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Local retention, dispersal and fluctuating connectivity among populations of a coral reef fish

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Abstract The persistence and resilience of marine populations in the face of disturbances is directly affected by connectivity among populations. Thus, understanding the magnitude and pattern of connections among populations and the temporal variation in these patterns is critical for the effective management and conservation of marine species. Despite recent advances in our understanding of marine connectivity, few empirical studies have directly measured the magnitude or pattern of connections among populations of marine fishes, and none have explicitly investigated temporal variation in demographic connectivity. We use genetic assignment tests to track the dispersal of 456 individual larval fishes to quantify the extent of connectivity, dispersal, self-recruitment and local retention within and among seven populations of a coral reef fish (*Stegastes partitus*) over a three-year period. We found that some larvae do disperse long distances (~200 km); however, self-recruitment was a regular phenomenon. Importantly, we found that dispersal distances, self-recruitment, local retention and the pattern of connectivity varied significantly among years. Our data highlight the unpredictable nature of connectivity, and underscore the need for more, temporally replicated, empirical measures of connectivity to inform management decisions.

Keywords Local retention · Self-recruitment · Dispersal kernel · Connectivity matrix · Metapopulation · Marine protected areas

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Introduction

Coastal marine fisheries and ecosystems are in global decline due to the increasing intensity and diversity of stresses in coastal waters (Hutchings 2000; Jackson et al. 2001). Marine protected areas (MPAs) have been advocated as one measure to facilitate continued ecosystem viability (Sale et al. 2005). However, the efficacy of MPAs as well as the persistence and resilience of marine populations in the face of disturbances in general are fundamentally linked to the scale of dispersal and the degree of connectivity among populations (Eckert 2003; Botsford et al. 2009). In addition, dispersal and connectivity drive population genetic differentiation and thus play key roles in the evolution of local adaptation (Bradbury et al. 2008; Walter et al. 2009).

The degree of temporal stability in larval dispersal connecting marine populations has not been empirically tested, yet temporal variability in dispersal and connectivity will determine predictability in population dynamics and will impact population genetic structure (Larson and Julian 1999; Selkoe et al. 2006; Hogan et al. 2010). In fact,

temporal changes in larval migration patterns have been implicated as a source of spatial and temporal patchiness in the genetic structure of marine populations (Selkoe et al. 2006; Hogan et al. 2010). Therefore, not only must we improve our understanding of larval dispersal pathways, local recruitment rates and population connectivity, we also need empirical estimates of the temporal component of variation in those variables for the effective management and conservation of marine populations (Sale et al. 2005; Levin 2006; Jones et al. 2007). It is logistically difficult to track the dispersal of small pelagic larvae in the marine environment, although technologies have improved in recent years such that connectivity studies are more feasible (Thorrold et al. 2002). Despite recent advances in the field of marine connectivity, relatively few empirical studies have measured the magnitude or pattern of contemporary connections among populations of marine fishes (Sale et al. 2005; Jones et al. 2009). In fact, most studies only estimate self-recruitment, the ratio of locally produced settlement to settlement from elsewhere (Jones et al. 1999, 2005; Swearer et al. 1999; Almany et al. 2007; Christie et al. 2010). Although self-recruitment is important, in order to assess population persistence we need estimates of local retention, the ratio of locally produced settlement to the total number of settlers locally produced, not self-recruitment (Botsford et al. 2009). This metric is much harder to estimate as it requires information about larval exchange among a network of populations. Few studies have tracked larval dispersal among populations (Miller and Shanks 2004; Becker et al. 2007; Planes et al. 2009; Shima and Swearer 2009); fewer still have empirically estimated temporal variation in dispersal (Miller and Shanks 2004); and none have empirically investigated the degree of temporal stability in connectivity among a network of populations.

Coral reef fishes live in spatially patchy reef environments where populations are connected primarily by pelagic larval dispersal via ocean currents (Sale 1980). The duration of the pelagic larval stage in coral reef fishes is typically weeks or months (Leis 1991), providing the opportunity for long-distance dispersal. Biophysical models have estimated that the spatial scale of connectivity among reefs in the Caribbean is on the order of tens to hundreds of kilometers (Cowen et al. 2006). Recent empirical studies have shown that reef fish larvae have the ability, and perhaps the propensity, to return to their natal reef following a residency in the pelagic environment (Jones et al. 2005; Almany et al. 2007); they also may act to minimize long-distance dispersal (Fisher and Bellwood 2003). Thus, local processes have the potential to contribute substantially to the demography of reef fish populations.

