersal eggs until the larvae hatch and disperse.

To detect larval connectivity among islands, we took tissue samples from adults and newly settled recruits at each island population. Fish were collected for genetic analysis at three reefs per island, and samples were taken during 10 separate summer monthly reproductive periods (July 2005 and June–August during 2006–2008). Individuals were genotyped at 10 highly polymorphic microsatellite loci and parent–offspring pairs were recorded ( $n_{\text{adults}} = 1,348$ , ~337 per island,  $n_{\text{recruits}} = 1,930$ , ~482 per island; see Pusack et al. 2014 for full details). Parentage was analyzed by a Bayesian exclusion method (Christie 2010), which does not require knowledge of the proportion of candidate parents sampled, and provides strict control over type I error rates (Christie 2013, Christie et al. 2013, Anderson and Ng 2014). This procedure allowed us to track the start points and endpoints of dispersal and to quantify uncertainty associated with these findings by resampling putative parent–offspring pairs by their probability of type I and type II errors (Appendix S1). Basic results of the parentage analyses have been published previously (Pusack et al. 2014), but the data on demography (which were collected during the same time period as the tissue samples used for genetic analyses) are presented here for the first time. In this study, we concentrate on the estimation of offspring production at each island, and we demonstrate how information on offspring production and larval dispersal can be combined to estimate demographic connectivity between local populations.

### *Post-settlement survival, growth, and reproduction*

From 2006 to 2008, we measured post-settlement demography at each island. Measuring demography in the field was a very labor-intensive process, and demography was measured at two of the three study reefs per island. We

assume that average rates of demography that were estimated from the two reefs per island were representative of the island population as a whole. Among-reef variation in demography was subsumed within our analyses and reflected in the uncertainties associated with demographic parameters estimated for each island. Study reefs averaged ~1.6 ha in area, and within each reef we established 11–22 permanent plots. Plots were approximately  $2 \times 2$  m and centered on large coral heads that were inhabited by groups of bicolor damselfish. Within each plot, all fish were individually tagged and subsequently measured throughout the study (overall sample size = 1,894 fish). Fish were tagged with subcutaneous injections of elastomer, and tags were color and location coded to identify individuals. Additional details regarding techniques of tagging and monitoring are described by Johnson and Hixon (2011) and Hixon et al. (2012). Individual growth in each local population was estimated by fitting growth curves to data on changes in body size, and size-dependent survival was estimated using logistic regression (see Appendix S2 for details).

We measured reproductive output by measuring the area of egg masses within artificial nests (Hixon et al. 2012). We calculated per capita reproduction at each reef on each sampling day by summing the area of eggs produced and dividing by the number of adults (fish >6 cm total length [TL]; Schmale 1981). Reproductive activity of bicolor damselfish follows a lunar cycle (Robertson et al. 1988, Johnson and Hixon 2011, Hixon et al. 2012). To account for this pattern, we described per capita reproduction as a periodic function of lunar day

$$f_t = \exp\left(b + A\left(\cos\left(\frac{2\pi}{29.5}\right)(t - t_{\text{MAX}})\right)\right) \quad (1)$$

where  $b$  describes average offspring production,  $A$  is the amplitude of the increase/decrease of reproduction with lunar day, and  $t_{\text{MAX}}$  is the lunar day when reproduction is maximal. We used a mixed-effects modeling framework to select a variant of Eq. 1 to describe how reproduction varied among the local populations (i.e., islands). For the full model, we allowed all three parameters to vary among islands. We used AIC values to evaluate whether simpler models (e.g., with some parameters held constant across islands) would provide adequate summaries of the data (Burnham and Anderson 2002, see Appendix S2). Clutches of eggs were laid in contiguous monolayers, so the area of each clutch was proportional to the number of eggs therein. Thus, egg number was estimated by multiplying egg mass area ( $\text{cm}^2$ ) by 215 eggs/ $\text{cm}^2$ , the average density of eggs observed during our study.

We estimated lifetime egg production by combining the age schedule of survivorship (derived from estimates of growth and size-dependent survival at each island) with the age schedule of reproduction (defined as 0 before maturity;  $f_t$  afterward, and included a seasonal component; see Appendix S2). These quantities were multiplied, and lifetime egg production was calculated by integrating this product from age 0 to infinity.

### *Estimating demographic connectivity*

If one considers genotyped individuals to be “tagged,” then demographic connectivity between populations ( $c_{i,j}$ )

can be estimated by dividing the number of tagged recruits that were spawned at population  $j$  and recruited to population  $i$  (i.e.,  $R_{i,j}$ ) by the total number of tagged offspring produced at population  $j$  (i.e.,  $\widehat{O}_j$ ):

$$c_{i,j} = \frac{R_{i,j}}{\widehat{O}_j} \quad (2)$$

Which stages are considered to be offspring will depend on the goals of the analyses and the information available, but connectivity is usefully expressed as the number of tagged recruits per egg produced (Burgess et al. 2014). In this form, connectivity measurements implicitly include survival during the egg, larval, and early juvenile stages. In this study, we calculated tagged offspring produced at an island population as

$$\widehat{O}_j = N_A \times \int_{t_1}^{t_2} f_i dt \quad (3)$$

where  $N_A$  is number of genotyped adults in a sample, the function  $f_i$  describes per capita egg production (as it varies with lunar day; see Eq. 1), and  $t_1$  and  $t_2$  are days of the lunar cycle marking the start and end points of a reproductive period.

For each of 10 reproductive periods examined in this study, we knew how many of the newly settled recruits sampled at island  $i$  were spawned by parents sampled at island  $j$ . In our analysis, we calculated the average values of demographic connectivity ( $c_{i,j}$ ) that were most likely to have produced the observed number of parent–offspring pairs for each pair of islands and for all 10 dispersal events. In this analysis, we pooled data for all 10 events and thus estimated average values of connectivity. The method is capable of estimating connectivity on an event-by-event basis, but additional analyses suggested that a simpler model in which connectivity was the same over time was preferred to a more complicated model in which connectivity values varied among events (Appendix S1). Connectivity was estimated at our pre-defined spatial scale (5 ha), but because the area of habitat we searched during recruit collections was much smaller than the total area available, we treated our observed number of parent–offspring pairs as realization of a random variable. We assumed that the number of genetically tagged recruits observed at each island–time combination followed a Poisson distribution, with the expected value ( $E[N_{PO}]$ ) set by connectivity between islands (which was unknown), offspring production ( $\widehat{O}_j$ , which was known), area searched ( $A_{\text{Searched}}$ , which was known), and total area ( $A_{\text{Total}}$ , set to 5 ha)

$$E[N_{PO}] = \frac{A_{\text{Searched}} \widehat{O}_j c_{i,j}}{A_{\text{Total}}} \quad (4)$$

This approach was appropriate because we were able to search only a small fraction of the total habitat available and the chances of observing parent–offspring pairs were naturally low. Note that the expected number of tagged offspring observed in a sample is normalized by area searched, not by the total number of recruits collected in that sample. Our calculations of connectivity are not sensitive to the

number of recruits that came from other locations (see Bode et al. [2017] for an illuminating discussion of such dilution effects).

Our approach was to estimate likelihood profiles for demographic connectivity estimates by calculating the probability of obtaining the observed number of genetically tagged recruits per island pair, given different levels of connectivity (see Appendix S1 for additional details). In this way, we could describe plausible values of connectivity, even when the number of parent–offspring pairs were few. This method derives statistical power from the total number of adults genotyped and is informative when “tagged” offspring are either found or not found. For example, even if no parent–offspring connections were found between two local populations, if offspring production was high and we searched a large proportion of the habitat, then we could be fairly certain that connectivity was low. On the other hand, if offspring production was low and/or if little of the available habitat was searched, then we would be less certain that connectivity values were near zero. This information was assessed for each cohort and island pair and was reflected in our estimated confidence intervals for the connectivity values. We note that there will be an appreciable amount of uncertainty in estimates of demographic connectivity. In most natural systems, it is not practical to collect offspring from a large proportion of the available habitat, and a proper account of demographic connectivity will require that uncertainty in components such as reproduction are incorporated into the final estimate. Our estimates of connectivity are therefore interpreted in a probabilistic context, and with a focus on regions of high confidence surrounding the point estimates. When the goal of the analysis was estimation, we concentrated on both the point estimates and their confidence intervals. When estimates of demographic connectivity were used to infer higher-order properties such as realized connectivity and metapopulation growth (see below), uncertainty in the estimates of connectivity was explicitly incorporated into these calculations.

In addition to measuring demographic connectivity as the number of eggs produced at population  $i$  that ultimately recruited to population  $j$ , we also estimated average connectivity by using the expected number of recruits as our measure of offspring production. We refer to this measure as conditional connectivity because it is conditional on early life survival. It estimates the probability that an offspring from population  $i$  dispersed to population  $j$ , given that it survived to the age at which collection occurred. In other words, it may be used to summarize what proportion of the total number of juveniles produced from population  $i$  recruited to population  $j$ . Conditional connectivity was calculated as the number of tagged recruits divided by the total number of recruits that were spawned at a particular population and survived to the age at collection ( $\sim 13$  d post-settlement). This latter quantity was calculated by multiplying  $\widehat{O}_i$  by estimated values of survival during the egg stage (0.60; Johnson et al. 2010), larval stage ( $1.02 \times 10^{-3}$ ; Johnson et al. 2015), settlement (0.307; Almany and Webster 2006) and the early post-settlement stage (mean = 0.77; this study). Rates of survival may of course vary, but because we were interested in calculating average connectivity values between islands and over a period of several years, it was



reasonable to use average survival values in these calculations. When estimating conditional connectivity, we incorporated the uncertainty in our estimates of both production and survival (Appendix S1).

