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REPORT

Modeling vertical coral connectivity and mesophotic refugia

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Abstract Whether mesophotic reefs will behave as refugia for corals threatened by global climate change and coastal development depends on vertical exchange of larvae between diverse habitats. Here we use a biophysical model of larval dispersal to estimate vertical connectivity of a broadcasting (*Orbicella faveolata*) and a brooding (*Porites astreoides*) species of coral in the US Virgin Islands. Modeling predicts subsidy to shallow areas by mesophotic larvae of both species based on local hydrology, adult reproductive characteristics, larval traits, and a wide range of scenarios developed to test depth-sensitive factors, such as fertilization rates and post-settlement survivorship. In extreme model scenarios of reduced fertilization and post-settlement survivorship of mesophotic larvae, 1–10 % local mesophotic subsidy to shallow recruitment is predicted for both species, which are demographically significant. Although direct vertical connectivity is higher for the broadcaster, the brooder demonstrates higher local multigenerational vertical connectivity, which suggests that local *P. astreoides* populations are more resilient than those of *O. faveolata*, and corroborates field studies. As shallow habitat degrades, mesophotic–shallow subsidy is predicted to increase for both species. This study is the first of its kind to simulate larval dispersal and settlement between habitats of different depths, and these findings have local, regional, and global implications for predicting and managing coral reef persistence in a changing climate.

Keywords Mesophotic coral ecosystems · Ecological modeling · Population connectivity · Refugia · Coral reef resilience

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Introduction

Coral reefs face a daunting set of local and global challenges to their continued persistence in shallow tropical waters (Gardner et al. 2003; Hughes et al. 2007; Pandolfi et al. 2011). Further, the effects of habitat fragmentation on coral metapopulation connectivity are poorly understood and potentially severe (Tilman et al. 1994; Collingham and Huntley 2000; Hanski and Ovaskainen 2000). Although the environmental conditions that determine the abundance and distribution of coral reefs may be restricted, the extent and degree to which local and global coral reef stressors may disturb coral reefs are not uniform in space. Areas that provide natural resilience to local coral populations by reducing exposure to stress may have the potential to behave as refugia and be particularly important to coral reef persistence and recovery.

The "deep reef refugia hypothesis" (DRRH) developed out of observations that depth reduces thermal and light stress on coral organisms (Glynn 1996; Riegl and Piller

2003; West and Salm 2003). Depth has also been shown to mitigate the impacts of coastal sedimentation and pollution (Smith et al. 2008) and storm damage (Goldberg 1983). Deeper coral habitats could behave as refugia for corals and associated organisms, and as larval sources to shallower habitats during or after periods of adverse conditions. In particular, recent attention has been paid to the refugia potential of mesophotic coral ecosystems (MCEs) (Bongaerts et al. 2010a), defined as phototrophic coral ecosystems found below 30 m. Caribbean MCEs have been found to be in impressive condition compared to shallow Caribbean reefs (Bak et al. 2005; Menza et al. 2008; Smith et al. 2008).

Larval exchange between deep and shallow habitat is integral to the DRRH (Lesser et al. 2009). Despite this, very little evidence exists that supports or refutes that coral larval exchange actively occurs between deep and shallow habitats. Historical evidence of larval exchange, as shown by studies of coral population genetics, suggests that immigration between deep and shallow habitats is species and location specific. Bongaerts et al. (2010b) and van Oppen et al. (2011) found strong genetic divergence of *Seriatopora hystrix*, a brooding coral, across depth in northeastern Australia, but van Oppen et al. (2011) found evidence of vertical connectivity of the same species in northwestern Australia. In the Caribbean, spawning corals such as *Eunicea flexuosa* and *Montastraea cavernosa* demonstrate geographic variation in genetic divergence or connectivity with depth, with the latter showing considerable mixing in the US Virgin Islands (USVI) (Prada and Hellberg 2013; Serrano et al. 2014).

Understanding habitat quality and productivity is crucial in developing realistic population models of coral reef systems (Paris et al. 2005; Underwood et al. 2007; Botsford et al. 2009; Mumby et al. 2011). For some depth-generalist coral species, it appears larval production in MCEs may rival or exceed shallow larval production (Holstein et al. 2015), which potentially results in mesophotic subsidy to shallow settlement. Evidence of this subsidy in the form of genetic mixing can be difficult and expensive to obtain due to the spatial scales and stochastic nature of coral connectivity, and may not provide information on mechanisms that promote or limit subsidy. The goal of this study was to utilize a four-dimensional biophysical model (three spatial dimensions and time) of coral larval dispersal, parameterized with three-dimensional settlement habitat and species-specific coral reproductive and larval traits, to gauge the potential for mesophotic–shallow larval subsidy (MSS) in the northern USVI. Although three-dimensional flow velocities are often used to model particle dispersal in the ocean (Paris et al. 2007, 2012; Kool and Nichol 2015), this is the first model of its kind to explicitly model larval connectivity

between habitats of different depths. The effects of depth on coral gamete productivity, fertilization, and the post-settlement survivorship of coral larvae are largely unknown, but these are likely to be controlling mechanisms in vertical connectivity. The sensitivity of vertical larval connectivity to these factors was examined in order to estimate ranges that promote or limit MSS. Results of this study will inform local management and the study of genetic connectivity of coral reef metapopulations. The study also has implications for the validity of the DRRH and is an example of the utility of biophysical modeling in the prediction of coral reef persistence.

Materials and methods

To investigate vertical coral connectivity in the northern USVI, a multi-scale biophysical model, the Connectivity Modeling System ((CMS); Paris et al. 2013), was used to simulate larval transport of two depth-generalist coral species, *Orbicella faveolata* and *Porites astreoides*. *O. faveolata* is a threatened broadcast spawning species (NOAA 2014) and a principle reef-building coral in the Caribbean. *P. astreoides* is a brooding coral predicted to have different dispersal dynamics from *O. faveolata* and other broadcast spawning species, due to rapid larval competence. Throughout the methods and results, discussion of coral larvae and larval exchanges refers to simulated particles and modeled dispersal, unless explicitly noted. For a glossary of terms, see Table 1.

Hydrodynamic module

The CMS couples offline ocean current, GIS-based habitat, and biological submodels. To maximize accuracy in larval dispersion calculations, a hierarchy of oceanographic models was used, nested through the CMS Lagrangian scheme. The two larger oceanographic models were HYbrid Coordinate Ocean Model models (HYCOM, http://hycom.org) and included the HYCOM-Global 1/12 degree horizontal resolution (ca. 7-km grid) model and the Gulf of Mexico GoM-HYCOM 1/25 degree horizontal resolution (ca. 4-km grid) model. The smallest model was based on the Regional Ocean Modeling System framework (ROMS, Shchepetkin and McWilliams 2005), had 300-m horizontal resolution, and was centered over the northern USVI (Cherubin et al. 2011; Fig. 1). All models included horizontal and vertical flow velocities, temperature, and salinity. The first ten vertical layers (0–100 m) were extracted from HYCOM models. The ROMS model utilized 18 unequal vertical layers from 0 to 150 m in order to maximize resolution of shallow hydrology.

