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Uniting paradigms of connectivity in marine ecology

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Abstract. The connectivity of marine organisms among habitat patches has been dominated by two independent paradigms with distinct conservation strategies. One paradigm is the dispersal of larvae on ocean currents, which suggests networks of marine reserves. The other is the demersal migration of animals from nursery to adult habitats, requiring the conservation of connected ecosystem corridors. Here, we suggest that a common driver, wave exposure, links larval and demersal connectivity across the seascape. To study the effect of linked connectivities on fish abundance at reefs, we parameterize a demographic model for The Bahamas seascape using maps of habitats, empirically forced models of wave exposure and spatially realistic three-dimensional hydrological models of larval dispersal. The integrated empirical-modeling approach enabled us to study linked connectivity on a scale not currently possible by purely empirical studies. We find sheltered environments not only provide greater nursery habitat for juvenile fish but larvae spawned on adjacent reefs have higher retention, thereby creating a synergistic increase in fish abundance. Uniting connectivity paradigms to consider all life stages simultaneously can help explain the evolution of nursery habitat use and simplifies conservation advice: Reserves in sheltered environments have desirable characteristics for biodiversity conservation and can support local fisheries through adult spillover.

Key words: coral reef fish; larval dispersal; mangroves; marine protected area; migration; nursery habitat; seagrass; waves.

INTRODUCTION

The persistence of many species depends on individuals successfully migrating among multiple, connected, patches or habitats (Sale et al. 2005, Hastings and Botsford 2006). Connectivity has become a defining characteristic of marine ecosystems (Carr et al. 2003), where much of the science has blossomed (Roberts 1997, Cowen et al. 2006). Studies of connectivity have followed two paradigms: dispersal of larvae in the pelagic environment before they settle into a demersal stage (Cowen et al. 2006, Almany et al. 2007), and the ontogenetic migration of demersal juveniles from nurseries to adult habitats (Nagelkerken et al. 2000a, Mumby et al. 2004). Although each paradigm centers on a consecutive life stage, both fields of research have developed independently and led to fundamentally different conservation strategies: stratification of reserves in light of larval connectivity (Botsford et al. 2001) vs. connecting corridors of adjacent habitats to maintain ontogenetic migrations (Beger et al.

2010). However, abundance of adult fish depends both on the supply of larvae (Armsworth 2002, Hastings and Botsford 2006, Hufnagl et al. 2013), and the proximity of reefs to nursery habitats (Mumby et al. 2004, Hufnagl et al. 2013, Huijbers et al. 2013). Processes that facilitated linkages between larval and nursery connectivity could therefore have a considerable effect on the population dynamics of many marine species.

Uniting the two paradigms with a common driver that links larval dispersal to ontogenetic migrations could have important implications for conserving fish species and inform on the evolution of nursery habitat use. If larval and demersal migration are linked, the placement of marine reserves could take advantages of these linkages by identifying places where abundances are likely to be enhanced. Linking life-stages is also important for understanding the evolution of migratory life-histories. Evolutionary questions about nursery habitat use have tended to focus on the ecological benefits of its use in early ontogeny such as refuge from predation (Laegdsgaard and Johnson 2001), implicitly assuming that larval supply does not regulate the benefits of nurseries to fish species. The long larval phase of many fish, upward of a month for

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many species, seems inconsistent with the evolution of nursery habitat use, because nursery habitats are patchily distributed (Nagelkerken et al. 2008, Hufnagl et al. 2013), and longer larval phases are more likely to see larvae dispersed away from connected demersal habitats.

Here, we argue that the two connectivity paradigms are united by a common driver, exposure to wind and waves, which links larval dispersal to demersal migrations. We use tropical coral reef fish, which have become a model system to study both forms of connectivity (Swearer et al. 1999, Mumby et al. 2004, Cowen et al. 2006, Almany et al. 2007). Following this precedent, we hypothesize that exposure to wind and waves creates a direct coupling between the dispersal of reef fish larvae and the opportunity for juveniles to utilize mangrove nurseries, consequently benefitting from a low predation environment prior to undertaking an ontogenetic migration to adult habitats (Laegdsgaard and Johnson 2001). Specifically, we test the following hypotheses:

H_1 : Reefs in sheltered locations are less likely to experience strong directional (advective) currents and we predict that the dispersal of larvae will be relatively limited, implying higher local retention (Fig. 1).

H_2 : Sheltered conditions are conducive to the establishment of mangroves and dense seagrass beds in carbonate environments (Woodroffe 1990, Saunders et al. 2014), so we predict that reefs in sheltered conditions will have greater access to fish nursery habitats.

H_3 : Taking H_1 and H_2 together, we predict that larval retention and access to nursery habitats are positively correlated in space because of the codependence on wave exposure (Fig. 1).

H_4 : Finally, we predict that a coupling of larval and demersal connectivity will enrich fish biomasses on reefs.

MATERIALS AND METHODS

Study region

We test our hypotheses using spatial data and models from The Bahamas archipelago because it is one of the largest reef systems in the Atlantic, has among the highest range of wave exposures in the wider Caribbean (Chollett et al. 2012), and a broad range of nursery habitat availability that has been surveyed extensively (Harborne et al. 2008; Fig. 2). Further, The Bahamas is a conservative location to test our hypotheses because tidal circulation is strong, making circulation even less dependent on wave exposure as it is in micro-tidal areas of the western Caribbean (Kjerfve 1981). The region has also been relatively free from mangrove clearing, so the distribution of mangrove habitats is likely unaffected by transient dynamics, such as dispersal limitation. The main driver of mangrove distributions is availability of soft sediment habitat in sheltered areas (Woodroffe 1990). Further, extensive mangrove forests allow us to examine natural patterns of exposure with mangrove to reef connectivity. Nursery and larval connectivity have also been widely studied in the Caribbean (Cowen et al. 2006, Harborne et al. 2008), and can be easily parameterized for the Bahamas. We used a series of data sets and models to test each hypothesis in the Bahamas region.