Both connectivity and conditional connectivity are measures that depend on the spatial scale of interest. Total area of interest ( $A_{\text{Total}}$ ) is arbitrary but may be set by considerations such as sampling area or management goals (e.g., areas designated for marine reserve protection). In this study, we begin by considering a spatial scale of 5 ha. This is the approximate average of the cumulative area of reef that we surveyed at each of the four island populations we studied, and is a scale that is comparable to a variety of other studies of reef fishes (reviews by Sale 1998, MacNeil and Connolly 2015).

#### *Evaluating growth of the regional metapopulation*

The potential for growth of the metapopulation can be evaluated by calculating the dominant eigenvalue of the realized connectivity matrix, which is the product of lifetime offspring production and the demographic connectivity matrix (Armsworth 2002, Hastings and Botsford 2006). If the value is  $>1$ , then the metapopulation will grow; and if the value is  $<1$ , then the metapopulation will decline in the long term. This is a density-independent description of metapopulation growth, but one that will be adequate under many conditions (Armsworth 2002, also see Appendix S3). Here, we use the approach to describe the growth capacity of the metapopulation, based on average connectivity values and evaluated at the observed, average densities. To estimate potential growth of the regional metapopulation of bicolor damselfish, we generated the realized connectivity matrix by multiplying each column of the demographic connectivity matrix by lifetime egg production for each island population. To describe uncertainty in these estimates, 1,000 values of demographic connectivity and lifetime egg production were derived from resampled estimates of the parameters describing demography and parentage. In this way, we used the interval estimates of connectivity, which was more appropriate than the point estimates (i.e., in cases where no parent-offspring pairs were observed in our sample, we could be confident that average connectivity was low, but it was unlikely to be a true value of zero). The mean values of the realized connectivity matrices were used to evaluate the potential for a regional metapopulation of four island populations, each measuring 5 ha, to grow with no external input. We assume that patterns of demographic connectivity are stable, and while we acknowledge complexities such as stochastic variation in connectivity (e.g., Guizien et al. 2014) and density dependence may affect the accuracy of long-term projections, we believe that the eigenvalue of the realized connectivity matrix can provide a useful estimate of a metapopulation's potential for growth. To evaluate the relative contribution of the local population inhabiting each island to the dynamics of the four-island metapopulation, we calculated the sensitivity of metapopulation growth to changes in the elements of the realized connectivity matrix by calculating the partial derivative of the eigenvalue with respect to the small changes in the elements of the realized connectivity matrix (Appendix S3). We also calculated

sensitivities of metapopulation growth rate to lifetime egg production at each of the four study islands (Appendix S3).

Finally, we conducted an exploratory analysis where we adjusted  $A_{\text{Total}}$  and calculated  $\lambda$  in order to answer the question of how large in area four island populations would have to be in order for the metapopulation to maintain positive growth on its own without external input. This analysis assumes that patterns of demography and larval connectivity among the areas sampled are similar to those within the larger area to which inferences are made. As long as the extent of spatial scaling is not so large as to include major changes in habitat or ocean currents, such analyses can provide a useful assessment of metapopulation dynamics. In addition, this analysis can be used to evaluate how large four marine protected areas in this network would need to be in order to ensure protection of a species whose combined patterns of lifetime reproduction and demographic connectivity (and not necessarily life history characteristics) are similar to our study species. Although our data are for a non-fished species, there are multiple reasons to believe that patterns of realized connectivity may be similar for a variety of species within our study region. First is that patterns of larval exchange may be strongly influenced by ocean currents, and currents that connect two locations may facilitate transport of larvae of multiple species (e.g., Kool et al. 2010, Watson et al. 2011b, Treml et al. 2012). Second is that our measure of metapopulation growth, the eigenvalue of the realized connectivity matrix, is a measure of the potential for an individual to replace itself within the metapopulation. For a population to grow, a typical individual must at least replace themselves within their lifetimes, and basic life history theory suggests that species may achieve replacement via different strategies (e.g., by producing many offspring with relatively low survival rates, or by producing fewer offspring with higher survival rates; Stearns 1992, Roff 2002). Because species' capacities for demographic replacement may be similar, variation in realized connectivity may be more sensitive to larval dispersal. If multiple species release their larvae into the same ocean currents, then these species may have similar patterns of realized connectivity between locations.

## RESULTS

### *Post-settlement survival, growth, and reproduction*

The major difference in post-settlement demography among islands was survival, although somatic growth rates differed slightly (Appendix S2). Survival rates were higher at Lee Stocking Island and the Exuma Cays Land and Sea Park and substantially lower at Cat Island and Eleuthera (Appendix S2). As a result, the age schedules of survivorship were markedly different among the four populations (Fig. 1). Assuming that fish matured at 6 cm TL (Schmale 1981), we estimated that 21.2% of settlers survived to maturity at Lee Stocking Island, whereas only 9.1% of settlers survived to maturity at Cat Island. Overall, survival rates were low for recently settled recruits (for example, monthly survival for a 2 cm TL fish was  $\sim 0.60$ ) and higher for adults (monthly survival for a 7 cm TL fish was  $\sim 0.85$ ).

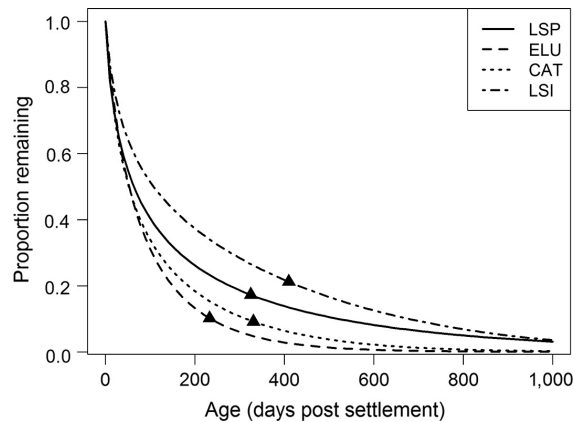


FIG. 1. Estimated age schedules of survivorship. Estimated time of maturation for each population is indicated by the solid triangles. LSP, the Exuma Cays Land and Sea Park; ELU, Eleuthera; CAT, Cat Island; LSI, Lee Stocking Island.

Per capita reproduction also varied substantially among islands. A model in which average reproduction varied among islands (independent of lunar periodicity) provided the most parsimonious explanation of the variance in reproduction. The AIC value for this model (823.6) was substantially lower than the full model (in which all three parameters of Eq. 1 varied among islands; AIC = 829.7), and lower for all other combinations (Appendix S2: Table S1). Based on this analysis, the average egg production per capita during monthly reproductive periods was very high at the Exuma Cays Land and Sea Park (6,634 eggs per month), lower at Lee Stocking Island (4,193 eggs per month), and lower still at Eleuthera and Cat Island (3,298 and 2,095 eggs per month, respectively). Differences in survivorship combined with differences in per capita reproduction resulted in strong differences in lifetime egg production, which was high at Lee Stocking Island and the Exuma Cays Land and Sea Park, but low at the other two islands (Fig. 2).

#### Demographic connectivity

For each of the 16 dispersal pathways we investigated (four islands acting as both start and endpoints), we tested for parent–offspring pairs in 10 different sampling events (monthly cohorts that settled in July 2005, and in June, July, and August of 2006–2008). Although the detection of parent–offspring pairs was naturally low in this system, connectivity was observed for six of the dispersal pathways we investigated (Fig. 3A). For the 10 pathways where no parent–offspring pairs were detected, these data were still informative because values of zero parent–offspring pairs were likely only if demographic connectivity was relatively low. Monthly egg production varied considerably among the study islands (Fig. 3B) and this variation in production affected estimates of connectivity. For example, local retention of offspring was observed twice at both the Exuma Cays Land and Sea Park and Cat Island, but because per capita reproduction was much lower at Cat Island, these results suggest that local retention was much higher at this location (see interval estimates in Table 1a, medians in

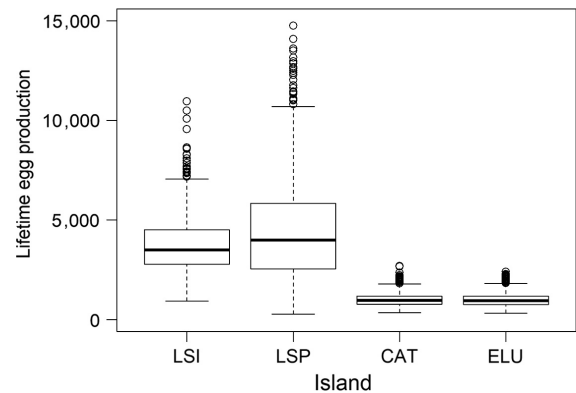


FIG. 2. Lifetime offspring production. Estimated number of eggs produced by an average, newly settled recruit at each island (i.e., each local population). Distributions were generated by a resampling procedure in which each of the parameters for the functions describing growth, survival, and reproduction were sampled at random from their estimated distributions. Boxplots represent the distribution of 1,000 resampled estimates of offspring production; mid line, median; box edges, 25th and 75th quantiles; whiskers, 95th quantiles; circles, observations beyond the 95th quantiles. LSP, the Exuma Cays Land and Sea Park; ELU, Eleuthera; CAT, Cat Island; LSI, Lee Stocking Island.

Fig. 3C). Values of connectivity were appreciable in the northern and eastern regions of Exuma Sound, and Lee Stocking Island did not appear to be well connected to the other three islands (Table 1a; Fig. 3C).