Table 1 Definitions of terms used, including terms relating to larval ecology and terms related to graph theoretical analysis of connectivity networks

Glossary of terms	
Migration	The movement of a larva from one habitat, or node, to another
Recruit	A larva that has settled and survived any post-settlement mortality
Recruitment	The act of a larva recruiting, or generally refers to the accumulation of recruits, or the degree or magnitude of that accumulation
Settler	A larva that has encountered settlement habitat and completed its pelagic larval phase
Settlement	The act of a larva settling, or may refer to the number or magnitude of settlers in a specific habitat
Larval subsidy	The supply of settlers from exogenous sources. In this case, mesophotic larval subsidy to shallow reefs is the supply of settlers from mesophotic reefs to shallow areas
Local retention	The percent or proportion of larvae produced within the model domain that also settle within the model domain
Mesophotic–shallow subsidy	A proportion describing the settlement in shallow areas (0–30 m) that is due to mesophotic (31+ m) larval input (subsidy) as compared to shallow larval retention
Network or connectivity network	An arrangement of habitats that are intersected by larval exchange
Node	A point or vertex that describes the location of reef habitat. A node is assigned a depth between 0 and 50 m
Edge	A connection between two habitats that represents larval exchange in a specific direction
Shortest path	The minimum number of steps through connected habitats, or generations, required to connect two habitats
Average shortest path	The mean minimum number of steps, or generations, required to connect every node in a network to every other node
Betweenness centrality	A measure of the importance of a habitat or node to the integrity of a network. Highly central habitats are likely to behave as corridors for multigenerational connectivity

Habitat module

Coral reef habitat was parameterized spatially explicitly in three dimensions. 1 km^2 gridded polygons were overlaid on several coral habitat basemaps: (1) shallow (1–30 m) coral habitat maps developed by the National Oceanic and Atmospheric Administration's National Centers for Coastal Ocean Science (NOAA NCCOS; Kendall et al. 2001), (2) a high-resolution MCE map of the Marine Conservation District (Rivera et al. 2006), and (3) estimates of hardbottom habitat extent from multibeam and side-scan soundings (NOAA NCCOS). Polygons intersecting coral habitat were retained. Reef polygons were limited geographically to the spatial extent of the highest resolution oceanographic model. Each reef polygon was assigned a depth of 0–10, 11–20, 21–30, 31–40, or 41–50 m. If a reef polygon intersected with habitat in multiple depth strata, a polygon for each strata was retained. From this, 518 reef polygons were generated (Fig. 1). The centroid of each reef polygon was the release location for virtual larvae, and the extent of each reef polygon was settlement habitat.

Particle tracking module

The CMS tracked virtual larvae and recorded their positions over 2 yr (2007–2008) of hydrographic forcing. If a competent larva crossed over suitable settlement habitat, it settled to that location. Habitat was suitable only if within the same depth strata as the larva. This settlement condition allowed for fine-scale modeling of vertical connectivity. Reef habitat and larvae produced deeper than 30 m were classified "mesophotic", and shallower were classified "shallow."

Biological module

Virtual larvae-specific gravity changed realistically over time to simulate growth and bottom-seeking behaviors. Buoyancy characteristics were species specific and parameterized from the literature (*O. faveolata*: Szmant and Meadows 2006, Vermeij et al. 2006, Tay et al. 2011; *P. astreoides*: Gleason et al. 2005, 2009) and laboratory observations (Holstein 2013; Electronic Supplementary Material, ESM, Table 1).

Larvae were released from each habitat node according to species-specific reproductive seasons. Actual *O. faveolata* populations experience one to two mass spawning events per year in late summer, 6–9 d after the full moon (Szmant 1986; Szmant et al. 1997). To account for variability in spawning months, simulated larvae were released over 4 d, at 6–9 d after the full moon, at 2100 hrs, in August, September, and October of 2007 and 2008 (12 release times per year). All 518 nodes released 200 larvae
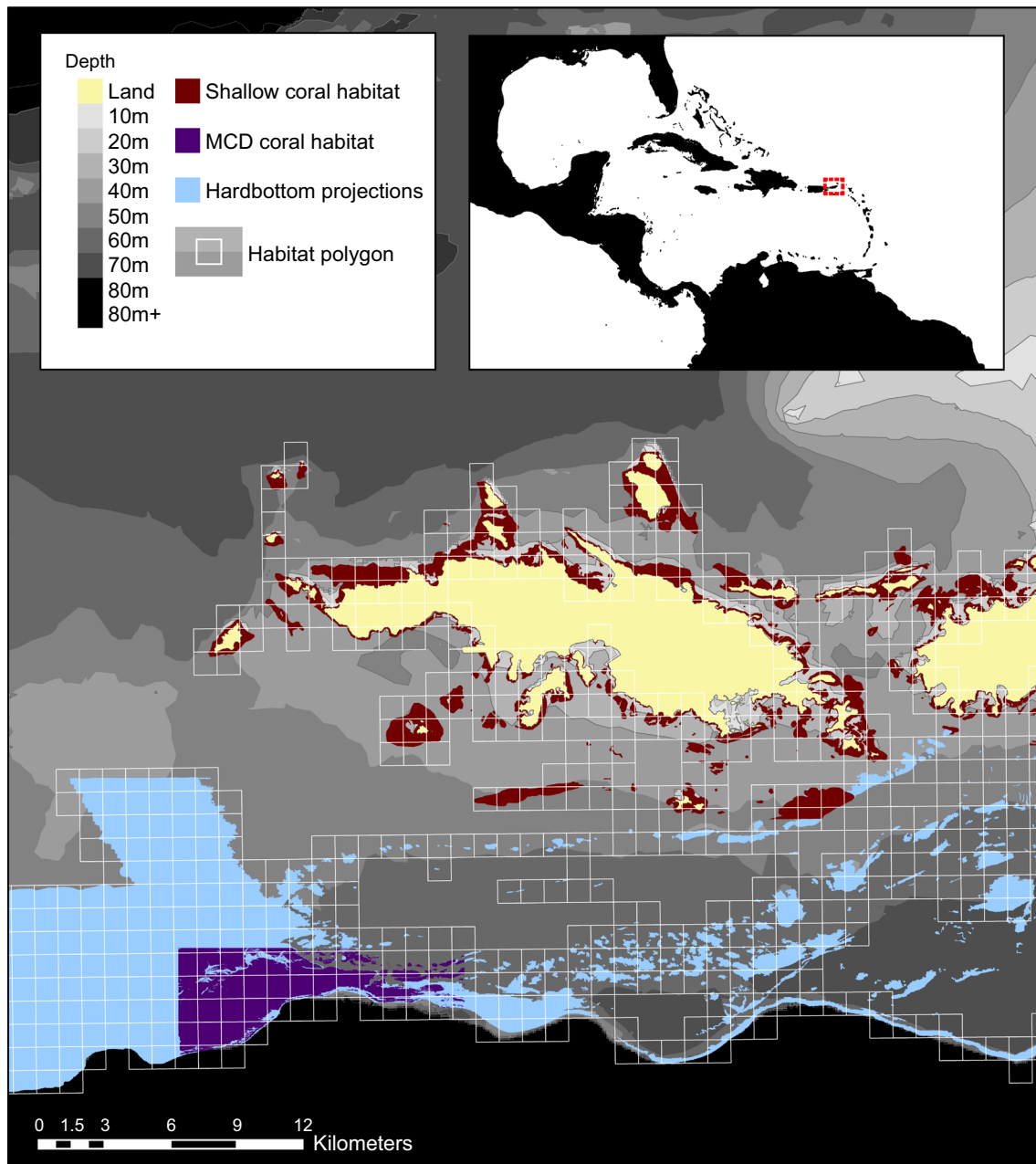
Fig. 1 Spatial extent of the study (and ROMS model) in the northern USVI. Shallow benthic habitats (*red*) and habitats in the Marine Conservation District (*purple*) are well classified. Hardbottom projections (*blue*) are un-verified predictions of mesophotic coral ecosystems. *White squares* represent 1 km² habitat polygons used in dispersal modeling

simultaneously at each release time, resulting in 2,486,400 simulated *O. faveolata* larvae.