Several recent population-genetic studies of a common Caribbean coral reef fish, *Stegastes partitus* (bicolor damselfish), shed some light on the spatial and temporal scales of gene flow (i.e., historical connectivity) among populations. Only one of these studies investigates contemporary connectivity (Christie et al. 2010). Purcell et al. (2009) found weak population structuring across the Caribbean basin suggesting high levels of gene flow at the largest scale (thousands of kilometers). However, they did find evidence of more restricted gene flow (isolation by distance) in the Eastern Caribbean. Salas et al. (2010) showed weak genetic structuring within (hundreds of kilometers) and among ($\sim$1,000 km) regions in the Western Caribbean (Costa Rica–Panama and the Mesoamerican Barrier Reef System (MBRS), concluding that gene flow is significant within the two subregions, but likely restricted between subregions. At smaller spatial scales, Ospina-Guerrero et al. (2008) found genetic homogeneity among sites within the Columbian Caribbean ($\sim$400 km), suggesting high levels of gene flow at this scale. However, three studies found weak (Hepburn et al. 2009; Hogan et al. 2010) to strong (Villegas-Sanchez et al. 2010) genetic structuring at a similar scale in the MBRS, showing evidence of more restricted or variable gene flow. Christie et al. (2010) found direct evidence of larval retention (i.e., self-recruitment) in Bahamian populations of *S. partitus*, on a backdrop of high gene flow among sites ($\sim$250 km). Furthermore, two studies found that genetic structure among populations was temporally unstable at the scale of seasons (Hepburn et al. 2009) and years (Hogan et al. 2010), and this was attributed to fluctuations in connectivity among reefs (Hogan et al. 2010).

Despite recent advances, there are currently insufficient empirical data to make generalizations on expected patterns and temporal variation in connectivity among coral reefs, particularly for contemporary connectivity. Such generalizations would be valuable for validating and updating biophysical models that estimate general patterns of connectivity, and are used explicitly to design marine protected areas. Here, we empirically estimate the scale of larval dispersal, the level of self-recruitment and local retention within populations, and the spatial and temporal variation in contemporary connectivity among populations of the coral reef fish *S. partitus* at a spatial scale relevant to conservation and management. We use genetic assignment tests to track dispersal movements of individual larvae to assess connectivity among seven locations (reefs) in a $\sim$6,000 km^2 region of the Mesoamerican Barrier Reef System (MBRS) in the western Caribbean (Fig. 1). We sampled from seven sites in Belize and Mexico and we repeat the sampling over three years. Here we provide the first empirical estimates of temporal variation in local

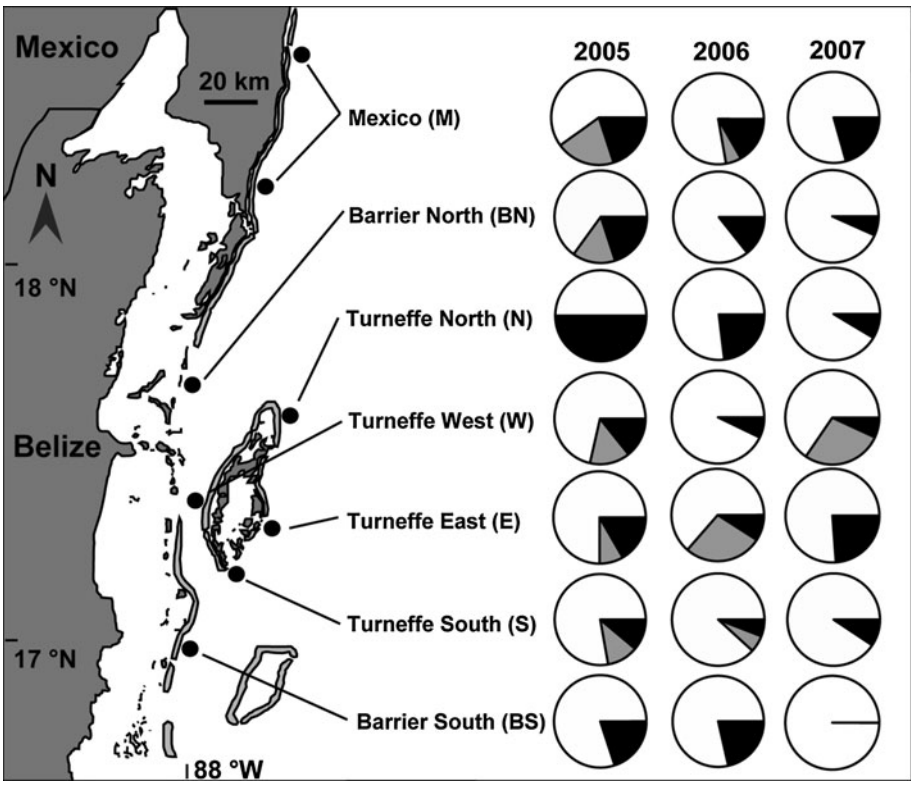

Fig. 1 Map of the sampling sites in the Mesoamerican barrier reef system with assignment results. The map shows sampling sites from Mexico (M), Belize Barrier Reef North (BN), Turneffe Atoll North (N), Turneffe Atoll West (W), Turneffe Atoll East (E), Turneffe Atoll South (S) and Belize Barrier Reef South (BS). *Pie charts* indicate the proportion of assignable juveniles collected at a given site in 2005, 2006 and 2007 that were assigned to another sampled site (*white*), self-assigned (*black*), or excluded from all possible sampled populations (*gray*)

retention and connectivity among a network of marine populations.

Methods

Study species

Stegastes partitus is a small territorial damselfish (Pomacentridae) that is common on reefs throughout the tropical Western Atlantic. Adults spawn demersally following a unimodal lunar cycle with year-round reproduction and seasonal reproductive peaks from April to November (Robertson et al. 1988). The males of the species provide parental care to the eggs; however, after hatching ($\sim$3.5 days), larvae enter the pelagic environment and the pelagic larval duration ranges between 24 and 40 days (Robertson et al. 1988; Wellington and Victor 1989). After settlement, the adults are sedentary, defending small feeding territories indefinitely (Myrberg 1972). This life history is ideal for connectivity studies because connectivity among reefs is determined exclusively by larval dispersal.