Despite the fact that the total population size of bicolor damselfish in Exuma Sound is very high (possibly on the order of hundreds of thousands; Christie et al. 2010), and the fact that areas of habitat that we studied were small compared to the total habitat available (Fig. 3), demographic connectivity among our study islands was appreciable. This pattern is most apparent when examining patterns of conditional connectivity (measures that factor out survival of eggs, larvae, and early juveniles; Table 1b). For many of the island combinations, conditional connectivity was estimated to be on the order of 1–11%, and an estimated 41% of the offspring that were produced at Cat Island (and survived to the recruit stage) returned to that local population, which was the maximum retention among the four islands (Table 1b).

#### Growth of the regional metapopulation

The realized connectivity matrix indicated that at the spatial scale of populations inhabiting 5-ha reefs, the levels of exchange among local populations were appreciable, yet not enough to ensure metapopulation growth without external input (Table 2). No local population was self-sustaining (no individual cell was  $\geq 1$ ) and the regional metapopulation would not grow on its own (dominant eigenvalue, median = 0.347, 95% CI = 0.178–0.736). Our results suggest that metapopulation growth was most sensitive to changes in connectivity values from Cat Island (Table 2b). In particular, local retention of larvae at Cat Island had the largest influence on metapopulation growth. However, both Cat Island and Eleuthera had appreciable exchange of larvae with each other, indicating replacement pathways that acted in addition to local retention. For example, an

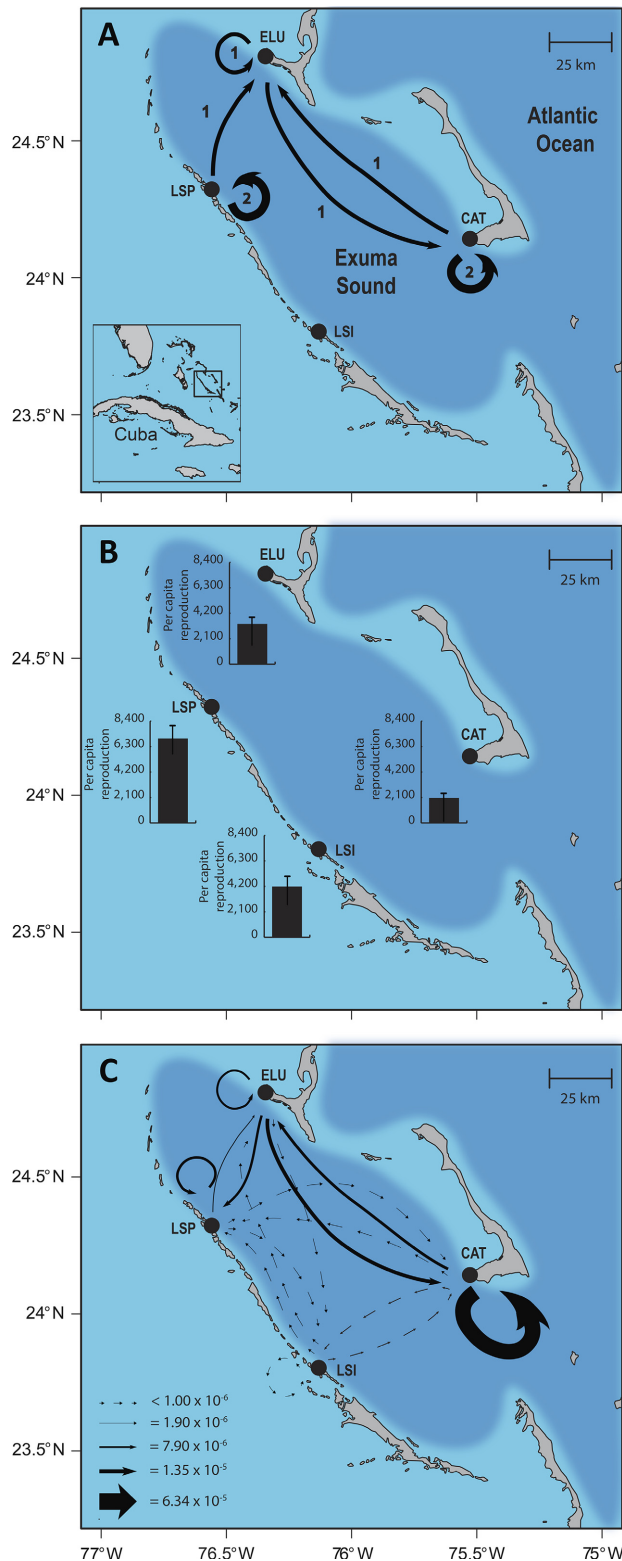


FIG. 3. Maps showing values of (A) detected larval connectivity, (B) per capita egg production, and (C) demographic connectivity (integrating A and B) among four local populations of bicolor damselfish in Exuma Sound, Bahamas: Eleuthera (ELU), the Exuma Cays Land and Sea Park (LSP), Cat Island (CAT), and Lee Stocking Island (LSI). (A) Arrows indicate larval dispersal pathways detected by parentage analysis and numbers indicate how many times dispersal was confirmed along each path (Pusack et al. 2014).

appreciable number of eggs produced at Cat Island recruited to Eleuthera (and vice versa), suggesting that grand offspring of fish at Cat Island may have recruited back to Cat Island and contributed to the replacement of their grandparents. Metapopulation growth was somewhat sensitive to changes in these rates of exchange (see the corresponding, off-diagonal cells in Table 2b).

We also examined sensitivity of metapopulation growth to changes in lifetime egg production at each of the four islands. These calculations resulted in median sensitivity values of 0.025, 0.015, 0.040, and 0.019, for the Exuma Cays Land and Sea Park, Eleuthera, Cat Island, and Lee Stocking Island, respectively. The absolute values are low because they represent the effects of a small change in lifetime egg production (mean value = 2,574 eggs), and these changes are also proportional to connectivity values, which reflect mortality during the egg, larval, and early juvenile stages, and are naturally low (Table 1a). The relative values indicate that metapopulation dynamics are most sensitive to changes in lifetime egg production at Cat Island (and to a lesser extent, the Exuma Cays Land and Sea Park) than changes in lifetime egg production at Lee Stocking Island or Eleuthera (Table 2c). Despite high lifetime egg production for the Lee Stocking Island, the observation of very low connectivity with other islands and little-to-no replacement suggests that changes in production at this island would have a relatively small effect on growth of the regional metapopulation.

An exploratory analysis indicated that if local populations inhabited reefs  $\geq 65$  ha in size, then we could be confident that the regional metapopulation would persist via network effects (dominant eigenvalue: median = 2.09, 95% CI = 1.03–4.94). Assuming a linear scaling between local population area and connectivity, metapopulation growth rate would be expected to increase by  $\sim 0.03$  units for every 1 ha increase in area of reef inhabited by the four local populations. These results suggest that for species whose patterns of demographic connectivity are similar to those for bicolor damselfish (regardless of differences in life history), a network of four, 65-ha marine reserves in this region would maintain positive growth without external input.

DISCUSSION

Despite the very large number of bicolor damselfish inhabiting coral reefs lining the Exuma Sound, the relatively small areas of reef we studied, and the substantial distance between study islands, demographic connectivity among our study populations was appreciable. This pattern was most apparent when considering conditional connectivity, a

FIG. 3. (continued) For pathways where no parent–offspring pairs were observed, the data suggest low, but not necessarily zero, dispersal. (B) Estimated number of eggs produced per adult and per dispersal event at each of the study populations (mean  $\pm$  SE). (C) Demographic connectivity estimated by combining parentage and demographic analyses (i.e., data from panels A and B). Demographic connectivity represents the proportion of eggs produced at each population that survived and dispersed as larvae to other populations (arrows connecting sites) or returned to their natal populations (circular arrows). Arrow thickness reflects estimated rate of exchange.

TABLE 1. Estimates of connectivity among populations at the four study islands.

	From LSP	From ELU	From CAT	From LSI
a) Demographic connectivity				
To LSP	$9.8 \times 10^{-6}$ ( $1.10 \times 10^{-6}$ , $3.20 \times 10^{-5}$ )	0 (0, $2.55 \times 10^{-5}$ )	0 (0, $2.72 \times 10^{-5}$ )	0 (0, $1.28 \times 10^{-5}$ )
To ELU	$1.9 \times 10^{-6}$ ( $2.00 \times 10^{-7}$ , $1.79 \times 10^{-5}$ )	$7.9 \times 10^{-6}$ ( $1.00 \times 10^{-6}$ , $5.91 \times 10^{-5}$ )	$1.09 \times 10^{-5}$ ( $1.60 \times 10^{-6}$ , $6.12 \times 10^{-5}$ )	0 (0, $1.27 \times 10^{-5}$ )
To CAT	0 (0, $2.44 \times 10^{-5}$ )	$1.39 \times 10^{-5}$ ( $2.2 \times 10^{-6}$ , $1.28 \times 10^{-4}$ )	$6.34 \times 10^{-5}$ ( $1.67 \times 10^{-5}$ , $2.28 \times 10^{-4}$ )	0 (0, $3.38 \times 10^{-5}$ )
To LSI	0 (0, $1.65 \times 10^{-5}$ )	0 (0, $3.49 \times 10^{-5}$ )	0 (0, $4.29 \times 10^{-5}$ )	0 (0, $2.22 \times 10^{-5}$ )
b) Conditional connectivity				
To LSP	0.07 (0.01, 0.35)	0 (0, 0.22)	0 (0, 0.22)	0 (0, 0.11)
To ELU	0.01 (0.001, 0.16)	0.05 (0.001, 0.52)	0.07 (0.01, 0.57)	0 (0, 0.11)
To CAT	0 (0, 0.21)	0.11 (0.02, 0.94)	0.41 (0.07, 0.97)	0 (0, 0.29)
To LSI	0 (0, 0.15)	0 (0, 0.31)	0 (0, 0.35)	0 (0, 0.19)

Notes: In a, demographic connectivity is expressed as the proportion of eggs produced at island  $j$  that survived and recruited to island  $i$ . In b, conditional connectivity is expressed as the proportion of surviving recruits that were produced at island  $j$  that survived and recruited to island  $i$ . Note that diagonals represent local retention. Values represent maximum likelihood estimates; numbers in parentheses represent 95% confidence limits. LSP, the Exuma Cays Land and Sea Park; ELU, Eleuthera; CAT, Cat Island; LSI, Lee Stocking Island.