In situ, *P. astreoides* colonies brood larvae internally and release nearly competent larvae in a loosely synchronized fashion focused around new moons from March through August (Szmant 1986; Chornesky and Peters 1987). Because *P. astreoides* are only found in low densities below 40 m, 50-m habitat was removed when modeling this species, leaving 377 reef polygons as larval

production and settlement habitat. Simulated larvae were released over 5 d, focused around the new moon, at 2100 hrs, in March through August of 2007 and 2008. All nodes released 200 larvae simultaneously at each of 30 release times, resulting in 4,524,000 simulated *P. astreoides* larvae.

See ESM Tables 1 and 2 for species-specific larval traits, including time to competency and pelagic larval mortality.

Model output and analysis

Connectivity output from the CMS records source (i) and settlement (j) habitats of individual settling larvae, the amount of time larvae were in the ocean (*age*), and arrival depth. From this information, raw migration matrices (i, j) were compiled, which quantify cumulative settlement at node j of virtual larvae originating from node i over release period, T.

Raw migrations were scaled by pelagic mortality, expressed as a half-life in seconds (h), and each larva's mortality was calculated individually as an exponential decay. Thus, each raw migration (m_{ij}) was scaled by a probability of pelagic survival ($s_{m_{ij}}$) from 0 to 1 based on the larva's age (in seconds) at the time of settlement.

$$s_{m_{ij}} = \frac{1}{2^{\text{age}_{m_{ij}}/h}} \tag{1}$$

Our focus was to estimate local retention of locally produced larvae. Thus, it was assumed all local habitat was known, and proportional (nonnormalized) migration matrices were used for analysis. Migration matrices were further scaled according to depth-specific productivity by a productivity coefficient, K_i, which ranged from 0 to 1 at each production node. Thus, scaled migrations are represented by the probability:

$$p_{ij} = K_i \times s_{m_{ij}} \tag{2}$$

And the mean probability of migration from i to j, $\bar{p}_{ij}$, is calculated as follows:

$$\bar{p}_{ij} = \frac{\sum_{m_{ij}=1}^{M_{ij}} K_i \times s_{m_{ij}}}{M_{ij}} \tag{3}$$

where M_{ij} is the total number of simulated larvae migrating from i to j. A new matrix, P_T, contains the number of probable migrations within the model scenario over time T, from any node to any other:

$$P_{T_{ij}} = \bar{p}_{ij} \times M_{ij} \tag{4}$$

Mesophotic–shallow subsidy

MSS was estimated by transforming P_T into vertical matrix, V_T, which summed all probable migrations between depth strata, monthly. MSS was then defined as the proportion of settling virtual larvae in shallow habitat (0–30 m) that originated from MCEs (31–50 m).

MSS was calculated assuming literature estimates for larval half-life (Edmunds et al. 2001; Vermeij et al. 2006; ESM Table 3) and larval productivity (Holstein 2013; Holstein et al. 2015; Table 2). Larval productivity was expressed as a function of adult colony density and adult

Table 2 Depth-specific habitat productivity based on empirical reproductive study of *Orbicella faveolata* and *Porites astreoides*

Depth (m)	*O. faveolata*	*P. astreoides*
10	0.31	1
20	0.38	0.31
30	0.92	0.54
40	1	0.38
50	0.08	–

Productivity is a product of adult coral cover and fecundity per area. Values are scaled to the maximum value (taken from Holstein 2013; Holstein et al. 2015)

fecundity per area, and each habitat polygon was assigned a productivity based on how these factors change with depth. *Orbicella faveolata* maximum productivity was at 40 m, and maximum productivity for *P. astreoides* was at 10 m. The sensitivity of the model to this differential productivity was unknown, and sensitivity analyses were performed by estimating MSS in 100 discrete scenarios chosen to represent a gradient of linear relationships of depth and productivity (Fig. 2).

Depth-specific rates of fertilization and post-settlement survivorship are critical for estimating levels of mesophotic–shallow connectivity. However, how depth affects coral fertilization is poorly understood, and fertilization in broadcasting species, which generally occurs at the air–sea boundary, may be depressed with depth due to distance from the benthos to the sea surface (Levitan et al. 2004). Additionally, coral larvae produced in deeper habitats may be more sensitive to ultraviolet radiation and may have reduced survivorship in shallower habitats (Gleason and Wellington 1995; Wellington and Fitt 2003; Gleason et al. 2005). In order to test the effects of depth-specific fertilization and post-settlement survivorship on vertical connectivity, 10,000 discrete scenarios of fertilization and post-settlement survival were investigated. In these scenarios, depth-specific fertilization ranged in comparison with a maximum rate, set at 10 m. Depth-specific fertilization was expressed by scaling migrations according to their depth of origin. Fertilization varied with each increasing 10 m depth strata by a power law (Babcock et al. 1994) applied to a differential (d_f) that ranged from 0 to 1. Fertilization at each depth strata was calculated based on the number of 10-m steps that strata were away from the 10-m isobath (steps) (Fig. 3a; ESM Table 3):

$$\text{Fertilization}_{\text{bin}} = d_f^{\text{steps}} \tag{5}$$

Similarly, post-settlement survivorship of each settled larvae was modeled according to the vertical distance between source and settlement habitat using a power law
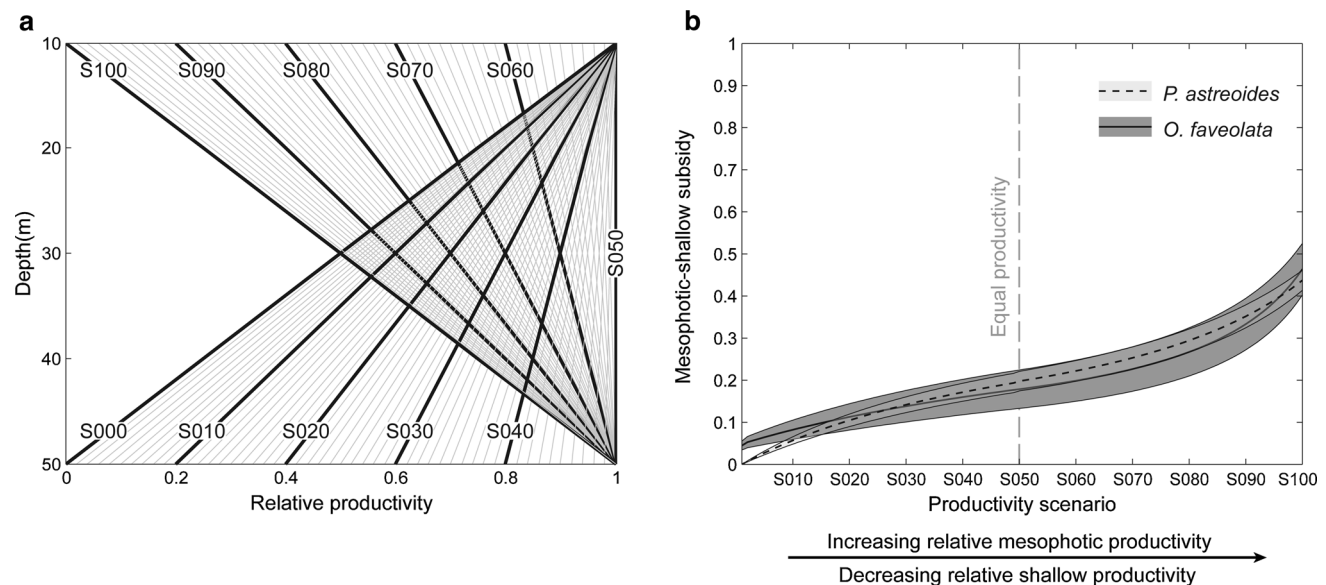
Fig. 2 **a** Productivity scenarios representing 100 potential linear relationships of depth and productivity. Each linear relationship was used to model mesophotic–shallow larval subsidy (MSS). **b** Sensitivity of MSS to productivity scenarios in each species (mean and SE)