To test hypotheses 1–3, we combine maps of mangrove, seagrass, and coral reef habitats from The Bahamas seascape with empirically forced physical models of wave exposure and larval dispersal. Taking the estimates of connectivity derived from testing hypotheses 1–3, we parameterize a life-history model of fish migrations, to make predictions about how adult populations will respond to linkages between larval and ontogenetic

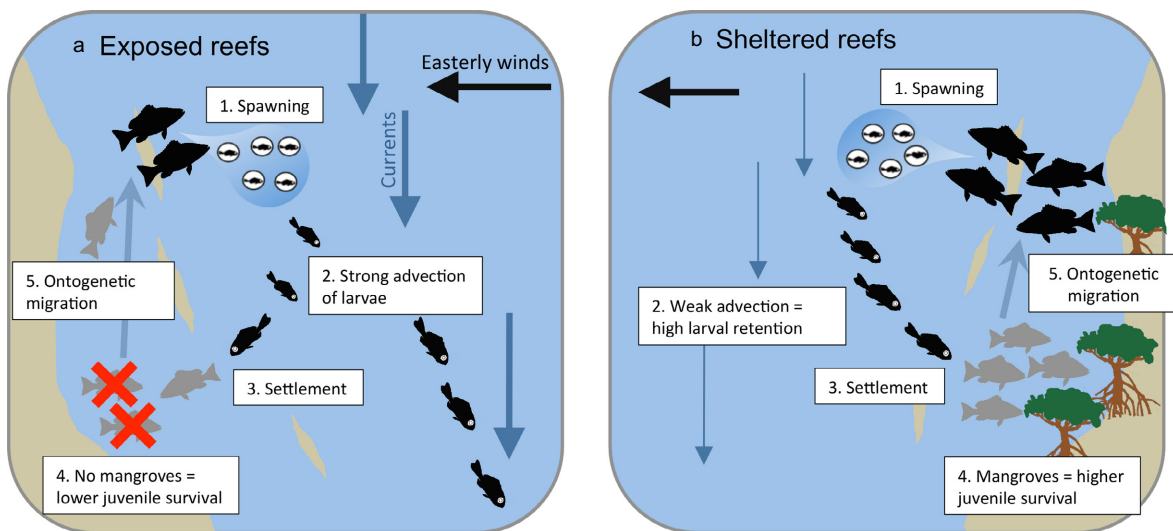


FIG. 1. Hypothesized linkage between larval and ontogenetic migrations. (a) Exposed spawning sites with high advection and no mangroves and (b) sheltered spawning sites with little advection so larvae are retained near mangroves.