Field sampling

We sampled seven sites in the Mesoamerican barrier reef system in the spring months each year for 3 years. Sampling occurred from 10 June–5 July 2005, 19–29 April 2006 and 19 May–1 June 2007. At each site, approximately 100 adult (3.8–7 cm TL) and 50–100 recently settled juvenile (1.2–2.5 cm TL) *Stegastes partitus* were collected by scuba divers (Table S3). We sampled three sites along the Belize and Mexican Barrier Reef and four sites around Turneffe Atoll in Belize (Fig. 1). Due to logistical issues, the Mexican site sampled in 2005 could not be sampled in 2006, so a site was chosen further north for 2006 and 2007. All fish were collected from a site in a single day except at Turneffe East in 2005, where adults were collected over a two-week period and juveniles were collected in one day. Fin tissue was removed from each fish and preserved in RNA Later® for transport to the lab.

Genotyping

Genomic DNA was extracted from samples using a plate-based extraction method (Elphinstone et al. 2003), and genotyping was performed as follows (full details are described in Hogan et al. 2010). In brief, nine microsatellite loci were chosen from the literature (Williams et al. 2003; Thiessen and Heath 2007) and screened for suitability. Polymerase chain reactions (PCR) were then performed to amplify specific loci with fluorescent dye-labeled forward primers to generate labeled PCR amplicons for sizing. The sizes of the PCR products were estimated using a LiCor

4300 DNA analyzer with GeneImagIR 4.05 software (BD Biosciences Bioimaging).

Population genetic analyses

This study represents a novel re-analysis of previously published genotype data (Hogan et al. 2010). In this study, we focus on genetic assignment tests, and although we present basic genetic analyses here, a detailed analysis of the genetics of these populations can be found in Hogan et al. (2010). Assignment tests are used to track the dispersal of individual larvae among populations by assigning them to population-level genetic "fingerprints." Genotype data were separated into adult and juvenile populations for all three sampling seasons at each of the seven sampling sites. A fish was included in the genetic analyses if there was genotype data for at least six of the nine microsatellite loci. Exact tests for goodness of fit to Hardy–Weinberg equilibrium (HWE) using the Markov chain method (1,000 permutation burn-in followed by 100,000 permutations) for each locus within each population were performed in Arlequin v.3.11; 39 of 189 exact tests showed significant differences from HWE within adult samples after sequential Bonferroni correction (Table 1). Tests for linkage disequilibrium were performed on all populations in Genepop; approximately 2% of the tests showed significant linkage disequilibrium. Loci were tested for possible genotyping errors and molecular or biological phenomena that could explain deviations from HWE using MicroChecker v.2.2.3. Homozygote excesses were found at four of the nine loci, which explained deviations from HWE in some populations at these loci. MicroChecker results showed that homozygote excesses were not attributable to genotyping errors, but null alleles could not be ruled out; nor could a Wahlund effect due to mixing of individuals from sources with different allele frequencies. We do not account for null alleles in our analyses because it is unlikely that null alleles are driving these homozygote deficits. In this study, no locus deviated from HWE in more than 8 of 21 adult populations, and deviations from HWE were not consistent across years—evidence that null alleles are an unlikely cause of disequilibrium. A Wahlund effect is much more likely to be causing HW disequilibrium; in fact, a detailed study of our populations found strong evidence of a Wahlund effect driving deviations from HWE (Hogan et al. 2010). Furthermore, a previous study of *S. partitus* (Purcell et al. 2009) suggested homozygote excesses in their populations were likely attributable to a Wahlund effect, but they ruled it out only because genetic differentiation among sites was low. However, it has been shown that even weakly divergent populations can experience a Wahlund effect (Johnson and Black 1984; Selkoe et al. 2006; Hogan et al. 2010). Regardless, Carlsson (2008) has shown that null alleles have only a weak effect on genetic assignment tests, and they result in a loss of assignment power. Our method of exclusion (see below) is robust to this effect by excluding individuals that have poor assignment power. Finally, *F*-statistics were calculated to quantify the extent of genetic heterogeneity among all populations within each year using MSA 4.05. Global F_{ST} values were low for each year (2005: 0.007, 2006: 0.001, 2007: 0.009), but were significantly different than zero in 2005 and 2007. Pair-wise (among sampling sites, within year) F_{ST} values ranged between 0.001 and 0.020 (Table S4).