applied to a differential of 0–1 (d_s), again in 10-m vertical steps (Fig. 3b; ESM Table 3):

$$\text{Survivorship}_{ij} = d_s^{\text{steps}_{ij}} \quad (6)$$

Survivorship was only affected when a larva migrated into shallower habitat. If a larva migrated to habitat at the same depth as its source, post-settlement survivorship was maximum (d_s^0). If a larva migrated to a habitat at one depth strata shallower than the depth of its source (steps = 1), post-settlement survivorship was scaled by d_s^1 (migrating two depth strata resulted in scaling by d_s^2, etc.). If a larva migrated into deeper habitat, post-settlement survivorship was not affected and modeled as d_s^0.

To estimate the number of generations necessary for local populations to be connected through larval exchange, Johnson's algorithm was used to find the shortest path (node-to-node steps) between all pairs of habitat polygons (Johnson 1977). "Average shortest paths" describes the minimum number of steps, or generations, that are required for all network habitats to be connected through larval dispersal. Coral generations are difficult to define because colonial coral organisms can be long-lived, but here it is defined as a larval recruit developing into a reproductive adult. Average shortest paths can identify how extensively networks are connected, and can also be used to show the relative "ease" of connectivity in different directions, such as from mesophotic to shallow or vice versa. Additionally, the importance, or centrality, of each habitat polygon was estimated by calculating betweenness centrality (Freeman 1977), with and without edge weights (connection

magnitude). This measure of centrality is based on the number of shortest paths that pass through any specific node, with more central nodes facilitating larval flux across a network. Additionally, betweenness centrality can be used to identify multigenerational corridors for larval connectivity (Treml et al. 2008; Holstein et al. 2014).

Results

Local retention

Model results focused on locally retained larval exchanges. Despite considerable larval advection out of the northern USVI model domain, monthly local retention of *O. faveolata* larvae ranged from 4.25 to 18.33 % (Fig. 4a). Monthly local retention of *P. astreoides* larvae was significantly higher (two-sample *t* test, $p < 0.0001$) and ranged from 26.21 to 58.35 % (Fig. 4b). *Orbicella faveolata* peak retention occurred in September in both years, and retention was generally higher in 2007 as opposed to 2008. In 2007, peaks in *P. astreoides* retention occurred in March and in late summer, and in 2008, peak retention occurred in May. Note that a single-habitat polygon experienced anomalously high recruitment in all simulations, caused by convergence in the oceanographic model's flow velocities close to the model boundary. This outlier was scaled to the third quartile of total recruitment experienced at each habitat, plus three times the interquartile range.
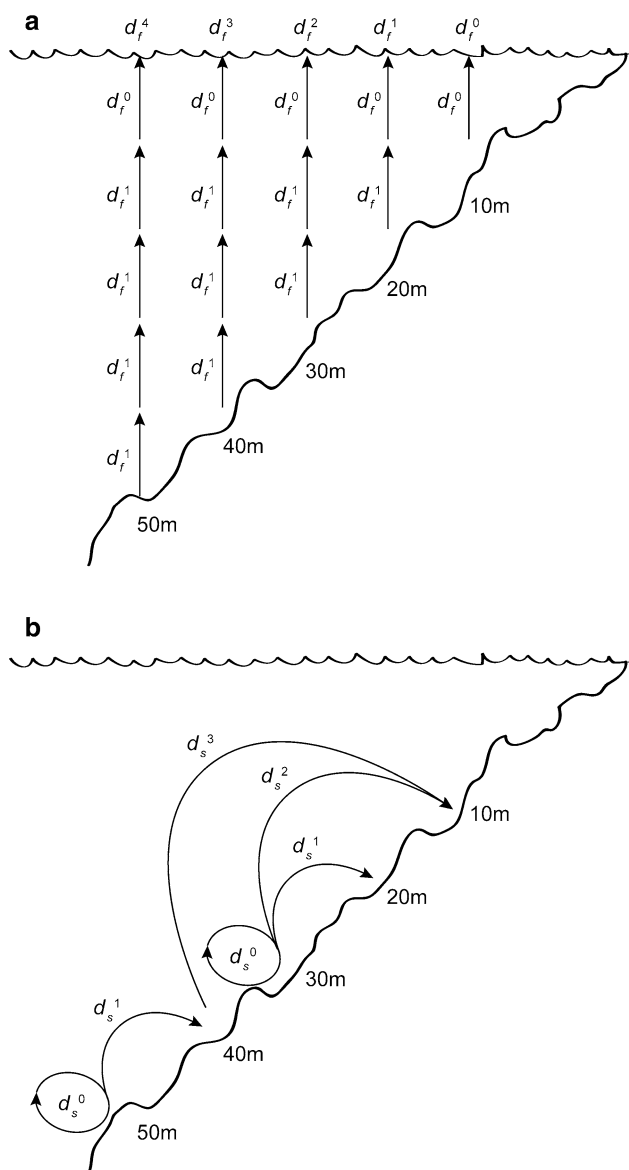
Fig. 3 a Design of 100 depth-specific fertilization scenarios for sensitivity analysis of mesophotic–shallow larval subsidy. Every 10 m that gametes must travel to reach the sea surface decreases fertilization by a factor of d_f^1 (Eq. 5). **b** Design of 100 post-settlement survivorship scenarios based on the vertical distance between production and settlement habitat. Every 10 m that a larva migrates upward post-settlement survivorship is scaled by a factor of d_s^1 (Eq. 6). Survivorship of larvae is not affected when migrating into deeper habitat

Fig. 4 Local larval retention of (**a**) *Orbicella faveolata* and (**b**) *Porites astreoides* in all modeled months in 2007 and 2008. **c** Mesophotic–shallow larval subsidy for both species trends with local retention