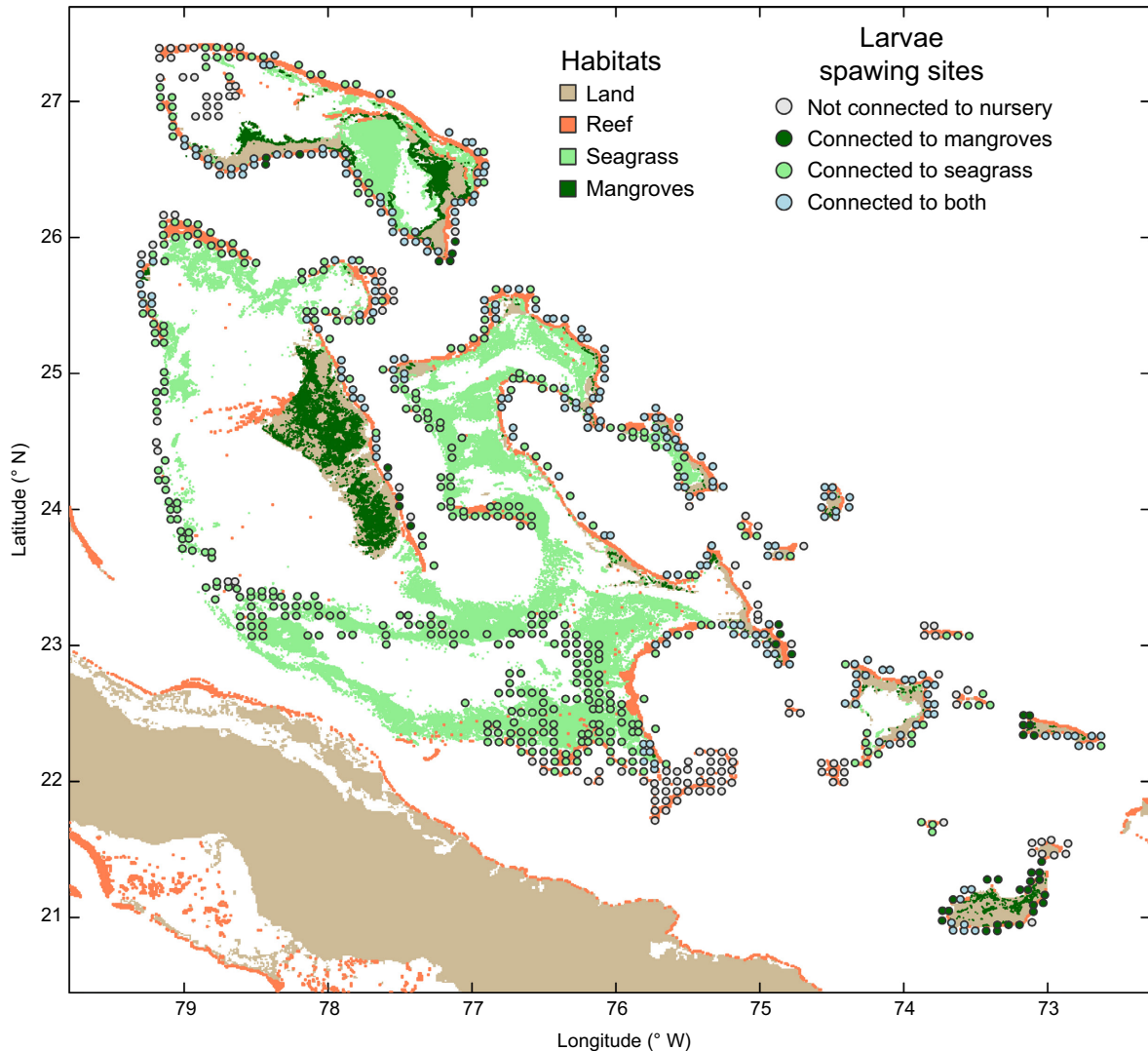


FIG. 2. The study region showing the distribution of seagrass, mangrove, and reef habitats, and larval production sites for the larval model.

connectivity. The approach combines habitat maps with empirically forced models so that analysis can be achieved on a larger scale than would be possible with purely empirical data.

Hypothesis 1: Local retention is higher when exposure is lower

To test whether local retention (Paris and Cowen 2004) is in fact higher in sheltered environments, we used a high-resolution three-dimensional model of larval dispersal (Cowen et al. [2006], updated with larval behaviors in Paris et al. [2007]) parameterized for reef fish with three sets of life history traits: a species with shallow vertical migration of larvae and a maximum planktonic larval duration (PLD) of 47 d, a species with deep vertical migration of larvae and a PLD of 51d, and a species with

deep vertical migration of larvae and a PLD of 78 d. The three species represent species that benefit from mangrove and seagrass nurseries when they are available such as, a snapper (family Lutjanidae), the striped parrotfish (*Scarus iseri*), and the doctorfish (*Acanthurus chirurgus*) (Nagelkerken et al. 2000a).

We focus on local retention of larvae at their natal sites as a key component of larval connectivity, because it is critical to population persistence (Pinsky et al. 2012), and retention is independent of population dynamics. Local retention was calculated as

$$r_i = \frac{L_{i,i}}{Q_i} \quad (1)$$

where r_i is local retention at reef site i , $L_{i,i}$ is the number of settling larvae at site i that originated at site i , and Q_i

is the number of larvae spawned at reef i that settle at reefs.

The model used to calculate local retention was an individual based model of stochastic larval trajectories. Larval movements were controlled by both hydrodynamic forcing and larval behavior. Hydrodynamic forcing was generated using the Regional Ocean Modeling System (Shchepetkin and McWilliams 2005), which represented velocity fields in discrete space and time with 25 vertical layers and daily time steps. The hydrodynamic model's horizontal resolution was adaptively refined so that it could resolve velocity fields in topographically complex regions like The Bahamas (Paris et al. 2007). The hydrodynamic model was forced with 5 yr (2004–2008) of real wind data and the TPXO6 global tide model⁷. Larval behavior included vertical migrations and migrations of up to 9 km toward suitable reef habitat at the end of their pelagic dispersal period (Paris et al. 2007).

Contiguous reef habitat (including *Orbicella* reefs and gorgonian plains) was divided into 9-km segments for model simulations, resulting in 3,202 reef sites across the Caribbean. We cropped these to the $n = 789$ reef sites for The Bahamas and larvae that left The Bahamas were assumed to be lost to the country. While the connectivity model covers a larger area, >95% of larvae spawned within The Bahamas are retained there. Larvae are spawned at each reef site and settle at reefs within a 9-km sensory zone at the end of their larval period. The larval model tracked releases of 100 larvae originating from each reef site each month, and reports on annual settlement of larvae as an $n \times n$ association matrix. The assumption of constant larval production was appropriate because within the complex reef habitats we consider here there is little variation in fish community structure with exposure (Mumby 2016). Here, we take the mean settlement across the 5 yr of simulations to gain a longer-term picture of larval connectivity patterns.

Wave exposure has been mapped previously, and independently from the larval dispersal model, and was estimated based on wind-driven fetch and spatially explicit measurements of wind speed and direction using satellite data (Chollett et al. 2012). We took the exposure value (joules per cubic meter) at each of the 789 reef spawning sites as our measure of exposure.

Preliminary analysis for the dependence of local retention on exposure indicated that residuals were left skewed and contained many zeros. We therefore used hurdle models for further analyses (Zuur et al. 2009). The hurdle models of larval connectivity had two stages: (1) a binomial generalized linear model, with logit link, for whether any retention occurred, (2) a log-normal linear model for the amount of retention at sites with positive retention. At both stages we included exposure as a covariate. We then calculate expected mean retention across both binomial and log-normal processes as the product of the binomial and log-normal stages. Thus the expected mean retention was

$$E[r_i] = \left(\frac{e^{\alpha_1 + \beta_1 K}}{1 + e^{\alpha_1 + \beta_1 K}} \right) e^{\alpha_2 + \beta_2 K} e^{\frac{\text{MSE}}{2}}. \quad (2)$$

Where the first part of the equation in brackets is the model for the probability of retention occurring and the second part of the equation predicts how much retention occurs given there was retention. Variable K is exposure (J/m^3); α_1 and β_1 are the estimated effects of exposure on the logit probability of retention and; α_2 and β_2 were the estimated effects of exposure on the natural log of the proportion retained. The mean squared error (MSE) from the regression of exposure against log-larval retention controlled for retransformation bias (Duan 1983). We calculated 95% confidence intervals for $E[r_i]$ using nonparametric resampling (Davison and Hinkley 1997). All analyses were conducted using R (R Development Core Team 2014) using base packages raster (Hijmans 2014) and boot (Canty and Ripley 2014).