TABLE 2. (a) Estimates of the realized connectivity matrix; (b) sensitivity of metapopulation growth to changes in elements of the connectivity matrix; (c) sensitivity of metapopulation growth to changes in lifetime egg production at each of the four islands.

	From LSP	From ELU	From CAT	From LSI
a) Realized connectivity				
To LSP	0.151 (0.026–0.687)	0.017 (0.000–0.107)	0.018 (0.001–0.113)	0.031 (0.000–0.222)
To ELU	0.040 (0.002–0.286)	0.032 (0.002–0.151)	0.073 (0.013–0.267)	0.029 (0.001–0.216)
To CAT	0.065 (0.002–0.522)	0.082 (0.006–0.420)	0.161 (0.027–0.573)	0.080 (0.002–0.606)
To LSI	0.047 (0.001–0.370)	0.024 (0.001–0.153)	0.031 (0.001–0.161)	0.060 (0.001–0.395)
b) Sensitivity to matrix elements				
To LSP	0.129 (0.002–0.902)	0.148 (0.003–0.905)	0.396 (0.024–1.782)	0.141 (0.003–0.939)
To ELU	0.067 (0.002–0.358)	0.077 (0.003–0.393)	0.230 (0.012–1.107)	0.075 (0.003–0.444)
To CAT	0.103 (0.009–0.418)	0.128 (0.006–0.478)	0.469 (0.011–0.969)	0.110 (0.007–0.509)
To LSI	0.096 (0.002–0.515)	0.106 (0.003–0.599)	0.308 (0.010–1.609)	0.106 (0.001–0.739)
c) Sensitivity to lifetime egg production				
	0.025 (0.001–0.242)	0.015 (0.001–0.066)	0.040 (0.002–0.232)	0.019 (0.001–0.177)

Notes: Values represent the average number of individuals per new recruit at island  $j$  that successfully recruit and survive to maturity at island  $i$ . Similar to a transition matrix that describes age-structured population growth, these numbers summarize the effective transition of individuals among the islands during each generation. Note that diagonals represent local retention. LSP, the Exuma Cays Land and Sea Park; ELU, Eleuthera; CAT, Cat Island; LSI, Lee Stocking Island. Values are medians with 95% confidence intervals in parentheses.

measure of connectivity that was summarized per surviving recruit and thus factored out the high rate of mortality experienced by eggs and larvae of this species. Conditional connectivity between islands was 1.6% on average, and involved dispersal distances up to 129 km. Conditional, local retention was estimated to be 13.3% on average, and was estimated to be 41% at Cat Island (95% CI = 6.0–97.0%). We acknowledge that the 95% confidence intervals for many of our connectivity estimates are large (Table 1), but given the logistical challenges of measuring both reproduction and connectivity in large, marine populations, and the need to account for the accumulation of uncertainty, it is very difficult to estimate demographic connectivity with a high degree of precision. We emphasize that likelihood values were largest in the regions near our point estimates, and we may still be reasonably confident that some values of connectivity were small whereas others were appreciable. One reason for the relatively large connectivity values observed here may be the presence of oceanographic features that facilitate

dispersal among island populations and/or retention of larvae within populations. In particular, mesoscale gyres form seasonally within Exuma Sound (Colin 1995, Stockhausen and Lipcius 2001) and are especially prevalent in a region centered among the Exuma Cays Land and Sea Park, Eleuthera, and Cat Island, the three islands for which we observed connectivity and local retention of larvae, but not off Lee Stocking Island (Pusack et al. 2014). Depending on the timing of reproduction and larval behavior, these ocean currents may facilitate either dispersal to other islands or retention to the natal population (see Paris and Cowen 2004 for direct evidence that larvae of *S. partitus* can detect and make use of ocean currents). Relevant to our current study, Pusack et al. (2014) measured allele frequencies within each of our four study populations.  $F_{ST}$  comparisons suggest appreciable gene flow among three of our study islands (Eleuthera, Exuma Cays Land and Sea Park, and Cat Island), but a low degree of gene flow between Lee Stocking Island and the others. These patterns are consistent of our



estimates of little to no demographic connectivity between Lee Stocking Island and the other islands during the study period (Table 1).

This study underscores the importance of gathering concurrently and integrating data on both the production and the dispersal of larvae, i.e., both local demography and larval connectivity. The dynamics and persistence of a metapopulation depend critically on both of these phenomena and isolated information on one or the other may lead to unreliable conclusions. For example, we detected two instances of local retention for both the Exuma Cays Land and Sea Park and Cat Island. Without information on larval production, one might conclude that levels of local retention were similar. However, per capita egg production was lower at Cat Island, and the proportion of habitat searched was much smaller. This information suggested that local retention at Cat Island was  $\sim 6.5 \times$  higher than at the Exuma Cays Land and Sea Park. Similarly, data on reproductive rates were critical in revealing substantial connectivity between Cat Island and Eleuthera, and a lower, but still appreciable level of connectivity between the Exuma Cays Land and Sea Park and Eleuthera (Fig. 3C).

It is likely that the patterns of connectivity we observed were strongly influenced by ocean currents within Exuma Sound (Colin 1995, Stockhausen and Lipcius 2001). Because persistent ocean currents may influence the dispersal of larvae of multiple species (e.g., Watson et al. 2011b), patterns of connectivity among local populations of other reef species at these islands may be similar to those we observed for bicolor damselfish. If so, we would expect greater retention of larvae in the north and east regions of the sound. This pattern is consistent with Stoner et al.'s (1998) finding that late-stage veliger larvae of queen conch (*Strombus gigas*) were most abundant in the northeastern region of Exuma Sound, moderately abundant near Cat Island, and low near Lee Stocking Island, despite a moderate density of adults. Similarly, Lipcius et al. (2001) used a biophysical model to simulate the transport of larvae of spiny lobster (*Panulirus argus*) within Exuma Sound and inferred that local retention would be very high at Cat Island, moderate at Eleuthera and the Exuma Cays Land and Sea Park, and lowest at Lee Stocking Island. These patterns are also consistent with what we found for bicolor damselfish. It is also notable that the one marine reserve in our study (the Exuma Cays Land and Sea Park) exhibited both local retention of larvae and delivery of larvae to other islands. This marine reserve is effective at protecting fishes at multiple trophic levels (Mumby et al. 2006, Lamb and Johnson 2010), and it is plausible that many species within this reserve benefit from both local retention of larvae and export of larvae to other locations within Exuma Sound.

This study also revealed major differences in lifetime offspring production among islands, but again, the metapopulation-level consequences of these differences must be interpreted within the context of larval dispersal. Lifetime offspring production was relatively high at Lee Stocking Island and the Exuma Cays Land and Sea Park, but substantially lower at Eleuthera and Cat Island (where average survival to maturity was low). We believe that the differences in survival among islands was largely due to differences in the structural complexity of habitats at these locations.

Habitat structure often provides small fish with refuge space from predators and increased complexity typically increases survival (e.g., Beukers and Jones 1998, Johnson 2006, Scharf et al. 2006, Hixon et al. 2012). Habitats at Cat Island and Eleuthera were comprised of structurally simple corals (mainly massive *Orbicella*, formerly *Montastrea*), whereas habitats at the other two islands contained a variety of corals that were structurally complex (e.g., *Agarica* and *Porites*). Per capita reproduction was highest at the Exuma Cays Land and Sea Park, somewhat lower at Lee Stocking Island, and lower still at the other two islands (Fig. 3B). These patterns are correlated with spatial variation in habitat complexity, yet we believe they are influenced more directly by food availability. Current speeds within damselfish habitat were notably higher at the Exuma Cays Land and Sea Park, somewhat high at Lee Stocking Island, and lower at the other two islands. Bicolor damselfish routinely feed on plankton that drift near their home territories (Myrberg 1972, Johnson 2008), and among-island differences in reproductive rates may be driven by differences in the supply of planktonic food (e.g., Thresher 1983). Based on information on lifetime egg production alone, one might conclude that Lee Stocking Island and the Exuma Cays Land and Sea Park were most important for the functioning of the metapopulation. However, Cat Island had a relatively high degree of both local retention and connectivity with Eleuthera. When also considering larval dispersal, it is clear that regional metapopulation growth was more sensitive to variation in lifetime egg production at Cat Island than at the other sites we studied (Table 2b,c).

Our analysis of metapopulation dynamics was set to a scale of populations inhabiting 5-ha reefs at each of the four islands. At this scale, average replacement of individuals was low and the metapopulation would quickly decline if not for input of larvae from outside the regional metapopulation ( $\lambda = 0.34$ ). Scaling-up, our results suggest that four reefs of  $\sim 65$  ha in area would experience sufficient demographic connectivity that the metapopulation would persist entirely on its own ( $\lambda$  was significantly  $>1$ ). Although bicolor damselfish is not a fished species, these results may provide a useful guideline for designing effective networks of marine protected areas for species with similar combinations of dispersal and demographic patterns. Protecting four, 65-ha sections of coral reef in this region would help ensure the long-term persistence of species whose patterns of realized connectivity are similar to bicolor damselfish, regardless of any differences in life history.