Mesophotic–shallow subsidy

Average monthly scaled vertical migrations, V_T, for both species can be seen in Fig. 5. Assuming literature and empirical parameterization of pelagic mortality and larval production, and no depth effects on fertilization or post-settlement survivorship, mean (±SEM) monthly MSS for *O. faveolata* was estimated as 0.251 (±0.042) (25.1 %) and
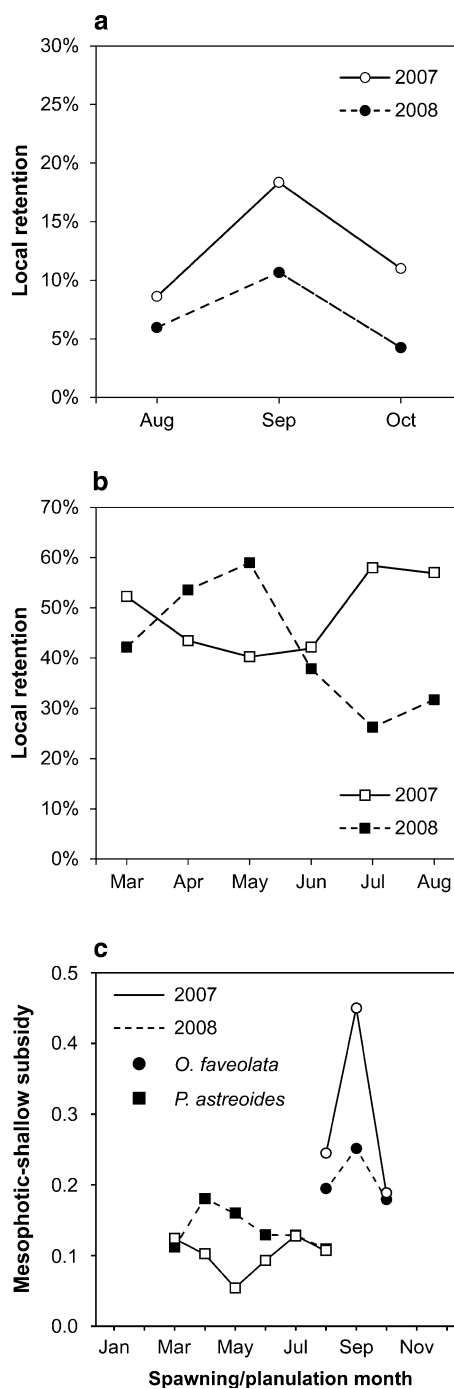
ranged from 0.179 to 0.45. MSS was significantly less in *P. astreoides* (independent two-sample *t* test with unequal variance, $p = 0.024$), averaged 0.119 (±0.009) and ranged from 0.054 to 0.181.
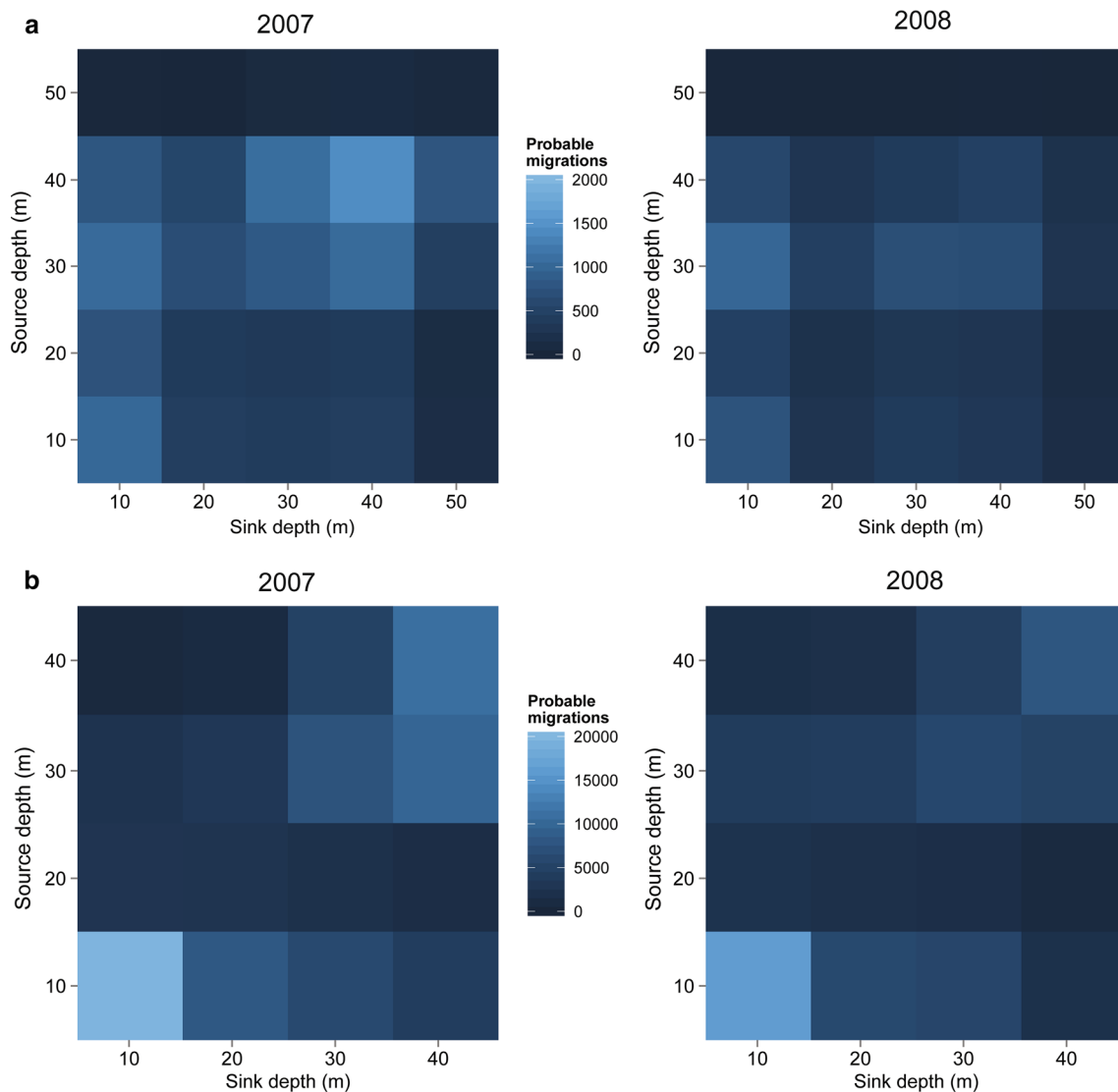
Fig. 5 Mean monthly probable vertical migrations in both modeled years, in 10 m depth strata, for (**a**) *Orbicella faveolata* and (**b**) *Porites astreoides*

Sensitivity analyses

Depth-specific productivity

For both species, MSS was 15–20 % when productivity was near equal at all depths (Fig. 2b). MSS was sensitive to depth-specific productivity and increased exponentially as mesophotic productivity increased relative to shallow productivity. The most extreme productivity scenarios tested resulted in a range of mean MSS from 0 % to over 50 %. Sensitivity of MSS to differential productivity scenarios appeared similar for both species.