Inspection of the residuals indicated that the hurdle model fit met the standard assumptions for binomial and log-normal errors. We also examined variograms of the residuals on over-water distance between reef sites using the Morans I statistic (Legendre and Legendre 1998). With the inclusion of exposure as a covariate, no statistically significant spatial autocorrelation was detected.

Hypothesis 2: Reefs with low exposure are more likely to have connectivity to nursery habitats

We next asked whether reefs in more sheltered environments are more likely to be within the range of ontogenetic migrations from juvenile nurseries. We examine both mangrove and seagrass nurseries.

We defined connectivity to nursery habitats based on likely maximum migration of juvenile fish from nurseries to reef habitat (10 km; Dorenbosch et al. 2006, Mumby 2006, Huijbers et al. 2013). We present results for mangrove to reef connectivity and seagrass to reef connectivity. Further, some species (e.g., striped parrotfish) use both seagrass and mangrove nurseries (Nagelkerken et al. 2008), so we analysed a third type of nursery connectivity: mangrove and seagrass to reef connectivity, where connected reefs were those that were within range of both seagrass and mangrove habitats.

We used generalized linear models to test for a relationship between each of the three types of nursery connectivity at reef sites (yes/no binomial response) and exposure. We chose to model exposure at reefs connected to nursery habitats, rather than exposure at lagoonal habitats directly, because the reef sites represent the spawning sites for the larval connectivity model and the fish species we are interested in are most likely to spawn near reefs. As such, the exposure at the reef, rather than at the mangroves or seagrass, will most strongly influence larval retention. We also point out that we focused throughout on the outermost coral reef zone, because this is the primary spawning habitat for reef fish and the

⁷ http://www.esr.org/polar_tide_models/Model_TPXO62_load.html

subject of the previous analysis of wave exposure impacts on larval retention.

Initially, we fitted the binomial models and examined the residuals for spatial auto-correlation using the global Moran's *I* statistic (Legendre and Legendre 1998). The three models for the different nursery habitats all had significant spatial auto-correlation, so we used the residuals autocorrelation approach to account for autocorrelation when estimating test statistics and effect sizes (Cruse et al. 2012).

Hypothesis 3: Reefs with connectivity to nursery habitats have higher retention

Our final statistical analysis was to test for a correlation between larval and nursery connectivity types. We analysed for a dependence of each fish species' retention on nursery habitat connectivity at reef sites (nine analyses in total, three fish species by three nursery habitat types). We used the same hurdle models as in hypothesis 1, but this time with nursery habitat connectivity as the predictor variable. We did not include exposure and nursery connectivity simultaneously in this analysis because we expect these two predictors to be correlated, as per hypothesis 2.

We acknowledge that the larval connectivity model does not model larval connectivity from natal reefs to nursery habitats directly, rather it models reef-to-reef connectivity (Paris et al. 2007). However, reef to reef connectivity is likely more realistic for our example species, which commonly settle on patch reefs, then they may migrate to nursery habitats, before migrating back to reef habitats as adults (Nagelkerken et al. 2000a, b, Adams and Ebersole 2002, de la Morinière et al. 2002).

Hypothesis 4: Linkages between larval and nursery habitat connectivity contribute to enrichment of fish abundance on reefs near nursery habitats

We developed a simple population model to illustrate how differences in juvenile survival and larval retention between reef sites connected and not connected to nursery habitats affected abundance of fish on a reef. The model is generic, but we varied the parameters to represent our three fish types, and the effects of exposure on nursery habitat availability and retention.

Population abundance on the reef was described in continuous time (e.g., Walters et al. 2007)

$$\frac{dN}{dt} = g(L) - NM \tag{3}$$

where *M* was the instantaneous mortality rate of adults and *g(L)* was the recruitment rate as a function of the number of juveniles arriving at the reef. Recruitment followed a Beverton-Holt equation

$$g(L) = \frac{aL}{1+bL} \tag{4}$$

where *a* was the survival of settlers at low density and we defined $b = a/R_{max}$, where R_{max} was the asymptotic number of recruits to the reef, when migration rates from nursery to reef habitat are high. We chose to have direct density dependence because predators are likely attracted to reefs with large numbers of prey and settlers may compete for food at higher densities (White et al. 2010).

For simplicity and given that no contrary evidence is available in the literature (White et al. 2010), we assumed that pre-recruitment processes, including survival as larvae and survival in the nursery habitat are density-independent. Nursery habitats likely increase the early survival of fish (Chittaro et al. 2005) and we represented this nursery function of mangroves or seagrass by increasing the parameter *a*.

Settlers may be from larvae spawned locally by adult fish and retained within the population, or immigrants from other populations. Locally derived settlers were calculated by $L_{local} = N \times r$, where *r* is the proportion of larvae that settle in the local habitat. We do not account for adult fecundity explicitly, but this was captured implicitly in *a*, which scales the number of settlers as a function of adult abundance. We assumed the immigration of larvae from other sites is constant. Therefore

$$L^{eq} = N^{eq}r + L_{immigrant} \tag{5}$$

where L_{eq} and N_{eq} are the equilibrium larval supply and abundance respectively and $L_{immigrant}$ was the constant number of immigrant larvae. Because $L_{immigrant}$ is unknown, and cannot be estimated from the larval connectivity model, we vary it in sensitivity results as a fraction of the larval production from a population with 100% retention and zero immigration (i.e., a closed population).