Much effort has gone into estimating patterns of dispersal of marine larvae (reviewed by Levin 2006, Cowen and Sponaugle 2009, Hilário et al. 2015). Although such studies have been motivated by understanding how connectivity affects population dynamics, few have concurrently measured variation in reproductive output to fully evaluate demographic connectivity (Botsford et al. 2009). Our results suggest that spatial variation in offspring production can play a major role in the demographic connectivity and dynamics of marine metapopulations. Because understanding such effects is integral to the effective design of networks of marine protected areas (Palumbi 2003, Botsford and Hastings 2006, Burgess et al. 2014), additional studies that integrate data on both larval dispersal and local

demography will be exceedingly valuable for the successful conservation and management of marine species.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2343/supinfo>

## Appendix S1. Details regarding the estimation of connectivity

We measured dispersal during 10 separate events (monthly cohorts that settled in July 2005, and in June, July, and August of 2006-2008). For each of those 10 cohorts, we genotyped adults at island  $j$ , and could calculate how many genetically “tagged” eggs were produced at that island. For those same cohorts, we also knew how many of the newly-settled recruits that we sampled at island  $i$  were spawned by parents at island  $j$ . This design resulted in 16 dispersal pathways (4 islands acting as both beginning and endpoints). The overall goal of this analysis was to find the average values of connectivity ( $c_{i,j}$ ) between the four islands in our study that were most likely to have produced the observed number of parent-offspring pairs between each pair of islands and for all 10 dispersal events. For example, for eggs produced at Cat Island and recruits collected at Eleuthera, there were nine instances when none of the recruits that we sampled were from eggs produced at Cat Island and one instance when one of the recruits we sampled was spawned at Cat Island. The latter observation confirms that connectivity occurred, but quantifying the average magnitude of connectivity required additional steps.

Note that we were interested in connectivity among island populations inhabiting 5-hectare reefs, but at these spatial scales it was possible for divers to sample only a small proportion of the available habitat (~5%) when collecting recruits. The expected number of parent-offspring pairs in our samples needed to be adjusted to account for this. In our analysis we calculated the expected number of parent-offspring pairs ( $E[N_{PO}]$ ) as a function of area searched ( $A_{Searched}$ ), total area ( $A_{Total}$ ), offspring production ( $\hat{O}_i$ ), and connectivity ( $c_{i,j}$ ):

$$E[N_{PO}] = \frac{A_{Searched} \hat{O}_j c_{i,j}}{A_{Total}} \quad (S1)$$

Area searched, total area, and offspring production were known quantities. For a given level of connectivity, one could then calculate the expected number of parent-offspring pairs in a sample. Note that the expected value is akin to a long-term average. It can be a fractional value, but observed values of the number of parent-offspring pairs must take on an integer value (0,1,2,3, etc.). In our analysis we assumed that the number of parent-offspring samples between two islands and per cohort followed a Poisson distribution.



We found the values of connectivity that were most likely to have produced the observed number of cases where recruits collected at population  $i$  were produced by parents at population  $j$  (referred to as parent-offspring pairs in the tables below). Our actual calculations involved 10 dispersal events (monthly cohorts), but as a heuristic exercise, the following is an example for 3 dispersal events in which we observed 0, 1 and 0 parent-offspring pairs. For a given value of connectivity, we can calculate the expected number of parent offspring pairs, and the probability of observing 0, 1, and 0 parent offspring pairs in our samples  $[\text{Pr}(\text{obs}|\text{exp}) \cdot E[N_{PO})]$  for each cohort was calculated using equation S1, and  $\text{Pr}(\text{obs}|\text{exp})$  was calculated using a Poisson probability distribution with mean value of  $E[N_{PO})]$ . Likelihood was calculated as the product of the  $\text{Pr}(\text{obs}|\text{exp})$  values for all of the cohorts ( $n = 3$  in this example).

If connectivity was  $1 \times 10^{-6}$ , likelihood was calculated to be 0.014:

Production of genetically "tagged" offspring, $\hat{O}_j$	$\frac{\text{Area searched}}{\text{Total area}}$	Connectivity $c_{i,j}$	Expected # of Parent-offspring pairs $\hat{N}_{PO}$	Observed # of Parent-offspring pairs	$\text{Pr}(\text{obs} \text{exp})$
203 000	0.05	$1 \times 10^{-6}$	0.010	0	0.990
201 000	0.07	$1 \times 10^{-6}$	0.014	1	0.014
229 000	0.06	$1 \times 10^{-6}$	0.014	0	0.986
				<b>Likelihood:</b>	<b>0.014</b>

If connectivity was  $1 \times 10^{-5}$ , then likelihood was substantially higher.

Production of genetically "tagged" offspring, $\hat{O}_j$	$\frac{\text{Area searched}}{\text{Total area}}$	Connectivity $c_{i,j}$	Expected # of Parent-offspring pairs $\hat{N}_{PO}$	Observed # of Parent-offspring pairs	$\text{Pr}(\text{obs} \text{exp})$
203 000	0.05	$1 \times 10^{-5}$	0.102	0	0.903
201 000	0.07	$1 \times 10^{-5}$	0.141	1	0.122
229 000	0.06	$1 \times 10^{-5}$	0.137	0	0.871
				<b>Likelihood:</b>	<b>0.096</b>

This procedure was repeated for connectivity values ranging from 0 to 0.001 in increments of  $1 \times 10^{-7}$  until the maximum likelihood estimates for connectivity values were obtained.

However, our procedure for estimating connectivity relies on inputs that are estimates, and therefore subject to some uncertainty. To incorporate this uncertainty into our overall estimates of connectivity we used a resampling procedure. For each of 1000 iterations, input parameters describing offspring production were drawn from their estimated distributions (Table S1).

Table S1. Estimated means and covariances of the parameters used to calculate offspring production and survival.

<b>Input</b>	<b>Distribution of parameter estimates</b>	<b>Means</b>	<b>(Co)variance</b>	<b>Reference</b>
Egg density	Normal	215	56.7	Samhuri et al. 2009; This study
Ln[egg production] (in cm <sup>2</sup> ) Eq. 1 in main text	Multivariate normal	$b = -0.281$ $A = 1.31$ $t_{MAX} = 20.47$	0.0391 -0.00129 0.0107 0.00376 0.0018 0.121	This study
Egg survival	Normal	0.60	$1.25 \times 10^{-3}$	Johnson et al. 2010
Larval survival	Empirical	0.00108	$9.62 \times 10^{-7}$	Johnson et al. 2015
Instantaneous mortality at settlement (daily)	Normal [Survival = exp( $\mu$ )]	$\mu = -1.18$	0.34	Almany and Webster 2006
Juvenile survival (13 d <sup>-1</sup> )	Normal	0.771	$2.24 \times 10^{-4}$	This study

In addition, we incorporated uncertainty from our parentage analysis by resampling putative parent-offspring pairs by their probability of Type I and Type II errors. The method of parentage analysis we used (Christie 2010) maintains Type I error rates at conservatively low level (Christie 2013), and also provides a posterior probability of that parent-offspring pair being false, given the frequency of shared alleles ( $\Pr[\phi|\lambda]$ ).  $\Pr[\phi|\lambda]$  ranged from 0.011 – 0.043 (see Pusack et al. 2014 for actual values) and was influenced by the frequencies of alleles shared by parents and offspring. To simulate Type I error (i.e., observed parents were actually false, despite matching

alleles at 10 of 10 loci), in each of the 1000 iterations, each of the observed parent-offspring pairs was treated as a random variable and sampled as true with a probability of  $1 - \Pr[\phi|\lambda]$ . Type II error rates were simulated by considering whether some pairs of recruits and adults could be parent-offspring, despite matching at fewer than 10 of 10 loci. Such results would be possible because of genotyping error. In our study there were 42 recruit-adult pairs that matched at 9 of 10 loci. However, it was biologically possible that only 12 of these could be parent-offspring pairs (in many cases the adult was dead long before the recruits were collected; in other cases the adult was too young to be reproductive at the time the recruit was collected). In contrast, all eight identified pairs that matched at 10 of 10 loci were all biologically plausible parent-offspring pairs. Using our estimated genotyping error rate of 0.014 (Christie et al. 2010), a recruit-adult pair that matched at 9/10 loci may have been a true parent offspring pair if there was a genotyping error at one loci, but not the other nine. In that case, the probability would be  $0.014 \times (1-0.014)^9$ . However, because all putative parent-offspring pairs were reanalyzed from DNA extraction to genotyping (Pusack et al. 2014), the actual probability of Type II error was lower (approximately  $[0.014 \times (1-0.014)^9]^2$ ). To simulate Type II error rate, each recruit-adult pair was sampled as a true parent offspring pair, with probability equal to the estimated Type II error probability. Note that if recruits and adults mismatched at more than 1 locus, the probability of Type II error was negligible ( $[(0.014)^2 \times (1-0.014)^8]^2 = 3.06 \times 10^{-8}$ ), so these cases were not included in our simulation.