Table 1 Summary statistics for nine microsatellite markers comparing adult populations of *Stegastes partitus* over three years ($n = 21$ populations)

Locus	Global F_{ST}	HWE (%)	Ho	Na
*Sp*GATA$_{40}$	0.001	38.0	0.84	31.1
*Sp*AAT$_{40}$	0.002	0.0	0.88	16.6
*Sp*AAC$_{44}$	0.044	28.6	0.34	11.1
*Sp*AAC$_{33}$	0.002	28.6	0.77	17.0
*Sp*TG$_{16}$	0.006	28.6	0.87	29.3
*Sp*GGA$_{7}$	0.025	4.8	0.55	6.1
*Sp*TG$_{53}$	0.002	9.5	0.88	35.4
*Sp*TG$_{13}$	0.018	14.3	0.64	8.9
*Sp*GT$_{10}$	0.003	4.8	0.82	17.3

HWE Percentage of adult populations that deviated from Hardy–Weinberg equilibrium at a particular locus (all years pooled). *Ho* Average heterozygosity by locus across all adult samples. *Na* Average number of alleles by locus across all adult samples

Genotype assignment method

Juveniles were assigned to putative adult populations based on their multi-locus genotype probabilities using a two-step method. First, a Bayesian assignment method was used (Rannala and Mountain 1997), with probability estimates generated by 10,000 iterations of Monte Carlo re-sampling using a published algorithm (Paetkau et al. 2004) in Geneclass v.2.0. Second, a rank-based assignment method was applied where individuals are assigned based on their negative log-likelihood of belonging to one population relative to the other source populations (Rannala and Mountain 1997). Individuals were considered to be assigned when they met two criteria:

1. They must be assigned to at least one source population with a probability of >85% in the first Monte Carlo based assignment procedure (threshold determined in a sensitivity analysis described below). Individuals with a <5% probability of belonging to any site were excluded from belonging to any of the

source populations, and those between 5% and the threshold value (85%) were considered unassigned.

2. The individuals that met the 85% threshold in the first step were then assessed using the rank-based method. Individuals were assigned to the source population if the likelihood of assignment to the highest ranked source population was 50% greater than the likelihood of assignment to the next highest ranked population.

Ten independent iterations of the assignment tests were conducted, and only individuals that were assigned to the same site in a majority of these iterations were considered successfully assigned individuals. This procedure further increased the stringency of assignment and eliminated individuals assigned to more than one potential source site. Our analysis results in all juvenile fish being classified as (a) successfully assigned, (b) successfully excluded from all sites, or (c) unassignable with any confidence. The removal from further analysis of juveniles that failed to assign should not create a biologically meaningful bias in our dispersal and connectivity data. A biological bias could arise if there are certain genotypes that are prone to different dispersal modes (i.e., greater or lesser dispersal distance) and if certain genotypes are preferentially removed by the analysis. However, in a previous study, we found that our genetic markers are neutral to selection in the populations studied here (Hogan et al. 2010), and it is unlikely that biologically meaningful biases exist among our assigned juveniles (relative to the sampled population). Furthermore, the sample size of assignable juveniles ($n = 453$) remains large, and thus we expect that our dispersal estimates are robust and representative of the sampled populations.

Assignment sensitivity analysis

We used an assignment sensitivity analysis to objectively determine the threshold of assignment stringency that we used in the first step of our assignment analysis. Because of the low-level genetic differentiation among our sites and across the entire Western Caribbean (Purcell et al. 2009), there are likely to be errors in the assignment of some juveniles, especially those with common genotypes. We used an information criterion to set an assignment threshold to reduce the number of erroneous juvenile assignments and at the same time to maximize sample size to increase statistical power. We assigned only those juveniles that met the determined threshold of assignment stringency, those that have high levels of certainty in their assignment. First we ran the assignment tests (as described above) using adult and juvenile samples from 2007 at ten different levels of assignment stringency (thresholds ranging from 5 to 95%). Next we plotted the percentage of juveniles assigned at each threshold (Fig. S1). We found a trend toward a general decline in the percent of juveniles assigned as assignment stringency increases (Fig. S1). Next we plotted the rate of change in the percent of juveniles assigned between successive thresholds (Fig. S2). This clearly shows where the greatest difference in percent assignment between successive thresholds occurs. The greatest difference in the percent of juveniles included in the assignment analysis occurred between the 95% threshold and the 85% threshold. This difference is more than double that of any other difference between successive thresholds. Therefore, the 85% assignment threshold provides the greatest balance between stringency of assignment and sample size.

Dispersal distance analysis

We calculated expected, random distributions of dispersal distance (assuming straight-line paths between pairs of sampling sites) to test whether the observed distributions were different from those expected due to random dispersal. Because the distances between sampling sites were not evenly distributed among distance categories (bins), we calculated the expected frequencies of dispersal events based on the proportion of possible dispersal pathways between sampled sites in each distance bin. We compared observed dispersal distance distributions to the expected distribution using Kolmogorov–Smirnov tests (Fig. 2b).

Dispersal direction analysis

We calculated the net dispersal direction vector in each year to test for directionality in dispersal. Each individual dispersal event was assigned to a direction bin (in 22.5° increments). Because the directions between sampling sites were not evenly distributed among direction bins, we calculated the expected frequencies of dispersal events based on the proportion of possible dispersal pathways between sampled sites in each direction bin (assuming straight-line dispersal). Directional frequencies were corrected in the same manner as for distance (above), and net dispersal direction was then calculated as the sum of all corrected dispersal directions (red arrows; Fig. 2c).