Depth-specific fertilization and post-settlement survivorship

The empirically parameterized model's predictions of MSS were also sensitive to depth-specific rates of fertilization and post-settlement survivorship (Fig. 6). MSS was more sensitive to reduced fertilization at depth than to differential survivorship in shallow habitat, but the two factors have the potential to interact and reduce subsidy nonlinearly. Conservatively, the model predicted >1 % subsidy for *O. faveolata* if d_s and d_f remained above 0.3 and 0.5, respectively. In this scenario, relative survivorship of 40-m larvae at 10 m
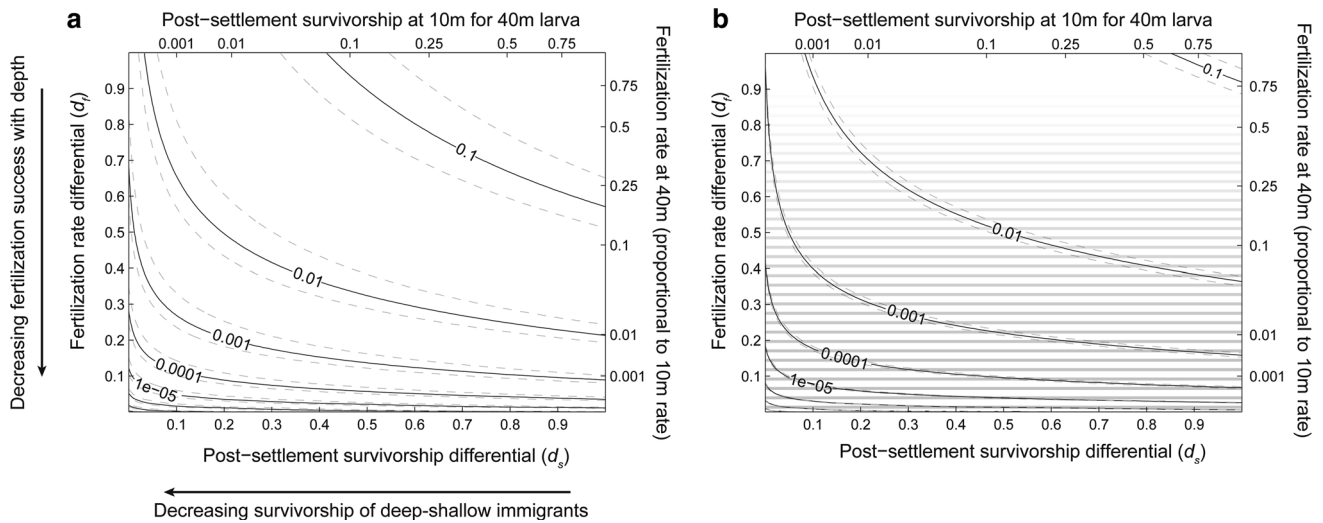
Fig. 6 Sensitivity of mesophotic–shallow larval subsidy (MSS) to depth-specific fertilization rates and post-settlement survivorship for (**a**) *Orbicella faveolata* and (**b**) *Porites astreoides*. See Fig. 3 and ESM Table 3 for more information regarding figure axes. MSS is more sensitive to changes in mesophotic fertilization than to changes in mesophotic larval post-settlement survivorship in shallow habitat. Because it is a brooding species, *P. astreoides* fertilization potential is not expected to be reduced by depth (hatching). *Solid curves* represent mean values indicated; *dashed curves* represent standard error

was ∼3 %, while the relative fertilization success at 40 m compared to the rate at 10 m was ∼12.5 %. When fertilization rate and post-settlement survival of mesophotic larvae were both reduced by ∼50 %, MSS of greater than 10 % was predicted. The sensitivity of *P. astreoides* MSS was similar to that of *O. faveolata*; however, mesophotic subsidies were lower for this species. Fertilization rate differentials were not considered important for *P. astreoides* mesophotic–shallow connectivity, and >1 % vertical subsidy could be maintained so long as d_s remained above ∼0.1 (∼0.1 % post-settlement survivorship of 40-m larvae at 10 m relative to shallow larval survivorship).

Multigenerational connectivity and habitat centrality

Average shortest paths were significantly different between species despite overlapping standard deviations due to very large *n* (Table 3). The *P. astreoides* network had a significantly smaller average shortest path than that of *O. faveolata* (Welch two-sample *t* test, *p* < 0.001), which implies higher local connectivity. Despite the statistical significance, average

shortest paths were between 1 and 2 for both species, which suggests, on average, all habitats in the northern USVI are connected within two generations for both species.

Comparisons of average shortest paths in different vertical directions were made by averaging shortest paths between and among mesophotic and shallow habitats (Table 3). All averages were less than two and significantly different between species and directions (Welch two-sample *t* tests, all *p* <0.001, *n* = ∼43,000 to ∼95,300, depending on comparison). *Orbicella faveolata* shallow–shallow connections had the shortest average shortest path, followed by shallow–mesophotic connections, mesophotic–shallow connections, and finally mesophotic–mesophotic connections (Table 3). The *P. astreoides* network displayed different vertical shortest path dynamics, where mesophotic–mesophotic connections had the smallest average shortest path, followed by shallow–shallow connections, shallow–mesophotic, and mesophotic–shallow connections.

Without edge weights, *O. faveolata* shallow habitat had higher betweenness centralities than MCEs. When edge weights were applied, maximum centrality occurred at 30 m, and 50-m habitat had low centrality. When edge

Table 3 Total average shortest path (±SD) from the adjacency matrix for each species, as well as vertical shortest paths

	Total	M–M	M–S	S–M	S–S
Orbicella faveolata	1.68 (0.49)	1.79 (0.44)	1.74 (0.45)	1.62 (0.49)	1.42 (0.50)
Porites astreoides	1.40 (0.50)	1.23 (0.43)	1.54 (0.50)	1.41 (0.49)	1.39 (0.50)

Smaller numbers indicate a tighter, more connected network

M–M mesophotic to mesophotic shortest paths, *M–S* mesophotic to shallow, *S–M* shallow to mesophotic, *S–S* shallow to shallow
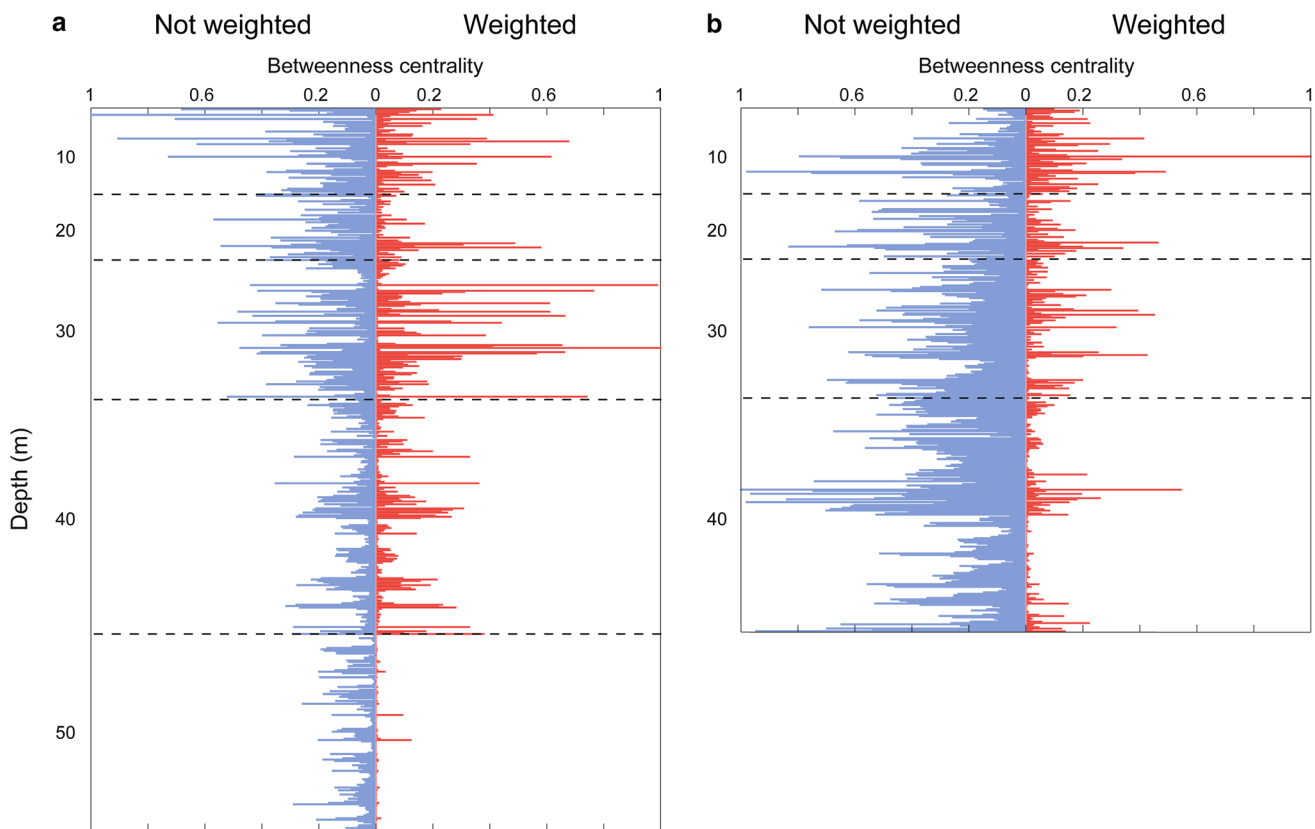
Fig. 7 Estimates of habitat betweenness centrality calculated using unweighted adjacency matrices and edge weights extracted from P_T (connection magnitude) for (**a**) *Orbicella faveolata* and (**b**) *Porites astreoides*. With edge weights, highly productive habitats are most central