Based on resampled values of demographic parameters and number of parent-offspring pairs, a likelihood profile for demographic connectivity values was calculated. Assuming that the number of parent-offspring pairs found in each sample of recruits followed a Poisson distribution, we calculated the probability of observing the data for connectivity values ranging from 0 to 0.001 in increments of  $1 \times 10^{-7}$ . To summarize the overall likelihood profile for connectivity, we averaged all 1000 probabilities associated with each connectivity value. The resulting likelihood profiles represent both the inherent variability of sampling recruits (described by the Poisson distribution) and the uncertainty of estimates of offspring production and parentage (described by our resampling procedure). These likelihood profiles were used to generate 95% confidence intervals for each estimate of connectivity. The range of values whose log likelihood lies within  $\frac{\chi_{\alpha,1}^2}{2}$  units of the maximum defines a confidence interval at the  $\alpha$ -1 level

(Meeker and Escobar 1995). To calculate upper and lower confidence limits, we found the upper and lower values of connectivity that were 1.92 units of log likelihood below the maximum likelihood estimate. We used a similar procedure to describe the likelihood profiles for conditional connectivity, but these calculations involved the additional steps of resampling values of survival during the egg, larval, settler, and early juvenile stages. Parameters describing survival during each of these stages were sampled from their estimated distributions (Table S1). For each level of conditional connectivity, we resampled 1000 different sets of parameters describing both offspring production and offspring survival, and for each of these 1000 iterations, we calculated the probability of observing the parentage data (with genotyping error included as described above). We calculated likelihoods for levels of conditional connectivity ranging from 0 to 1 and in increments of  $1 \times 10^{-4}$ .

Although our analyses concentrated on estimating *average* connectivity values, it is possible that values of connectivity between islands changed over time. To evaluate whether it was reasonable to assume that patterns of connectivity were stable, we compared measures of fit (AIC values) for two models: one in which connectivity among islands was allowed to vary during each reproductive event, and one in which connectivity among islands was assumed to be constant across reproductive periods. Support for the constant-connectivity model was overwhelming ( $AIC_{\text{constant}} = 80.67$ ,  $AIC_{\text{variable}} = 336$ ), largely because the variable-connectivity model (which was much more complex and required the estimation of many more parameters) provided only a marginal increase in likelihood.

We note that one reason for choosing a simpler model is the challenge of estimating variable connectivity. The regional population size of bicolor damselfish is large, and although we concentrated on 4 focal islands, there are many other locations that may contribute offspring to our study islands. Within this system it was possible to sample only a relatively small proportion of the adults and offspring in the populations of interest, and it would be difficult to detect moderate to small changes in demographic connectivity. Similarly, it is difficult to say whether temporal variation in larval exchange (a pattern discussed in our earlier study; Pusack et al. 2014) was truly indicative of spatial and temporal variation in demographic connectivity. Guided by parsimony, we chose a model in which patterns of demographic connectivity are temporally consistent. This choice was appropriate considering that the goals of the study were



to estimate average values of connectivity among the study islands, and that there is some evidence to suggest that the spatial patterns of connectivity we detected may remain consistent over much larger timescales (see Pusack et al. 2014, and discussion in the main text).

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## **Appendix S2: Measuring post-settlement demography and calculating lifetime egg production**

We calculated lifetime egg production for each of the four study populations by combining estimates of post-settlement growth, survival, and reproduction. Lifetime egg production (LEP) summarizes the number of eggs that a typical, newly-settled recruit will produce in its lifetime. LEP was calculated as:

$$LEP = \frac{1}{2} \int_{\alpha}^{\infty} l_t m_t dt \quad (S1)$$

where  $l_t$  is the age-schedule of survival,  $m_t$  is the age-schedule of fertility,  $\alpha$  is age at maturation, and age ( $t$ ) is expressed as days post settlement. We calculated  $l_t$  by combining information on growth (i.e., a function describing size at age) and a function describing size-dependent survival (see below for further details).  $m_t$  is a function that describes per capita reproduction of adults (fish > 6cm TL; see main text), and  $\alpha$  is age at maturation. Because previous studies have indicated that bicolor damselfish mature at ~6 cm TL (Schmale 1981),  $\alpha$  was calculated as the average age at which size was 6cm and was estimated from the growth function for each island (see below). Equation S1 considers offspring of a single sex and assumes a 1:1 sex ratio at birth.

In our study, populations were censused at monthly intervals during the summer (June, July, and August). During these censuses all bicolor damselfish in our study plots were (re)captured and measured. We searched for missing individuals on nearby reefs, though as in previous studies of this species, movement away from the study reefs was negligible (Carr et al. 2002, Hixon et al. 2012). We collected information on survival and growth during ~30 day intervals in the summers and during ~310 day intervals between summers.

### *Somatic growth*

To describe growth (total length at age), we fit a Richards function to our size-at-recapture data. The Richards function describes an asymptotic growth pattern in which small fish grow quickly and growth approaches zero at the largest sizes. The Richards function provides a good description of growth for this species and is flexible enough to describe variation in growth trajectories among populations (Hixon et al. 2012). The mark-recapture version of this equation (Ebert 1980) describes size at recapture ( $L_{t2}$ ) as a function of size at previous capture ( $L_{t1}$ ), time interval between captures ( $\Delta t$ ), asymptotic size ( $L_\infty$ ), a growth constant ( $k$ ), and a scaling exponent ( $n$ ):

$$L_{t2} = [L_\infty^{(-1/n)}(1 - e^{-k\Delta t}) + L_{t1}^{(-1/n)}e^{-k\Delta t}]^{-n} \quad (\text{S2})$$

Equation S2 can be rearranged to describe size-at-age  $L_t$ :

$$L_t = L_\infty(1 - Be^{-kt})^{-n} \quad (\text{S3})$$

where  $B$  is a scaling parameter equal to  $(L_\infty^{(-1/n)} - L_0^{(-1/n)})/L_\infty^{(-1/n)}$ , and  $L_0$  is size at settlement (estimated to be 1.5cm TL). Equation S2 was fit to our data using a nonlinear regression in R (R Development Core Team 2016). Once growth parameters were estimated for each island, average age at maturity was calculated as:

$$\alpha = -\ln\left(\frac{1 - \left(\frac{L_0}{L_\infty}\right)^{(-1/n)}}{B}\right)/k \quad (\text{S4})$$

where all parameters are as in the Richards growth equation.

### *Survival*

To estimate post-settlement survival, we assigned each individual a value of 1 if it survived through the census interval and a value of 0 if it disappeared. Because previous studies established that movement of this species away from the study reefs was negligible (Carr et al. 2002, Hixon et al. 2012), and because we exhaustively searched nearby reefs for missing fish, all disappearances were interpreted as mortality. We used logistic regression to describe survival as a function of size. The data suggested a complex pattern of mortality, so we included squared body size as a predictor of monthly survival. For the calculation of lifetime egg production, the age schedule of survival  $l_t$  was calculated as the product of daily survival, which was a function of body size ( $L_t$ ):

$$l_t = \prod_0^t \left( \frac{1}{1 + \exp(-(\beta_0 + \beta_1 L_t + \beta_2 L_t^2))} \right)^{1/30} \quad (S5)$$

where  $t$  is age post settlement, and  $\beta_0$ ,  $\beta_1$ , and  $\beta_2$  are parameters of the logistic regression relating body size to probability of survival during a 30-day interval.

### *Reproduction*

We measured reproduction by supplying males with artificial nests (see Johnson et al. 2010, Hixon et al. 2012 for additional details). Spawning occurs during a one-hour period following dawn (Knapp and Kovach 1991, Knapp 1993) and our censuses occurred between 09:00 and 15:00. During each monthly census and at two separate reefs per island population, we recorded egg number estimated as the area of monolayer clutches. We also recorded the age and spawning date of eggs based on their color (yellow = laid that day; brown = laid 1-2 days earlier; grey = laid 3 days earlier). Thus, for each census, we estimated egg production on each of three days before that census (with counts of eggs that were laid 1-2 days before the census were averaged and treated as if they were laid 1.5 days prior). For each day reproduction was measured, we calculated per capita reproduction at each reef by summing the total number of eggs produced and dividing by the number of adults (fish > 6 cm TL; Schmale 1981). In 2006, daily measurements of egg production were taken at Lee Stocking Island from June 8th to August 30th and these data were also included in the analyses.

We described daily, per capita reproduction as a periodic function of lunar day:



$$f_t = \exp(b + A(\cos(\frac{2\pi}{29.5})(t - t_{MAX}))) \quad (S6)$$

where  $b$  is the average reproductive output,  $A$  is the amplitude of the increase/decrease with lunar day, and  $t_{MAX}$  is the lunar day when reproduction is maximal. We used a mixed-effects modeling framework to select a variant of equation S6 to describe how reproduction varied among the islands. We fit multiple versions of equation S6 to the data (e.g., with combinations of parameters held constant across islands), and used AIC to select the most parsimonious model.

Reproduction also follows a seasonal cycle, and in the Bahamas, reproduction peaks in the summer months (June-September; see Johnson and Hixon 2011). In this study, our estimates of reproduction were for the summer months. Although these estimates were appropriate for calculating connectivity, they may overestimate lifetime egg production because reproduction diminishes during the wintertime. Estimates of lifetime reproduction were adjusted for seasonality (see below).

#### *Lifetime egg production*

Lifetime egg production (LEP) was calculated by using the framework described in equation S1. Functions describing growth and survival were used to generate  $l_t$ . The growth function (S3) was nested within the size-dependent survival function (S5) so that survival was a function of age. The age schedule of reproduction ( $m_t$ ) was based on equation S6, with one modification. To account for seasonal patterns of reproduction, we assumed that seasonal variation at all of our study islands was similar to seasonal variation previously described for study populations near Lee Stocking Island (Johnson and Hixon 2011). Reproduction was multiplied by a sinusoidal function that was maximal (a value of 1) at time zero and minimal (0.575) at time = 182.5 (i.e., half a year after the peak recruitment season). The age-schedule of reproduction ( $m_t$ ) was calculated as

$$m_t = f_t \left( 0.787 + 0.213 \left( \cos\left(\frac{2\pi}{365}\right)t \right) \right) \quad (S7)$$

where  $t$  is time (in days). For our calculations of LEP, day zero was set as a new moon in the middle of summer. Although this decision was arbitrary, it is logical because most recruitment occurs in the summer (Hixon et al. 2012). Choosing alternative starting points had negligible

effects on estimates of LEP, in part because lunar cycles are small relative to the expected, post-settlement lifetime of a recruit of this species.