Analysis of randomized adult populations

Using the 2007 data, we created 10 randomized adult populations in order to test the validity of the assignments made by the software program Geneclass 2.0. Adult multilocus genotypes were preserved, but they were assigned randomly among our seven sampling sites, preserving the original sample sizes. The juvenile genotypes were then assigned to the randomized genotype "populations"

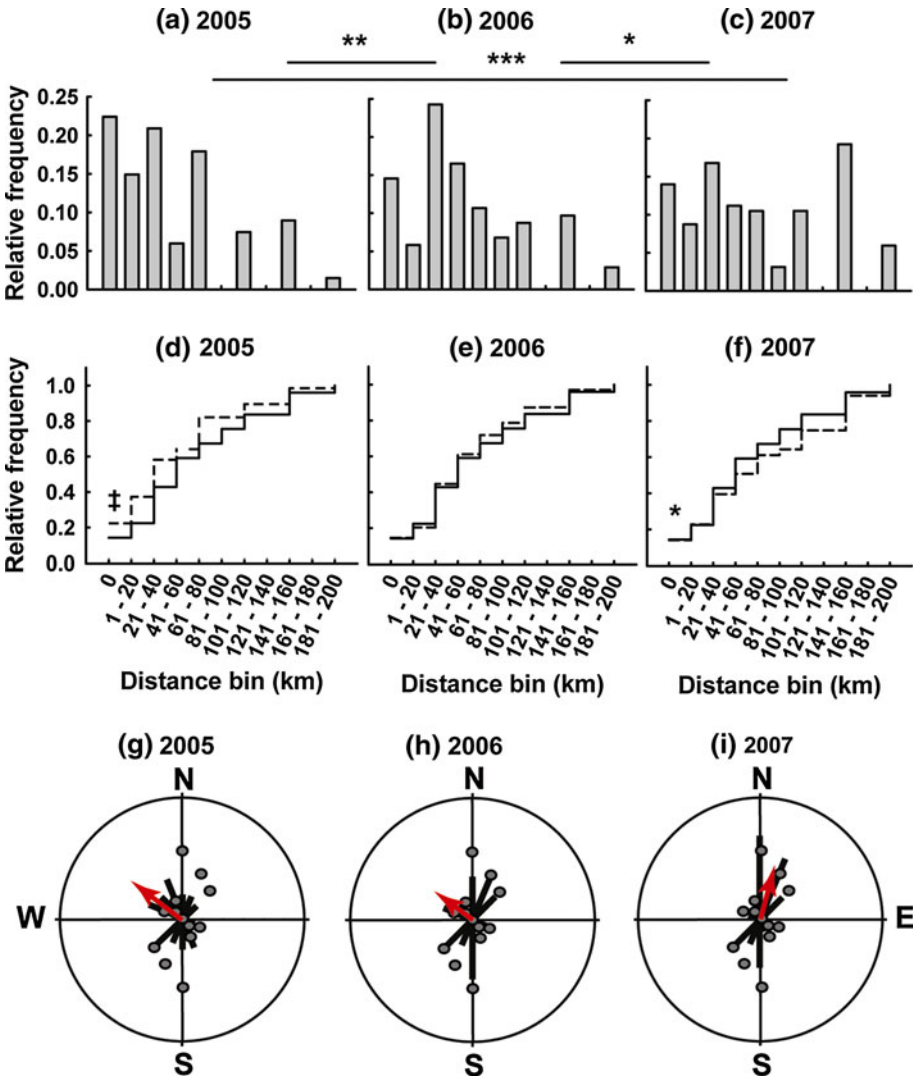

Fig. 2 Spatial and temporal dispersal within the Mesoamerican Barrier Reef System. All data for a given year are presented in the same column. **a–c** Frequency distributions of dispersal distances. Significant differences among years in distribution were determined by Kolmogorov–Smirnov tests ($k = 11$, $n = 99$) and are shown as *bars above the graphs* ($^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$). **d–f** Cumulative frequency distributions of expected, random dispersal (*solid line*) and observed dispersal (*dashed line*) with increasing dispersal distance. Significant differences between observed and random distributions were determined by Kolmogorov–Smirnov tests ($k_{all} = 11$, $n_{2005} = 67$; $n_{2006} = 103$; $n_{2007} = 286$) and are indicated on the figure ($^{*}P < 0.05$, ‡ power analysis indicates significant difference after small 8% increase in sample size). **g–i** Frequency distributions of dispersal directions (assuming straight line dispersal). *Gray dots* indicate the null expected frequencies based on the distribution of our sampling sites. *Red arrows* indicate the net direction of dispersal after correction for biases in dispersal among directional categories

following the assignment method described above. We compared the dispersal kernels generated from these ten randomizations with the results yielded by the actual data. To test for a statistical difference between random assignment and actual assignment results, we compared chi-squared distributions between random kernels and the actual data. The chi-squared distribution for the ten random kernels was generated by comparing each kernel to all other random kernels and generating chi-squared values for each comparison. Next we compared the actual dispersal kernel to each of the ten random kernels, generating a chi-squared value for each comparison. We then compared the two chi-squared distributions to each other to test for a difference between random and actual assignment results. Both chi-squared distributions were approximately normal (i.e., skew and kurtosis $-1 > x < 1$), and the two distributions did not overlap at their 95% confidence intervals, so the actual assignment results were significantly different from results generated by assignment to randomly generated adult populations.