weights were used, shallow habitat (10 m) showed the highest centrality for *P. astreoides* (Fig. 7).

Discussion

The model predicted demographically significant mesophotic contributions to shallow settlement for both a spawning and a brooding coral in the USVI, even under extreme scenarios of mesophotic larval post-settlement mortality and reduced fertilization. Productivity, or habitat quality, appears to have dramatic implications for model predictions of vertical connectivity.

The fates of advected simulated larvae and the input of larvae from upstream reefs are not addressed in the current model, and thus, vertical migration may occur on spatial scales larger than described here. MCEs are often peripheral to shallow habitat (Locker et al. 2010), which could suggest dispersing larvae receive cues and settle in this habitat before reaching shallow reefs. Indeed, recruitment to MCEs may be a pervasive aspect of coral reef population connectivity. The fates of advected mesophotic larvae thus have important implications for conservation and management; northern USVI MCEs may

be important both as local and as remote recruitment sources.

Annual variability

Hydrographic conditions can vary considerably inter-annually. The USVI falls within a region with high hurricane frequency (Foster et al. 2013); in 2007 four tropical systems passed over or near the USVI during late summer, and in 2008 there were two, including Hurricane Omar which became a major hurricane in October. For this reason, it is ideal to simulate larval dispersal over multiple years of hydrography in order to capture inter-annual variability in prevailing currents. Two years of high-resolution hydrographic data were available for use in this study, and inter-annual variability in patterns of simulated settlement was observed in both species. *Orbicella faveolata*-simulated larval retention was consistently higher in 2007 than in 2008. During late summer in 2007, simulated larvae became entrained in a persistent sub-mesoscale eddy that returned larvae that may otherwise have been advected away. High *O. faveolata*-simulated larval retention in September of 2007 highlights that recruitment events for this species may be stochastic (Miller et al. 2000; Edmunds

and Elahi 2007) and that modeling dispersal using many years of hydrography may be necessary to predict realistic estimates of local larval retention. However, the pattern of simulated larval retention appears similar for *O. faveolata* between years, with peak retention following September spawning. *Orbicella faveolata* spawning has been observed in September in the USVI (Holstein et al. 2015), which may indicate an adaptive response to consistently enhanced local retention of larvae in this month.

Patterns of *P. astreoides*-simulated larval retention were nearly opposite between years. This again highlights the need to model dispersal using multiple years of hydrography (Kough and Paris 2015); however, total simulated larval retention for this species appears similar between years. For both species, patterns of MSS tracked those of local retention (Fig. 4c), suggesting vertical connectivity is a consistent feature of local retention in this modeled system.

Mesophotic–shallow subsidy

The model predicted considerable flux of larvae between mesophotic and shallow habitat in the northern USVI for both species. In fact, *O. faveolata*-simulated larval migration from 40 to 10 m surpassed retention at 10 m in September in both modeled years (ESM Appendix 1.1). Simulated MSS was higher for *O. faveolata* than for *P. astreoides*, despite the fact that most simulated *O. faveolata* larvae were advected from the system. Early competency and short dispersal distances in *P. astreoides* increased the proportion of simulated larvae settling close to natal habitats, effectively reducing MSS. If the majority of actual coral recruitment in the northern USVI is expected to come from locally retained larvae, modeled subsidy estimates are almost certainly demographic in nature. Alternatively, if most local recruitment is of exogenous shallow-produced larvae, the model may overestimate mesophotic subsidies to local recruitment.

Simulated mesophotic larval retention was consistently as high as or higher than simulated shallow larval retention for both species, suggesting recruitment in USVI MCEs may substantially consist of locally produced mesophotic larvae. This has implications for the resilience of these habitats and for adaptation and speciation.

Depth-specific productivity

Using species- and depth-specific parameters should increase model efficacy in describing vertical connectivity. Modeled estimates of vertical connectivity were highly sensitive to scenarios of depth-specific productivity, suggesting accuracy in estimation of habitat extent, adult density, and adult fecundity is essential to developing

realistic models of dispersal (Hughes and Tanner 2000; Botsford et al. 2009) and thus, the accurate prediction of MSS in the USVI.

The sensitivity analysis performed on differential productivity could be used to predict changes in MSS after differential habitat fragmentation. Specifically, should shallow habitat degrade more quickly than MCEs, as it appears is the case (Smith et al. 2008), MSS should increase, and potentially exponentially.

Post-settlement survivorship and fertilization

The potential for elevated post-settlement mortality on larvae of deeper origin is one of the greatest caveats to the DRRH, as it implies it might be difficult for mesophotic larvae to replenish shallow corals, and that many coral populations may be speciating by depth. Deep corals may produce lower concentrations of mycosporine-like amino acids (MMAs), which protect coral tissues from ultraviolet radiation. This can result in lower concentrations of these proteins in eggs and larvae produced by deeper-living colonies, which may reduce reproductive success of mesophotic corals, particularly when mesophotic larvae enter shallow waters (Gleason and Wellington 1995; Wellington and Fitt 2003). Adult reciprocal transplantation experiments have suggested that commonly deeper-living color morphs of *P. astreoides* perform poorly when moved into shallow environments (Gleason 1993) and other coral species have shown similar differential mortality after transplantation (Bongaerts et al. 2011). Indeed, several studies have shown genetic structure in coral populations and their symbionts across depth gradients (Bongaerts et al. 2010b, 2013, 2015; Slattery et al. 2011; Serrano et al. 2014), which may support the assertion that deep-adapted corals have reduced recruitment success on shallow reefs. Without further study, it is difficult to determine to what degree genetic structure found in these studies is due to local habitat arrangement, hydrologic forcing, post-settlement survivorship, competitive effects, and/or larval traits.

To date, empirical estimates of any depth-related differences in post-settlement survivorship for *O. faveolata* or *P. astreoides* are sparse. Mid-depth (24 m) larvae of *Agaricia agaricites* experience higher mortality at 3 m than conspecific larvae brooded at 3 m (Gleason and Wellington 1995); however, the effect was not observed in settlers at 10 m. In a similar study, larvae of *O. annularis* and *O. franksi* from different depths (4–14 m) experienced similar, and low, survivorship under UVA and UVB treatments (Wellington and Fitt 2003). Both studies suggest survivorship in areas shallower than 10 m is likely to be low for larvae from all depths for these species. It is difficult to extract "likely" scenarios of differential post-settlement survivorship; however, *Agaricia agaricites* larvae brooded

at 24 m experienced about half the survivorship of shallower conspecifics at 3 m (Gleason and Wellington 1995). If this relationship is used as a benchmark (50 % reduced survivorship of 40 m larvae at 10 m, $d_s \approx 0.8$), the current model's predictions of MSS for *O. faveolata* become heavily dependent on fertilization rate.