To calculate variation associated with our estimates of LEP, we conducted a resampling procedure where each of the parameters of the component functions of equation S2 were sampled at random from their estimated distributions. Parameters were assumed to follow univariate or multivariate normal distributions, with the means and (co)variances estimated from the data. For each iteration, a set of parameters was drawn at random and LEP was calculated. This procedure was repeated 1000 times to generate a distribution of LEP estimates for each of the four study islands.

## **RESULTS**

### *Individual Growth*

Although patterns of growth varied somewhat among the four islands, in all cases growth rates were relatively fast during the early juvenile phase and decreased with the size of the fish (Fig. S1). Average growth rates approached zero at sizes between 7.50 cm TL (Eleuthera) and 9.97 cm TL (Exuma Cays Land and Sea Park). Growth was greater during longer intervals, but there did not appear to be a major, seasonal change in growth rates. A model with a single set of growth parameters for both seasons (but different parameters for islands) described the data reasonably well (Fig. S1).

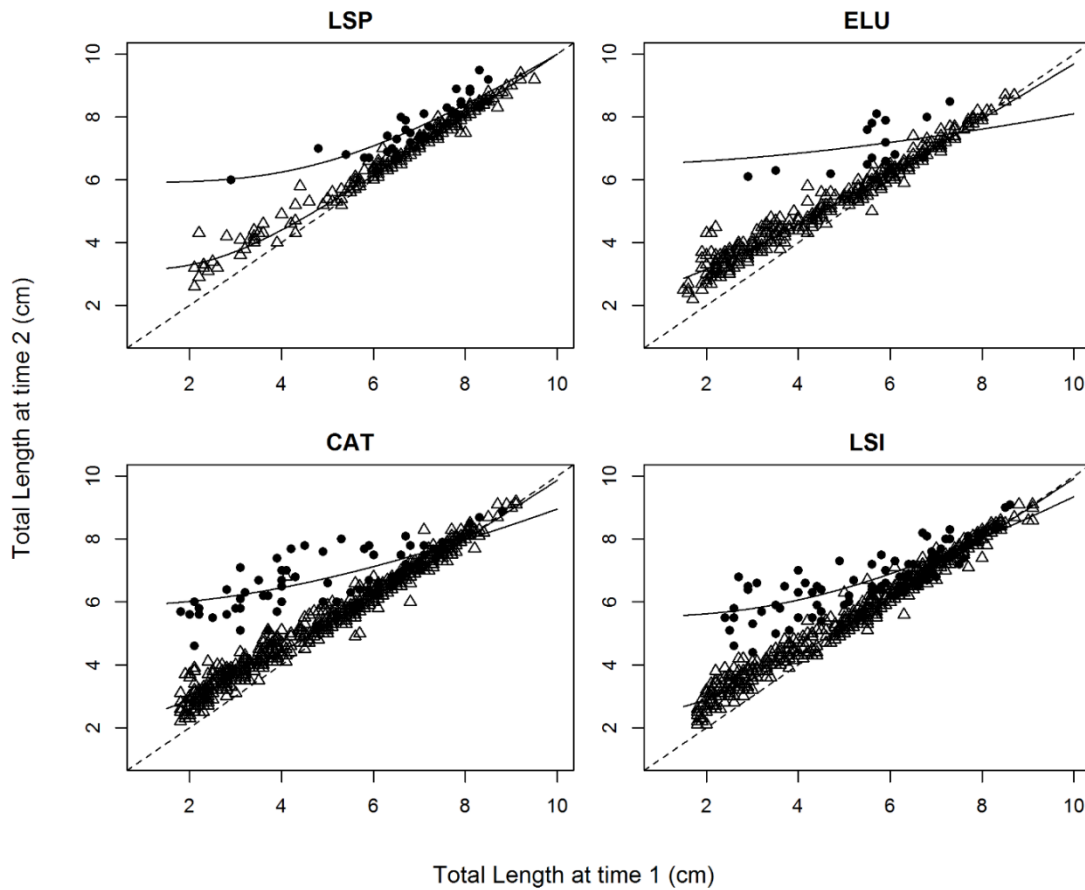


Fig. S1. Measurements of individual growth at each of the four islands. Open triangles represent growth during summer intervals (~30 days), solid circles represent growth during winter intervals (~310 days). Dash lines indicate 1:1 lines. Solid curves illustrate the fit of a Richards function predicting total length (TL) at time 2, given initial TL, average interval length, and estimated growth parameters for each island. LSP = Exuma Cays Land and Sea Park; ELU = Eleuthera; CAT = Cat Island; LSI = Lee Stocking Island.

The growth curves varied somewhat among the four islands (Fig. S2). Most notably, fish at Eleuthera grew relatively quickly as juveniles, but then leveled-off at relatively small adult sizes. Fish at the Exuma Cays Land and Sea Park grew very large as adults, and fish at Lee Stocking Island grew relatively slowly overall (Fig. S2).

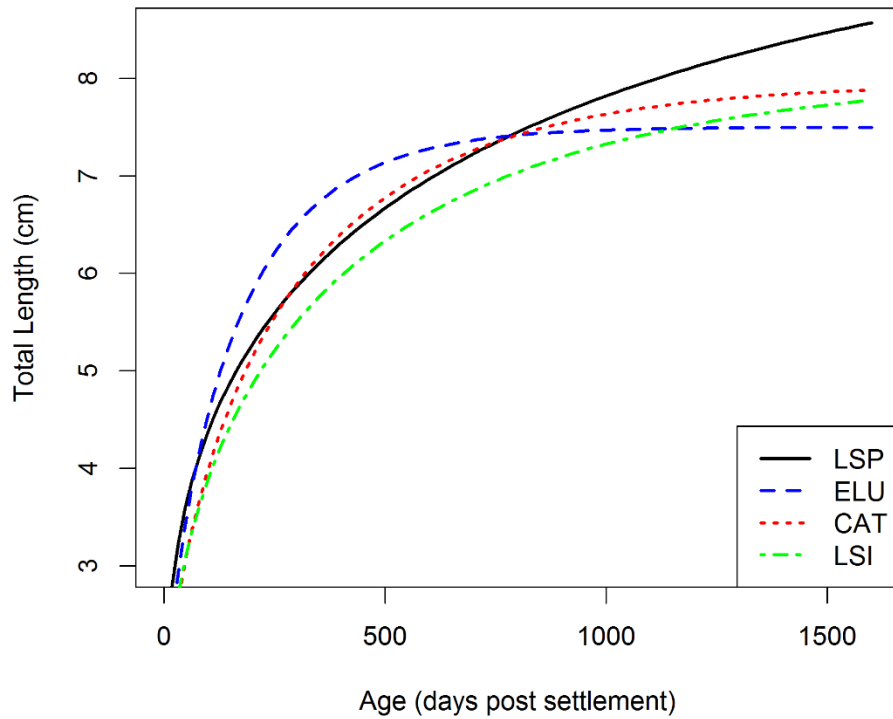


Fig. S2. Estimated individual growth curves for each of the four islands. Growth curves are based on the Richards function (equation S4) with parameters estimated from the data displayed in Fig. S1. LSP = Exuma Cays Land and Sea Park; ELU = Eleuthera; CAT = Cat Island; LSI = Lee Stocking Island.

### *Survival*

In general, survival increased as fish became older and larger, yet beyond this pattern, overall rates of survival varied among the study islands (Fig. S3). Survival rates of late juveniles and adults were higher at Lee Stocking Island and the Exuma Cays Land and Sea Park (upper left and lower right panels) and lower at Cat Island and Eleuthera (lower left and upper right panels; Fig. S3).