Results

Neutral microsatellite DNA markers were used to characterize adult (source) populations, and genotype assignment analyses were used to link individual juveniles back to their likely natal reefs. We genotyped 1,828 adult fishes from seven reefs, and re-sampled every year for three years. The average pair-wise F_{ST} value among adult populations was 0.005, and the maximum pair-wise F_{ST} value was 0.02 over the three years of sampling. Of the 1,291 juvenile samples collected and genotyped over the three years of sampling, 456 (35%) were assigned to a particular sampled site with high confidence. Of the successfully assigned juveniles, 70 (15%) were assigned back to the site at which they were caught (i.e., "returned home"), and the remaining 386 (85%) juveniles were assigned to one of the other sampled sites. The degree of self-recruitment (the ratio of juveniles returning home to juveniles coming from other source reefs) varied widely both among sites and across time (Fig. 1); however, the average self-recruitment rate across the region over all years was 15%, and was relatively consistent among the three years (2005: 22%; 2006: 15%; 2007: 14%; Fig. 2a). By comparison, the degree of local retention (the ratio of juveniles produced at a site that returned home to the total number of juveniles produced at that site) was on average higher than self-recruitment (21%), but yearly estimates were similar to estimates of self-recruitment (2005: 35%; 2006: 16%; 2007: 13%), albeit with notably higher local retention in 2005. When we enlarged our spatial scale from the site level, we found that an average of 65% of all assignable juveniles produced on Turneffe Atoll recruited back to populations on Turneffe over the three years of sampling, but local retention at this scale varied widely among years (2005: 84%; 2006: 70%; 2007: 58%). We also found that 1.7% ($n = 22$) of all juveniles sampled were excluded from all sampled sites with high confidence.

The distribution of the calculated dispersal distances (dispersal kernels) differed significantly among sampling years (Fig. 2), while the relative contribution of each source population to the recruitment at a given site changed dramatically over time (Fig. 3a). If there were predictable patterns of connectivity from year to year, we would expect to see a positive relationship in the strength of interaction between site pairs from one year to the next. However, we found that there was no predictability in the larval dispersal pathways from one year to the next (Fig. 3b). Also, 18% of the variation in self-recruitment was partitioned among years, and 26% was explained by the site-by-year interaction (log-linear analysis: Δchi-squared: $df_{\text{years}} = 2$, $\Delta\chi^2 = 99.9$, $p < 0.0001$; $df_{\text{site} \times \text{year}} = 12$, $\Delta\chi^2 = 22.3$, $p = 0.051$).

As a species with a larval duration of approximately 30 days, *Stegastes partitus* has the potential for long-distance dispersal. In our system, dispersing fish, sampled over the three years, traveled an average of 77 km (SEM ± 6 km). The majority of assignable juveniles recruited within a radius of 60 km or less around the natal reef in each year (Fig. 2a). Five percent ($n = 21$) of assignable larvae were shown to have traveled the full extent of our sampling region (187 km) during their larval lives. Furthermore, there was generally no decline in the strength of connectivity among sites with distance from the source (Fig. 3c).

We used the distributions of dispersal distances (dispersal kernels) and dispersal direction to test for patterns within and across the sample years. We test these patterns against null model expectations. The mean dispersal kernel in 2007 was significantly different from random expectation (Fig. 2b), and a power analysis revealed that, with only a small (8%) increase in sample size, the 2005 distribution was also significant (Fig. 2b). Deviation from random expectation in 2005 was driven by greater than expected short-distance recruitment, and in 2007 differences were driven by lower than expected levels of recruitment to middle distances (Fig. 2b). The 2006 distribution was not significantly different from random. When our results were compared to those of assignments to randomized adult populations, the observed dispersal kernels differed significantly from those generated from randomized trials (see "Methods"). Furthermore, the direction of dispersal was also not random, but rather biased in a northwesterly direction in both 2005 and 2006 and in a north-northeasterly direction in 2007 (Fig. 2c). In 2006 the overall directionality of dispersal was weak.

Discussion

Marine protected areas typically have two primary objectives: to conserve biodiversity and to enhance fishery yields. For both ends, quantified patterns of connectivity, estimates of self-recruitment and local retention, and measures of dispersal distance are important for determining the size and spacing of reserves that will maximize their effectiveness (Fogarty and Botsford 2007; Jones et al. 2007). Here we used highly polymorphic microsatellite markers and genetic assignment tests to identify natal sources of recently dispersed larvae of the coral reef fish *Stegastes partitus*.

We were able to identify or exclude natal sources for approximately 35% of all fishes sampled with a high degree of certainty. Our results show that self-recruitment occurs consistently at appreciable levels among natural populations of a common reef fish, the bicolor damselfish. Our data support the view that self-recruitment is a common and regular phenomenon in natural coral reef fish populations (Jones et al. 2005; Almany et al. 2007; Christie