Substituting Eqs. 4 and 5 into Eq. 3 and solving for abundance at equilibrium

$$\frac{dN}{dt} = \frac{a(Nr + L_{immigrant})}{1 + b(Nr + L_{immigrant})} - NM = 0 \tag{6}$$

which gave an equation quadratic in *N* that was solved by completing the square.

We varied retention across the exposure gradient, as predicted from the fish species models in hypothesis 2. We also vary parameter *a* across the exposure gradient. We assumed that survival of juveniles that had access to nursery habitats is doubled when compared to juveniles that did not have access to nursery habitats, a conservative estimate based on field studies (Grol et al. 2011). We therefore scale parameter *a* proportionally to the probability of nursery habitat connectivity, from a base value assuming no connectivity to nursery habitat, up to a maximum of twice the base value for reefs that have a 100% probability of being connected to nursery habitat (i.e., the most sheltered reefs).

We calculated the connectivity of reefs to nursery habitat using the models that fitted the probability of

nursery habitat to exposure (hypothesis 2). Thus, our predictions represented the expected mean abundance across all sites for a given level of exposure, rather than an expectation for a single site. We plotted three predictions for abundance across the exposure gradient: using only the retention effect, using only the juvenile survival effect and with the combined effects. We also plotted a fourth curve that represents the expectation for abundance if the retention and habitat effects had only additive effects on abundance. If the combined effects curve has a greater abundance than the additive effects curve, then the combined effects of habitat and larval connectivity have a synergistic effect on abundance.

For each species, estimates of adult mortality rates were taken from the same or similar species (Appendix S1: Table S1). For many species, numerous mortality estimates are available, so we used mid-ranged values, but also varied mortality rates in sensitivity analyses. For snapper, we used a mid-range value of $m = 0.45/\text{yr}$ (Nelson and Manooch 1982, Acosta and Appeldoorn 1992, Burton 2002). For parrotfish, no estimates of mortality in *Scarus iseri* were available, so we used a value of $m = 0.3/\text{yr}$, which is indicative of other similarly sized *Scarus* species and also other parrotfish species from the Caribbean (Choat et al. 2003, Taylor and Choat 2014). For tang, no direct estimates of *Acanthurus chirurgus* were available, so we used a value of 0.3 based on estimates from other Acanthurid species (Craig et al. 1997) and their relatively short lifespan (Choat and Robertson 2002).

We explored several alternative scenarios for parameters to account for multiple ecological hypotheses. Parameters a and the number of immigrant larvae are generally unknown for reef fish species, so we presented additional results with low and high juvenile survival and

immigration. Lower immigration may represent the lower survival of larvae that have travelled further from their spawning sites (Marshall et al. 2010). Finally, connectivity to nurseries can double the biomass of predators (Mumby et al. 2004) and may impact prey species biomasses (Harborne et al. 2016). We thus conduct analyses where adult mortality increased by up to two times on reefs connected to nursery habitat.

RESULTS

Hypothesis 1: Local retention is higher when exposure is lower

Larval retention increased by nearly three times (e.g., from 1.2% to 3.4% for snapper) from the most sheltered to the most exposed reefs, for all three fish “species” (Fig. 3). Fits of the hurdle models indicated a statistically significant effect of exposure on both the probability that retention was greater than zero (binomial stage) and the proportion of larvae retained given that retention was greater than zero (log-normal stage; Appendix S1: Table S2). For the three species, the effect of exposure on the probability of retention was positive, such that the probability of retention was low at very low exposure (<500 Joules/m³), and increased by ~20% at high levels of exposure. This effect runs counter to our main hypothesis, and is due to idiosyncratic features of the Bahamas seascape, with several sites with low exposure being positioned so that they had very low settlement rates at any reef site.

The effect of exposure on the proportion of larvae retained was negative (log-normal stage), so that larval retention decreased at reefs with greater exposure. The change in the proportion of larvae retained across the

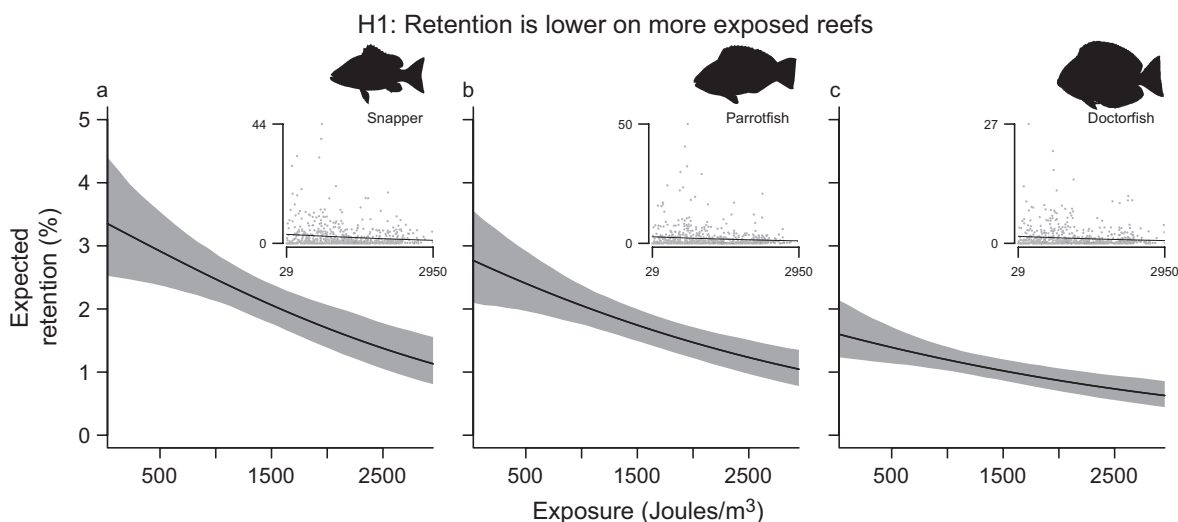


FIG. 3. Mean expected larval retention is lower on more exposed reefs for (a) snapper, (b) parrotfish, and (c) doctorfish larval types. Gray area indicates 95% confidence intervals. Insets show model fits (solid line) and all data points for retention at reefs, axes limits on insets indicate the ranges for exposure and retention.