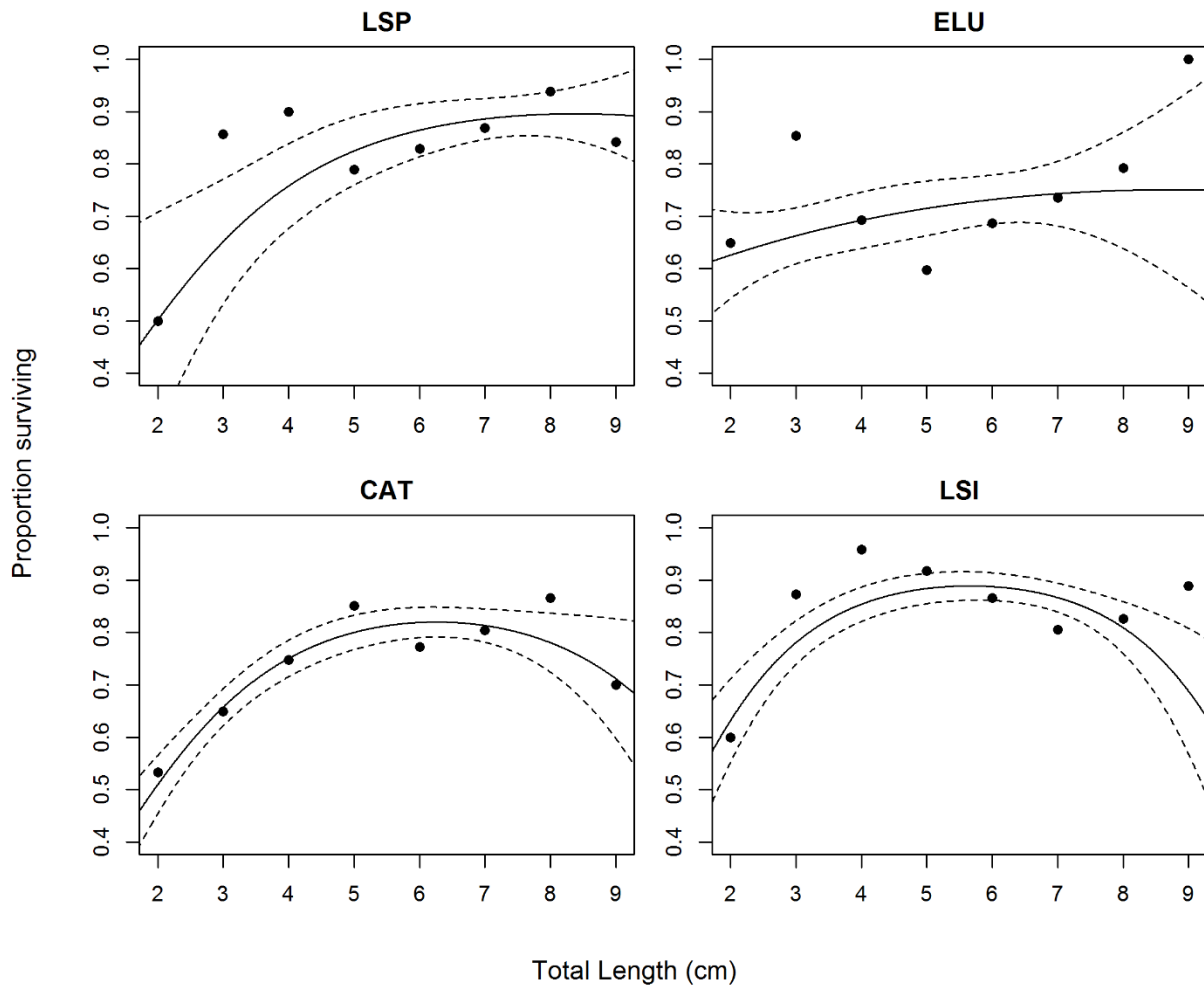


Fig. S3. Proportional survival over a 30-day period for each of the islands. Each dot represents average survival within 1cm size bins. Solid curve indicates the expected, proportional survival as a function of the size of fish. Dashed lines indicate 95% confidence bands. LSP = Exuma Cays Land and Sea Park; ELU = Eleuthera; CAT = Cat Island; LSI = Lee Stocking Island.

### *Reproduction*

Per capita reproduction followed the lunar cycle, with a peak in reproduction occurring around lunar day 21 ( $t_{\text{MAX}} = 20.47$ ; Fig. S4). A model in which the only the elevation of the curve ( $b$ ) varied among the islands provided the best fit to the data (Table S1). Although a model in which

both the amplitude and elevation of the curve varied among islands provided a similar fit ( $\Delta AIC$  0.5), we chose the simpler model to describe variation in reproduction. Parameter  $A$  was estimated to be 1.332, and estimates of  $b$  were 0.152 for Exuma Cays Land and Sea Park, -0.455 for Eleuthera, -0.547 for Cat Island and -0.327 for Lee Stocking Island. Note that reproduction was measured as egg area ( $\text{cm}^2$ ) and egg number was calculated by multiplied egg area by mean density of eggs ( $215 \text{ eggs cm}^{-2}$ ).

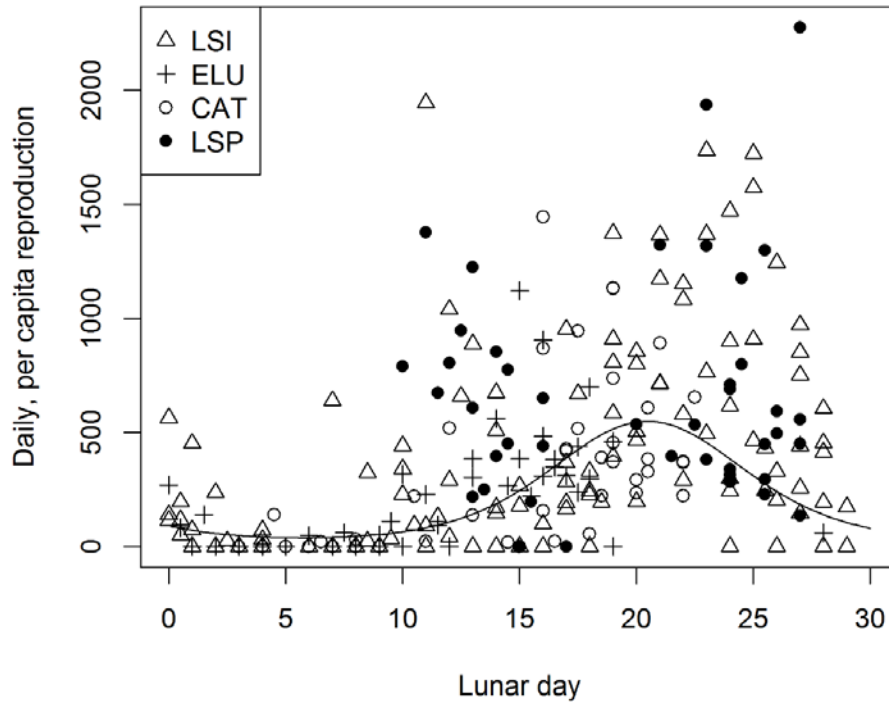


Fig. S4. Number of eggs produced per adult per day of the lunar cycle. Solid curve represents a modified sinusoidal function (equation S7) that summarizes average reproduction over time. Data suggest that overall reproductive output varied among islands, but that the islands did not vary with respect to timing of reproduction within the lunar cycle. LSP = the Exuma Cays Land and Sea Park; ELU = Eleuthera; CAT = Cat Island; LSI = Lee Stocking Island.



Table S1. AIC scores for candidate models used to describe variation in per capita reproduction of bicolor damselfish at each of the four study islands.

Parameters that varied among islands	AIC	$\Delta$ AIC
$b, A, t_{\text{MAX}}$	829.7	6.13
$A, t_{\text{MAX}}$	833.9	10.3
$b, A$	824.1	0.5
$b, t_{\text{MAX}}$	827.2	3.6
<b><math>b</math></b>	<b>823.6</b>	<b>0</b>
$A$	830.0	6.4
$t_{\text{MAX}}$	830.0	6.4
None (fixed effects only)	828.0	4.4

### *Lifetime egg production*

Lifetime egg production varied substantially among islands. Production was high for fish at the Exuma Cays Land and Sea Park (mean = 4545) and Lee Stocking Island (mean = 3757), but substantially lower for fish at Cat Island (mean = 1002) and Eleuthera (mean = 993). Even when variation in parameter estimates was accounted for, stark differences in LEP among islands were apparent (see Fig. 2 of main text). The main reason for these differences was variation in survival among islands (cf. Fig. S3 and Fig. 1 in the main text).

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### **Appendix S3. Sensitivity of metapopulation growth to changes in realized connectivity and lifetime egg production**

To evaluate the relative contribution of the local population inhabiting each island to the dynamics of the four-island metapopulation, we calculated the sensitivity of metapopulation growth to changes in the elements of the realized connectivity matrix. Metapopulation growth was measured by the dominant eigenvalue of the realized connectivity matrix ( $\lambda_1$ ), and sensitivity ( $S_{i,j}$ ) was measured as the effects that a small change in each matrix element ( $a_{i,j}$ ) would have on the dominant eigenvalue (holding all other matrix elements constant). Sensitivity was calculated as:

$$S_{i,j} = \frac{\partial \lambda_1}{\partial a_{i,j}} = \frac{v_i w_j}{\mathbf{v}' \mathbf{w}}$$

where  $\mathbf{v}$  and  $\mathbf{w}$  are the left and right eigenvectors of the realized connectivity matrix, respectively, and the ' symbol indicates matrix transposition (Caswell 2001).  $\mathbf{w}$  is a vector representing the stable state distribution of relative abundances at each island, and  $\mathbf{v}$  is a vector describing the contribution that fish at each island make to future growth of the metapopulation. We also examined sensitivity of metapopulation growth to changes in lifetime egg production at each of the four islands. Because changes in egg production affect multiple matrix elements (entire columns in this case), we calculated these sensitivities by taking the Kronecker product of the sensitivity matrix and the connectivity matrix, and then summing each of the columns.

We note that although the dominant eigenvalue of the realized connectivity matrix is a density-independent measure of growth, it will provide a good summary of metapopulation growth under most circumstances. Using the eigenvalue to summarize growth would be unreliable only in rare cases where lifetime egg production is strongly density dependent in local populations that have a high degree of local retention (through direct retention of offspring and/or indirect retention of grand offspring and other descendants; Armsworth 2002). Realized rates of retention were very low in our study (see Table 2 in the main text), and density dependence in local populations of bicolor damselfish is not so strong that it immediately dampens any variation in growth. In fact, patterns of population growth and/or decline for some populations of this species have been observed to continue across multiple generations, despite

clear patterns of density dependence in demographic rates such as survival to maturation and per-capita fecundity (Hixon et al. 2012). It is important to note that density dependence is not incompatible with sustained patterns of population growth or decline. Moderate levels of density dependence will typically restrict, rather than prevent growth variation (reviewed by Caley et al. 1996). Under such circumstances, and especially when rates of local retention are low (as they are in our study), the dominant eigenvalue of the realized connectivity matrix can provide an accurate summary of metapopulation growth (Armsworth 2002).

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