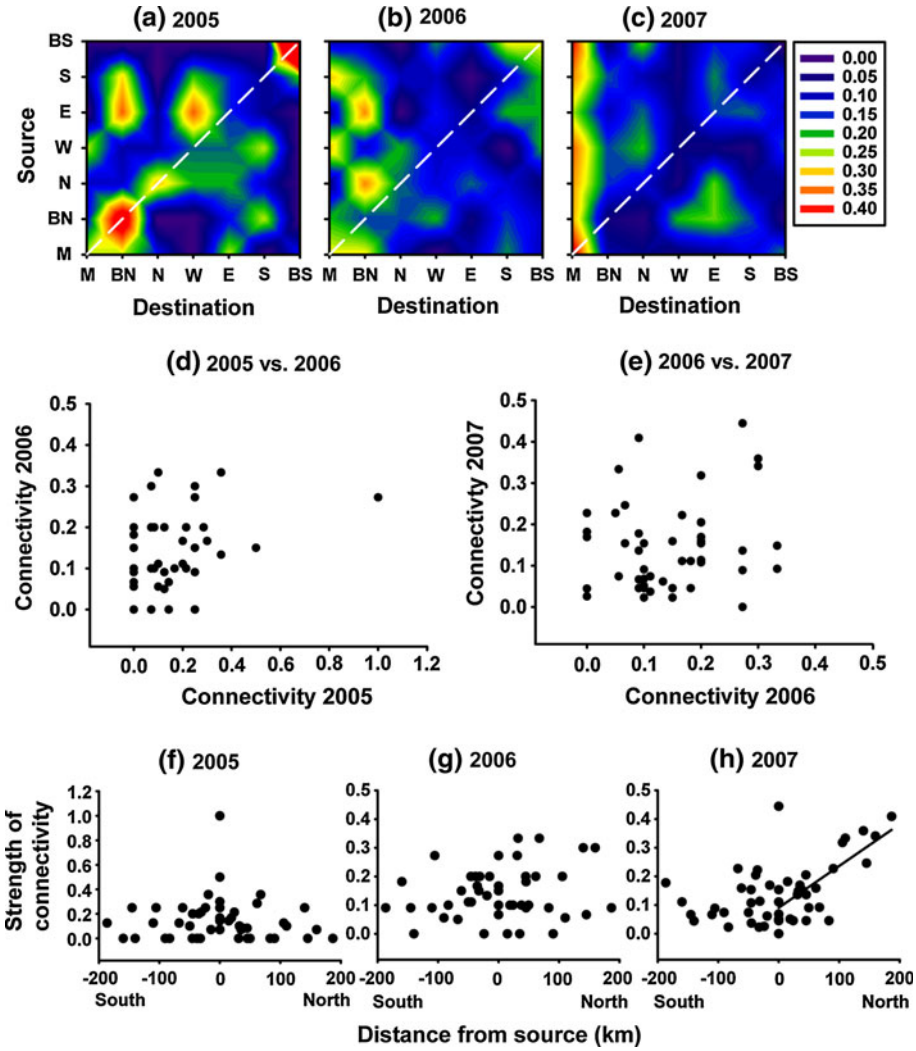

Fig. 3 Spatial and temporal connectivity and source–destination interactions. **a–c** Matrices of source–destination dynamics; *contours* indicate proportions of juveniles collected at a destination site (*columns*) that were assigned to a particular source site (*rows*). The proportions in each row add to give 1. The *diagonal dashed line* indicates local retention at a particular site. *Axis site codes* are the same as the codes in Fig. 1. **d, e** Change over time in source–destination interactions from one study year to the next. Plotted values are the strength of the source–destination connectivity measured as the proportion of juveniles produced at a source site (in a given year) that were collected at a particular destination population. If there was temporal consistency in connectivity we would expect to see a positive relationship between the source–destination interactions in consecutive years. **f–h** Variation in the strength of connectivity with distance from the source population (origin). The strength of connectivity is measured as the proportion of individuals produced at a particular source population. Positive distances from the origin are in a northerly direction and negative distances are in a southerly direction. The null expectation is an isolation-by-distance model whereby the strength of connectivity among sites declines with increasing distance. The *solid line* **(h)** indicates a relationship with a slope that is significantly different from zero (2007 North: $r^2 = 0.41$, $F = 18.2$, $P < 0.01$). There were no other significant relationships with geographic distance **(f, g)**

et al. 2010). Previous studies have estimated that self-recruitment to populations of coral reef fishes ranges from 15 to 60% for a single reef (Jones et al. 1999, 2005; Swearer et al. 1999; Almany et al. 2007). Our estimates range from 0 to 50% at individual reefs, and the average level of self-recruitment is 15%. However, spatial and temporal variability at the individual reef level underscores the unpredictability of self-recruitment at small scales. Therefore, spatially and temporally replicated estimates of self-recruitment are necessary to capture this variability.

By comparison, the levels of local retention at the site level were similar to levels of self-recruitment, albeit higher on average in 2005. Local retention is an estimate of the demographic independence of populations. If local retention is high, then the population is less reliant on larval subsidies from other populations, while self-recruitment is not explicitly an estimate of demographic independence. Therefore, it is interesting that our estimates of self-recruitment and local retention are similar, because this suggests that self-recruitment might be a good

estimator of local retention. As we scale up from the site level, we find that 65% of larvae produced at sites within Turneffe Atoll returned to populations in Turneffe. While the level of local retention reported here is not high enough to drive isolation (and genetic divergence) at the site scales, our results show that local retention plays a significant role in the replenishment of these populations, and that demographic independence increases with spatial scale. However, our estimates of local retention varied among years at both the site and atoll scales, suggesting that the influence of recruitment subsidies from neighboring populations and the level of demographic independence of populations vary temporally.