exposure gradient was a much stronger effect than the change in the probability of retention, so the overall effect was a decline in expected mean retention across the exposure gradient (Fig. 3; Appendix S1: Table S2), which is consistent with hypothesis 1.

Hypothesis 2: Reefs with low exposure are more likely to have connectivity to nursery habitats

A spatial analysis of the Bahamian seascape confirms that nursery habitat availability declines with exposure for mangroves, seagrass, and their intersection (Fig. 4 and Appendix S1: Table S3). The overall prevalence of seagrass in the Bahamas seascape was higher than for mangroves, so the probability that a reef was connected to seagrass was high (>0.5) for all reefs except the most exposed (>2,500 Joules/m³). The probability that a reef was connected to both seagrass and mangroves followed a similar trend with exposure as for connectivity to mangroves alone (Fig. 2d and Appendix S1: Table S3), because mangroves were the limiting habitat type in the Bahamas seascape.

Hypothesis 3: Reefs with connectivity to nursery habitats have higher retention

While we find evidence that wave exposure influences larval retention and nursery habitat availability, it does not necessarily imply that both forms of connectivity are correlated to each other. Since this is our ultimate question, we explored patterns of larval and demersal connectivity directly (Fig. 5). Critically, reefs connected to nursery habitats had consistently higher larval retention than reefs not connected to nursery habitats (Fig. 5, significance indicated by 95% bootstrapped confidence intervals). This result was found for all three fish life histories. For the doctorfish, for example, retention

was up to 60% greater on reefs connected to mangrove habitats than those lacking nurseries. Overall, connectivity to seagrass had a greater effect on expected mean retention than connectivity to mangroves, or the intersection of mangroves and seagrass (Fig. 5 and Appendix S1: Tables S4–6).

Hypothesis 4: Linkages between larval and nursery habitat connectivity contribute to enrichment of fish abundance on reefs near nursery habitats

In sheltered environments, larvae will remain relatively close to their natal reef. Moreover, they are more likely to encounter nurseries once they have completed their pelagic phase, settle and commence recruitment. Retention near nurseries is a considerable advantage for species exhibiting ontogenetic migration, particularly for mangrove nurseries because the distribution of mangroves is patchy across the wider seascape. Only 35% of reefs have nearby mangroves and the probability of a larval fish encountering a reef near mangroves if spawned from a randomly located reef is low at 6–8% for all species. To estimate the magnitude of the retention advantage, we created a model of each fish species' population dynamics across seascapes from high to low exposure, parameterized using our analyses of exposure and connectivity (Figs. 3–5).

The seascape model predicts a non-linear decline in adult abundance as exposure increases, resulting in up to a 45% loss of abundance in the most exposed locations (Fig. 6). Disaggregating the contributions of each form of connectivity, we find that an elevated chance of encountering mangrove or seagrass nursery habitat had the greatest benefit (Fig. 6, red lines). However, the effect of elevated larval settlement also increases abundance, even in the absence of an effect of nursery proximity (Fig. 6 yellow lines). Importantly, when the effects of exposure

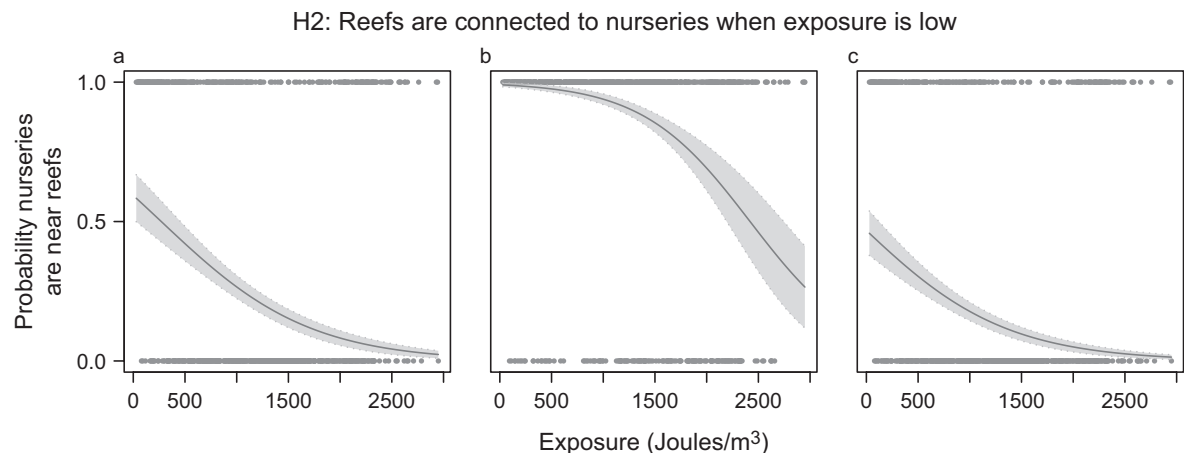


FIG. 4. The effect of exposure on the probability of reef connectivity to (a) mangroves, (b) seagrass, and (c) the intersection of mangroves and seagrass. Solid lines show mean expected probabilities, and shaded areas indicate bootstrapped 95% confidence intervals, points indicate measured values.

