

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 2×2 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_{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 (cm^2) by 215 eggs/ 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_{Searched} , which was known), and total area (A_{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 (~ 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 (1.02×10^{-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_{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_{Total} and calculated λ 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 ~ 0.60) and higher for adults (monthly survival for a 7 cm TL fish was ~ 0.85).

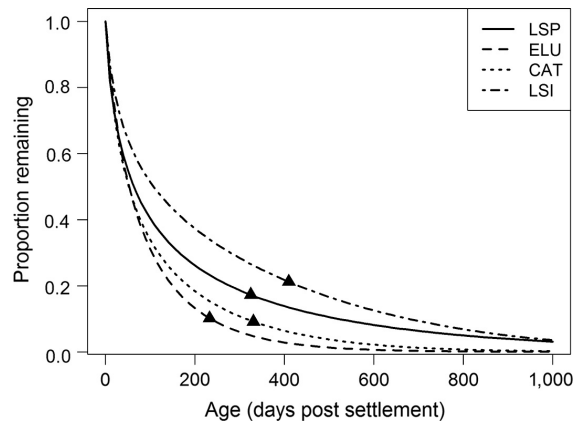


FIG. 1. Estimated age schedules of survivorship. Estimated time of maturation for each population is indicated by the solid triangles. LSP, the Exuma Cays Land and Sea Park; ELU, Eleuthera; CAT, Cat Island; LSI, Lee Stocking Island.

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

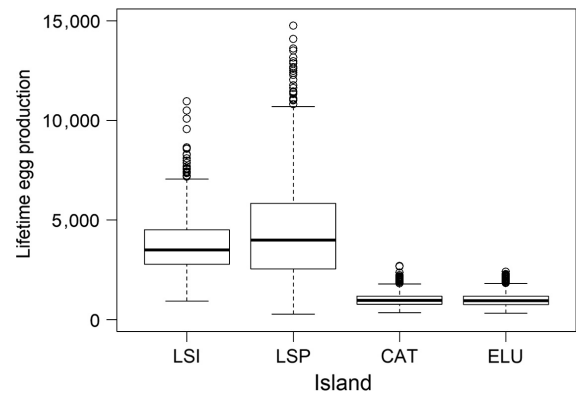


FIG. 2. Lifetime offspring production. Estimated number of eggs produced by an average, newly settled recruit at each island (i.e., each local population). Distributions were generated by a resampling procedure in which each of the parameters for the functions describing growth, survival, and reproduction 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 ≥ 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

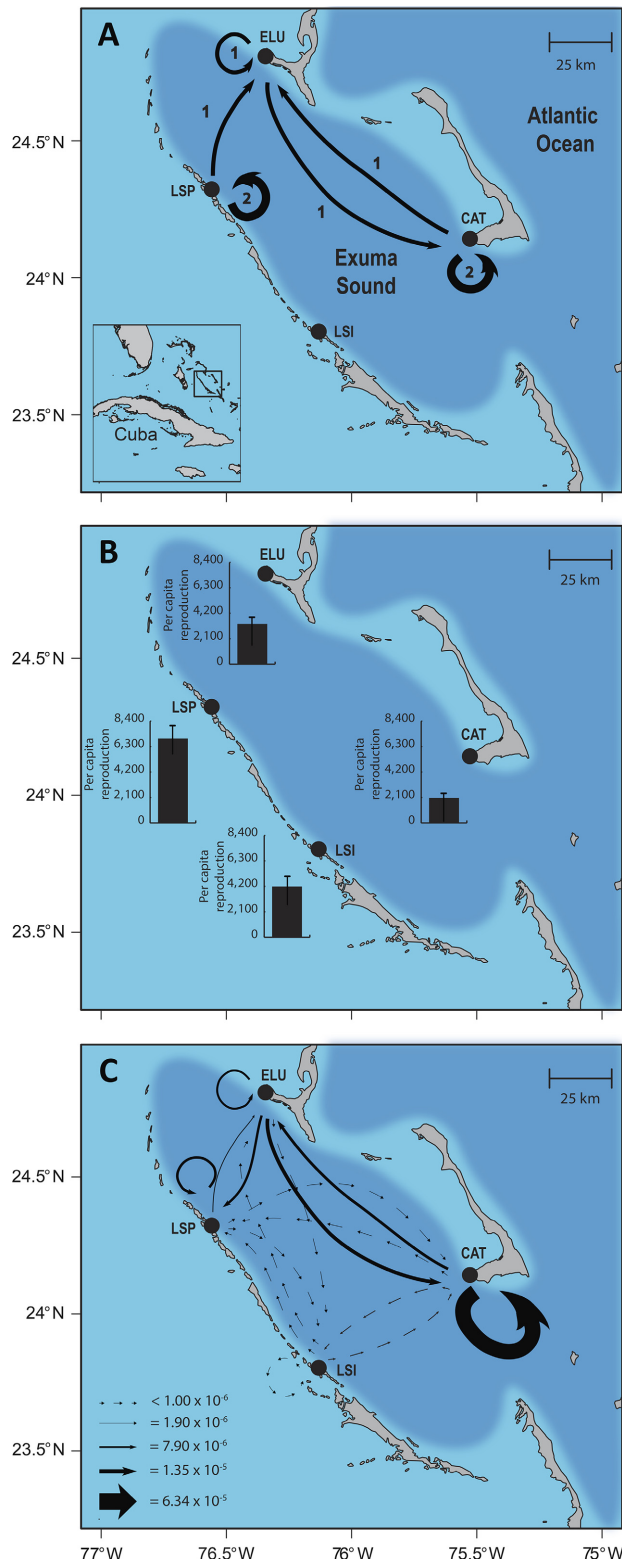


FIG. 3. Maps showing values of (A) detected larval connectivity, (B) per capita egg production, and (C) demographic connectivity (integrating A and B) among four local populations of bicolor damselfish in Exuma Sound, Bahamas: Eleuthera (ELU), the Exuma Cays Land and Sea Park (LSP), Cat Island (CAT), 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 ≥ 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 ~ 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	9.8×10^{-6} (1.10×10^{-6} , 3.20×10^{-5})	0 (0, 2.55×10^{-5})	0 (0, 2.72×10^{-5})	0 (0, 1.28×10^{-5})
To ELU	1.9×10^{-6} (2.00×10^{-7} , 1.79×10^{-5})	7.9×10^{-6} (1.00×10^{-6} , 5.91×10^{-5})	1.09×10^{-5} (1.60×10^{-6} , 6.12×10^{-5})	0 (0, 1.27×10^{-5})
To CAT	0 (0, 2.44×10^{-5})	1.39×10^{-5} (2.2×10^{-6} , 1.28×10^{-4})	6.34×10^{-5} (1.67×10^{-5} , 2.28×10^{-4})	0 (0, 3.38×10^{-5})
To LSI	0 (0, 1.65×10^{-5})	0 (0, 3.49×10^{-5})	0 (0, 4.29×10^{-5})	0 (0, 2.22×10^{-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 ~ 65 ha in area would experience sufficient demographic connectivity that the metapopulation would persist entirely on its own (λ 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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