We found that the average dispersing larva traveled ~77 km from the natal reef within this study region. However, the strength of connectivity between site pairs did not decline with distance, suggesting that larvae may disperse further than the boundaries of our sampling area. The 77 km distance found here is a conservative estimate of the average dispersal distance of larvae. In fact, a small percentage of the juveniles sampled (1.7%) were excluded from all possible sampling sites, suggesting that these fish were perhaps spawned in unsampled populations with markedly different genetic structure than any of our sampled populations, perhaps dispersing from some distant location. Long-distance dispersers may have a significant impact on genetic structure, acting to homogenize population structure over large geographic areas (Wright 1931). This is the case for *Stegastes partitus*, which shows weak genetic differentiation across the entire Caribbean basin (Purcell et al. 2009).

Our results suggest that significant demographic connectivity can occur at a spatial scale of ~200 km, and we found no evidence of a decline in the strength of connectivity with distance from the source population. Therefore, populations within the boundaries of a marine reserve can, perhaps, provide recruitment subsidies to areas as distant as ~200 km or greater from the reserve. Generally, the spatial scale of demographic connectivity in this system appears to match predictions from hydrodynamic models (Cowen et al. 2006) and recent empirical data (Becker et al. 2007; Planes et al. 2009) which suggest that populations are likely to receive significant larval inputs primarily from sources spaced less than 100 km away. The observed dispersal directions also appear to match model predictions. In 2005 and 2006, dispersal directions reflected the average prevailing currents in this region during the spring months (Tang et al. 2006; Soto et al. 2009). The variation from this pattern in 2007 likely reflects variability in regional current patterns not captured by models that average current patterns.

It has been shown in studies of natural and simulated populations that genetic assignment tests can be highly accurate in identifying source populations (Berry et al. 2004; Waples and Gaggiotti 2006). Assignment accuracy is related to the migration rate, and as a correlate, the genetic differentiation between subpopulations. The higher the migration rate between subpopulations, the more genetically similar those populations become, and the less accurate assignment will be (Berry et al. 2004; Waples and Gaggiotti 2006). However, studies have shown that even at quite low levels of differentiation ($F_{ST} \approx 0.01$–0.02), similar to those found among some of our populations, assignment tests can be quite accurate (Berry et al. 2004; Waples and Gaggiotti 2006). Furthermore, using many highly polymorphic loci and applying stringent threshold criteria to the assignment tests (as we have done here) reduces the percentage of incorrect assignments and improves assignment accuracy (Bjornstad and Roed 2002; Berry et al. 2004; Waples and Gaggiotti 2006). Also, the accuracy of assignments could be reduced if the allele frequency distributions of unsampled populations are very similar to one or more of our sampled populations, causing larvae to be falsely assigned to a site they did not actually come from. It is not logistically possible to sample all potential source populations for a marine fish such as *S. partitus*, which is very abundant and broadly distributed throughout the Caribbean. However, recent studies have shown that it is very unlikely that unsampled populations would have the same allele frequency distribution as one of our sites. A recent study of our populations showed that there were significant differences in allele frequency distributions among all of our sites, and weak but significant levels of genetic differentiation (Hogan et al. 2010). Other studies support this, showing weak to strong genetic differentiation among populations of *S. partitus* in the MRBS region (Hepburn et al. 2009; Salas et al. 2010; Villegas-Sanchez et al. 2010). Furthermore, our exclusion-assignment procedure is highly stringent and excludes individuals that have very common genotypes (those more likely to cause a false assignment). Finally, if our assignments were erroneous due to low assignment power, the patterns of the assignments would be random (Waples and Gaggiotti 2006), but we show that our patterns are significantly different from that expected at random. Overall, we cannot measure the effect of unsampled sites on assignment accuracy, and we acknowledge that some assignment errors are likely. However, we argue that this assignment procedure is highly stringent and robust, and that the overall patterns found are real.

The technique used here can be very useful for obtaining temporally replicated empirical estimates of connectivity for many intractable species—a task that will be necessary to validate predictive models of connectivity and ultimately provide general connectivity information for better marine management practices. We found that dispersal distance

distributions, dispersal directions, and the patterns of connectivity among sites were not stable through time. The unstable temporal pattern of connectivity indicates that consistent source–sink patterns do not exist for this species in this region. Given the nature of the temporal variability in connectivity, our results suggest that models estimating connectivity should match directly with the time frames of empirical studies to get the best validation of these models.

Temporal variability in connectivity has implications for the management and conservation of marine species. Variable connectivity can increase instability of population genetic structure (Hedgecock 1994; Larson and Julian 1999; Selkoe et al. 2006; Hogan et al. 2010). Furthermore, variability in source–sink interactions can act to stabilize metapopulations and prevent the extinction of local populations (Holland and Hastings 2008). Our results highlight the need for temporal connectivity data in other marine species, and emphasize the need for modeling studies to explore the effects of temporal variability in dispersal (Botsford et al. 2009). If temporal variability in the pattern and extent of connectivity is found to be a common phenomenon among reef fish populations, connectivity data from several years would be necessary for confidence in any source–sink patterns, especially when using this information explicitly for marine reserve network design.

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