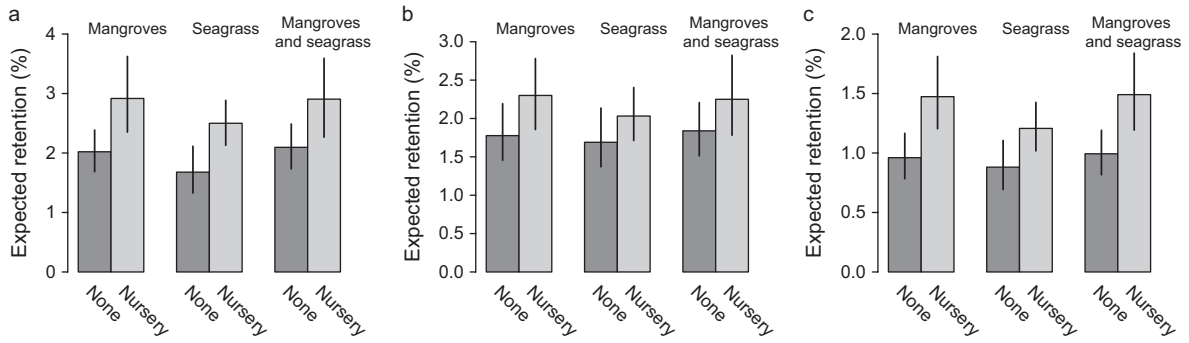


FIG. 5. Expected retention (mean \pm 95% confidence intervals) was greater on reefs connected to mangroves, seagrass, or the intersection of mangroves and seagrass than on unconnected reefs for (a) snapper, (b) parrotfish, and (c) doctorfish larval types.

on both forms of connectivity are combined they act synergistically (Fig. 6). Synergisms occur because a positive feedback loop emerges between reproduction and recruitment: higher adult abundance on reefs, as a result of improved juvenile survival in nurseries, means that more adults spawn and even more juveniles survive to recruit to the adult population. The synergistic effect is strongest for snapper, which had the highest adult mortality rate, so population dynamics were dominated by new recruits. The synergism is also strongest when larval supply from other sites is low, suggesting abundance of reef fish at more isolated reefs will increase the most from the local retention-habitat correlation.

Expected mean abundance across the exposure gradient as predicted by the seascape model was affected by several unknown population parameters, which may vary with local conditions and species (Appendix S1: Table S7). In particular, immigration of larvae from other sites and juvenile survival without nursery habitats were important. If immigration was high, then the effect of exposure on retention, and thus adult abundance, was small. The effect of retention also increased if immigrant larvae had lower settlement. If juvenile survival and immigration of larvae were both high, adult abundance was not limited by settlement or recruitment, so exposure had little effect on the population. Finally, if nursery

H4: Linked connectivities have a synergistic effect on abundance

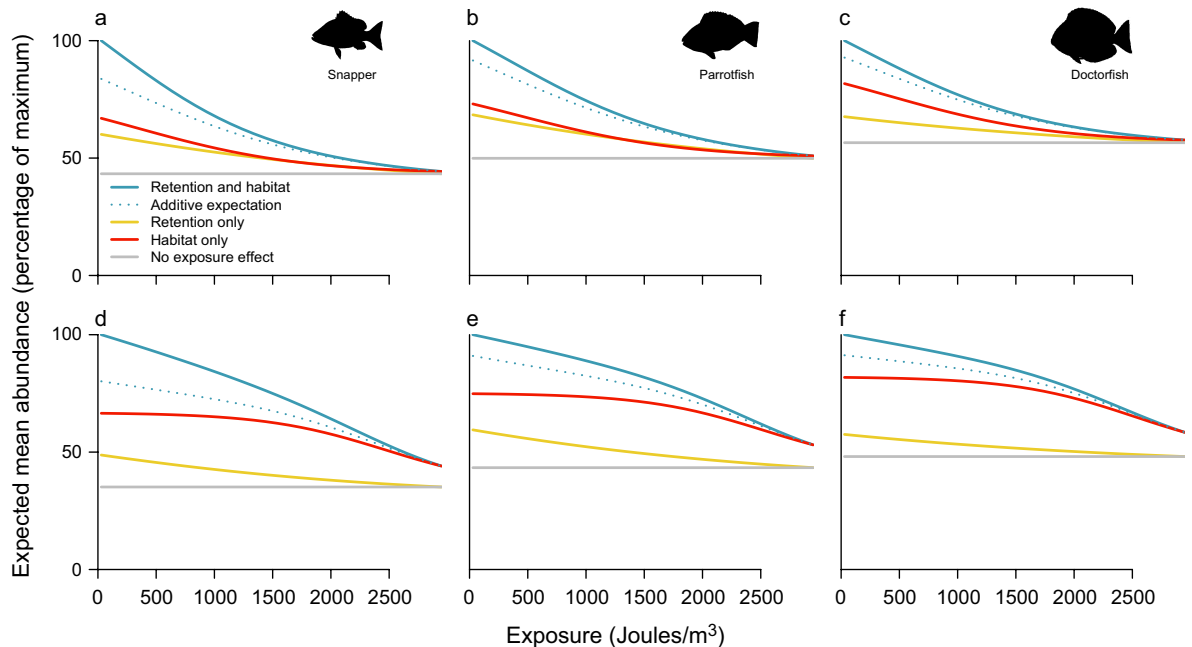


FIG. 6. Synergistic effect of larval and ontogenetic connectivity on fish abundance for (a, d) snapper, (b, e) parrotfish, and (c, f) doctorfish larval types with (a–c) mangroves as the nursery habitat and (d–f) seagrass as the nursery habitat. Results for models where the nursery habitat was defined as intersection of mangroves and seagrass are not shown, but are similar to (a–c).

habitats benefitted predator species and increased prey mortality by >42% there was no increase in recruitment close to nursery habitats, although the increase in retention was unaffected (Appendix S1: Fig. S1).