Consequently, reproductive success of corals may also be limited by fertilization (Lasker et al. 1996). Distance and sperm-dilution can reduce fertilization in benthic invertebrates (Oliver and Babcock 1992; Babcock et al. 1994), and thus fertilization in mesophotic broadcast spawning corals may be limited by gamete dilution if those gametes must be near the sea surface to fertilize. Empirical comparisons of fertilization rates at different depths are particularly difficult to perform in situ, and to date no studies are available with which to compare the sensitivity analyses performed in this study. Thus, the sensitivity analyses provide ranges in depth-specific fertilization rates that would still allow for demographically significant MSS in this system. For example, in order to maintain 1 % MSS in *O. faveolata*, assuming $d_s \approx 0.8$, fertilization rate at 40 m could be as low 1/100th of that at 10 m. The assumption that fertilization may be reduced with depth may not apply in *P. astreoides* because sperm are neutrally buoyant and fertilization occurs within the coral tissues, not at the sea surface. Therefore, differential fertilization was ignored for this species, and modeled mesophotic subsidy could be as high as 10 % assuming d_s of 0.8. So long as d_s remains above 0.1 (0.1 % survivorship of mesophotic larvae at 10 m relative to shallow–shallow survivorship), the model predicts *P. astreoides* mesophotic subsidy to remain demographic, and above 1 %.

Based on model predictions, vertical larval connectivity in the USVI appears possible based on local hydrology, active larval behavior, and a wide range of productivity scenarios—and appears robust to depressed fertilization and post-settlement survivorship of mesophotic larvae. *Orbicella faveolata* MSS is more sensitive to depressed mesophotic fertilization than to depressed post-settlement survivorship of mesophotic–shallow migrants.

A 1 % subsidy may be difficult to detect in genetic study; however, a 10 % subsidy should be detected if populations from different depths are sufficiently genetically differentiated. Recruitment of *O. annularis* corals in the Caribbean is stochastic and low, and estimates range from 0 to 0.78 colonies m^{-2} (Edmunds et al. 2011, and citations within). In the USVI, a majority of recruiting corals are poritids (Green and Edmunds 2011), and recruitment of this family is much more consistent. Thus, low-level MSS may be difficult to detect in *O. faveolata*, but easier to detect in *P. astreoides*. Because recruitment is stochastic and inconsistent across the region (Edmunds et al. 2011; Green and Edmunds 2011), it is currently best

to consider modeled subsidy estimates as relative to uncertain shallow recruitment rates. Further study of the effects of depth on fertilization of broadcast spawning corals and post-settlement survivorship of mesophotic larvae is necessary in order to fully understand vertical connectivity in this system.

Although not discussed here, sensitivity to pelagic mortality was also tested. For both species, MSS was robust to population-level changes in larval half-life. Only when mortality was very high, with larval half-lifes <2–3 d, was MSS affected negatively.

Multigenerational connectivity

The DRRH does not require mesophotic and shallow habitats to be connected directly through larval exchange, but rather that MCEs contribute to coral reef demography in general, and shallow reefs in particular. Differential post-settlement survivorship is a hurdle to vertical connectivity that could potentially be overcome through multigenerational vertical migrations, effectively connecting deep and shallow populations using mid-depth stepping-stones and avoiding mortality due to extreme environmental changes. It is possible that multigenerational larval pathways connect mesophotic and shallow reefs even where direct larval pathways between the two habitats are missing or rare. Within the current USVI model, investigation of multigenerational connectivity through shortest path analysis suggests that *O. faveolata* and *P. astreoides* networks are highly connected. In *O. faveolata*, migrating from any shallow habitat to any other shallow habitat requires, on average, the fewest steps. Connecting all MCEs requires the most steps, and connecting shallow and mesophotic habitats has less cost when it occurs shallow to deep. Despite the fact that simulated *O. faveolata* MSS is likely higher than that of *P. astreoides*, the local network of *P. astreoides* is significantly smaller than that of *O. faveolata*, suggesting fewer habitats are isolated from larval exchange, and potentially a higher degree of genetic connectivity. Mesophotic and shallow *P. astreoides* populations may be more connected than *O. faveolata* populations in the northern USVI over multiple generations.

Betweenness centrality can identify multigenerational corridors and habitats essential to the structure of a network. When betweenness centrality is calculated using edge weights (connection magnitude) highly productive habitats become more central. In this model, *O. faveolata* habitats with high betweenness centrality occur in the 30-m depth strata, suggesting these deeper habitats may behave as corridors of connectivity across the network, likely due to high productivity. In the simulated network of *P. astreoides*, shallow habitat appears more central than

deeper habitat due to greater productivity and larval exchange among habitats above 10 m. Thus, these two species seem to have distinct local management requirements, and local habitat fragmentation is likely to affect populations of these species differently. Average shortest paths results may help to explain field observations that brooding species like *P. astreoides* outperform larger spawning species in degraded shallow areas (Green et al. 2008), because their shallow-water larval exchange networks may be more connected and thus resilient.

Implications

The degree to which mesophotic and shallow coral populations are connected is a knowledge gap currently limiting the usefulness of the DRRH to coral reef management. To date, this knowledge gap has primarily been addressed using population genetics (Bongaerts et al. 2010b, 2013; van Oppen et al. 2011; Prada and Hellberg 2013; Serrano et al. 2014). Although this analytical tool is powerful, it has some limitations, including: (1) the spatial extent of sampling can alter conclusions, as larval exchange may occur at scales or in areas not addressed by genetic study; (2) a lack of genetic structure does not necessitate connectivity, but may be indicative of methodological shortcomings; (3) the longevity of coral genets can complicate conclusions, as potentially centuries-old colonies may or may not continuously contribute alleles to new cohorts; (4) the methods do not inherently reveal mechanisms that influence connectivity or isolation; and (5) genetic connectivity is a record of historical—potentially stochastic—connectivity and may not be predictive of future demographics. For these reasons, a biophysical modeling approach was employed here to complement ongoing coral population genetic studies (sensu Baums et al. 2006; Foster et al. 2012) and to investigate explanatory mechanisms that promote or limit connectivity. The model results predict a high potential for local MSS, but at levels (<10 %) that may be difficult to detect using traditional population genetic sampling.

We cannot make specific predictions regarding whether MCEs serve as sources of recovery for shallow populations without fully understanding how depth affects the fertilization and successful recruitment of mesophotic larvae. The sensitivity analyses described here provide benchmarks for future research addressing these aspects of vertical connectivity. Vertical coral connectivity in different geographic locations, at different spatial scales, and of different species will be dependent on local hydrologic forcing and species-specific adult and larval traits, which imply that the DRRH will not be equally applicable in space and time. As climate change and coastal development continue to fragment coral habitats, the competitive

dynamics for settling coral larvae may be difficult to predict, and a wide range of novel tools will be necessary to properly predict and manage coral reef persistence. Although projections of coral reef futures may be uncertain, the exchange of larvae between diverse habitats is likely fundamental to coral metapopulation persistence. Modeling has proven to be a useful tool for investigating the role of vertical larval connections in coral reef resilience and advancing our understanding of vertical larval pathways.

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