DISCUSSION

The beneficial effects of nursery habitats on adult reef fish populations (Nagelkerken et al. 2000a, Mumby et al. 2004, Olds et al. 2013) have mostly been explained as the alleviation of a population bottleneck in juvenile ontogeny (Laegdsgaard and Johnson 2001, Chittaro et al. 2005). Lagoons provide a relatively low, albeit variable, predation environment that offers easy access to a diversity of juvenile food sources (de la Morinière et al. 2003). Our results suggest that elevated larval retention may be another contributory and potentially synergistic mechanism explaining the widely observed enrichment of many reef fish species on reefs adjacent to lagoonal nurseries (Mumby et al. 2004, Unsworth and Cullen 2010, Nagelkerken et al. 2012, Olds et al. 2013).

The magnitude of the effect of exposure on adult abundance will vary across regions, with differences in mortality rate, and regional differences in the geography of seascapes, which affects the supply of larvae from other reef sites. Fish biomass on isolated islands with a strong exposure gradient will likely benefit the most, because supply of immigrant larvae will be low. Exposure to waves is likely to be the most useful proxy of adult biomass in seascapes like the Bahamas, where the combination of strong directional winds and islands means reefs with low exposure coincide with suitable substrate for mangroves and seagrass. The relationship between exposure and biomass could break-down in seascapes where sheltered nursery habitats are within the migration distance of juveniles fish to exposed reefs. For instance, in the southern Caribbean enclosed bays provide nursery habitat that services reefs on an exposed coast (Huijbers et al. 2013). Such seascapes could serve as important controls sites for field testing of the hypotheses we propose. However, the analyses also indicate there are considerable effects of exposure on adult abundance across a broad range of species life-history types and seascape configurations. Future empirical studies that seek to validate the hypotheses we have proposed here should consider the influence of species biology and seascape configurations.

Larval traits (Marshall et al. 2010) and ecological interaction (Harborne et al. 2016) will also modulate the synergistic effect of sheltered conditions on adult abundance. Locally retained larvae may have higher survival than immigrants, because they are locally adapted (Marshall et al. 2010). Lower survival of immigrant larvae increased the synergistic effect of exposure on abundance. The synergistic effect of exposure on abundance could be weakened by predation interactions. For instance, nursery habitats can also benefit a species' predators (Harborne et al. 2016) and larval dispersal of predators can covary with prey (White and Samhoury 2011) so that sheltered

areas may also have higher predation mortality. Field experiments should thus seek to investigate the relative roles of predation interactions and meta-population dynamics in shaping reef fish abundance.

We hypothesized that the evolution of ontogenetic migrations is inconsistent with extended larval dispersal, because larvae that spend weeks in the plankton are unlikely to settle near to patchily distributed nursery habitats. Yet, migration among reefs and nursery habitats has evolved in numerous fish lineages (Nagelkerken et al. 2000a, Seitz et al. 2014) and possibly several times independently within a single lineage (Tavera et al. 2012) suggesting that selective mechanisms have facilitated animals returning to preferred habitats. Exposure could be one such mechanism, though other mechanisms may be important. For example, some reef fish likely use olfaction (Dixson et al. 2014) or auditory senses (Simpson et al. 2004) to target settlement habitats. A particular benefit of higher larval retention is that it occurs throughout the pelagic phase over scales that are larger than the sensory zone of larvae, not simply towards later stages when post-larvae are sufficiently well developed to swim and influence their settlement habitat (Fisher et al. 2005). Consequently, linkages between larval and ontogenetic connectivity in sheltered areas may have facilitated the evolution of nursery habitat use; it increases the chance that larvae will settle near appropriate habitat.

Studies of marine connectivity are hindered by large spatial scales of animal movement and the ability to observe small organisms moving underwater (Cowen et al. 2006). Indeed, a full empirical test of the mechanisms we propose would have to track larval and demersal migrations across large spatial scales, which is logistically infeasible at this stage, although the rapid development of telemetry, larval tracking, and genetic parentage analysis provides exciting opportunities (Paris et al. 2007, Pusack et al. 2014, Hussey et al. 2015). We overcame these challenges by using the best available models and habitat maps for a large and regionally representative set of species and environments across The Bahamas. We note that many temperate species also utilize nursery habitats that occur in sheltered environments (e.g., seagrasses, salt marshes), suggesting that exposure may play a comparable role in the connectivity of many globally significant fishery species (Hufnagel et al. 2013, Seitz et al. 2014).

Fisheries management and conservation planning can both benefit from considering linkages between larval and demersal connectivity. While spatially realistic fisheries models have considered the importance of variable larval dispersal and patchy nursery habitat (Walters et al. 2007), the spatial coupling of connectivities has not been recognized yet might simplify conservation advice. Sheltered reefs may have greater self-sustaining larval retention, which is a desirable characteristic for biodiversity conservation (Hastings and Botsford 2003, Almany et al. 2007). Overall, the retention of larvae at a single reef site was low, even at sheltered sites, so protecting sheltered sites

could also provide spillover of larvae to fished areas. Thus, reserves in sheltered environments are good options to achieve biodiversity goals while also offering local fisheries benefits through adult spillover.

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