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REPORT

Modeled connectivity of *Acropora millepora* populations from reefs of the Spratly Islands and the greater South China Sea

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Abstract The Spratly Island archipelago is a remote network of coral reefs and islands in the South China Sea that is a likely source of coral larvae to the greater region, but about which little is known. Using a particle-tracking model driven by oceanographic data from the Coral Triangle region, we simulated both spring and fall spawning events of *Acropora millepora*, a common coral species, over a 46-yr period (1960–2005). Simulated population biology of *A. millepora* included the acquisition and loss of competency, settlement over appropriate benthic habitat, and mortality based on experimental data. The simulations aimed to provide insights into the connectivity of reefs within the Spratly Islands, the settlement of larvae on reefs of the greater South China Sea, and the potential dispersal range of reef organisms from the Spratly Islands. Results suggest that (1) the Spratly Islands may be a significant source of *A. millepora* larvae for the Palawan reefs (Philippines) and some of the most isolated reefs of the South China Sea; and (2) the relatively isolated western Spratly Islands have limited source reefs supplying them with larvae and fewer of their larvae successfully settling on other reefs. Examination of particle dispersal without biology (settlement and mortality) suggests that larval connectivity is possible throughout the South China Sea and into the Coral Triangle region. Strong differences in the spring versus fall larval connectivity and dispersal highlight the need for a greater understanding of spawning dynamics of the region. This study confirms that the Spratly Islands are likely an important source of larvae for the South China Sea and Coral Triangle region.

Keywords Larval connectivity · Coral reefs · Individual-based modeling · Coral Triangle · South China Sea

Introduction

The multi-national Coral Triangle region of the western equatorial Pacific (Veron et al. 2009a) has some of the highest abundance and diversity of corals and other reef species in the world (Barber 2009). Like elsewhere in the world, the Coral Triangle's reef ecosystem is threatened by anthropogenic climate change (Hoegh-Guldberg et al. 2007, 2009; Veron et al. 2009b), with many important environmental conditions (pH, sea level, temperature) expected to change as our climate warms. The Spratly Islands archipelago is a system of hundreds of reefs and small islands located in the South China Sea, west of the Coral Triangle (Fig. 1). Studies have looked at large-scale connectivity patterns in the Spratly Islands (Kool et al. 2011) and identified the Spratly Islands as an important source of larvae into the Coral Triangle region (McManus 1994; Kool et al. 2011), but little is known regarding fine-scale connectivity among the individual reefs of the Spratly Islands, or their importance as a supply of larval reef organisms to other reefs within the South China Sea.

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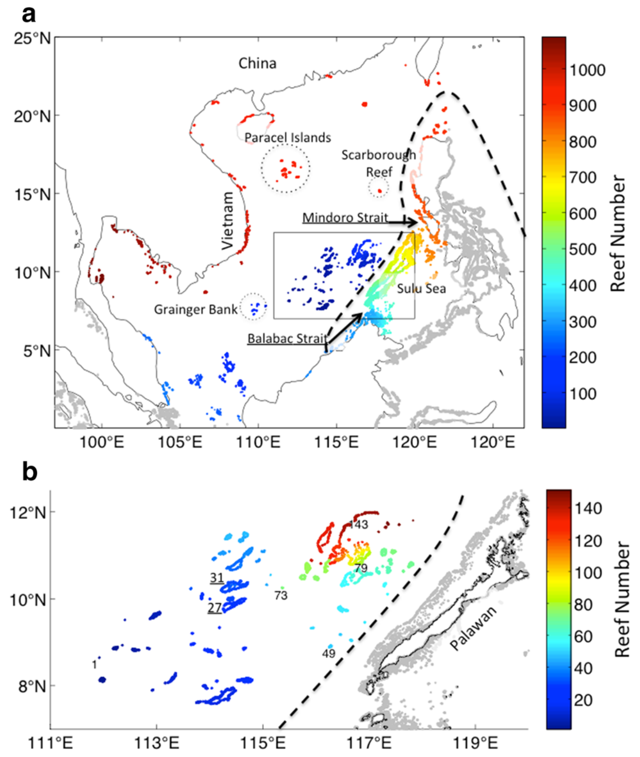

Fig. 1 Numbered reefs of **a** the South China Sea and **b** the Spratly Islands. Reef numbers assigned are used in the connectivity matrix plots (Figs. 3, 7). *Underlined numbers* (**b**) refer to reefs mentioned in the text; *non-underlined numbers* (**b**) correspond to the division lines on Fig. 3. *Black dashed line* represents the boundary of the Coral Triangle region (defined by Veron et al. 2009a)

Coral reef populations are generally considered to be open populations, with new recruits coming from external sources and spawned larvae dispersing to other reefs by virtue of their planktonic larval stage (Caley et al. 1996). The recruitment of new coral larvae to a reef is critical to maintain coral abundances, genetic diversity of populations (Ayre and Hughes 2004), and community ecosystem dynamics (Graham et al. 2006). These factors also impact the ability of reef ecosystems to remain resilient, defined as being both resistant to and able to recover from disturbances (McClanahan et al. 2012). Thus, understanding the recruitment pathways, or connectivity, between reefs can help identify reefs of particular importance to the larger meta-population of interconnected reefs (Cowen and Sponaugle 2009). Information on connectivity is thus of critical importance in the management and conservation of reef ecosystems (Fernandes et al. 2005; Jones et al. 2007; Almany et al. 2009).

Connectivity between reefs is a product of both physical and biological factors. Local currents and bathymetry play a role in the transport of larvae to new settlement locations (Graham and Largier 1997; Gaines et al. 2003; Largier 2003), and larval biological traits, including ability to settle (competency), mortality, and behavior (Sponaugle et al. 2002; Gerlach et al. 2007) determine when and where larvae may settle. Post-settlement behavior and mortality (Hunt and Scheibling 1997), as well as larger community and ecosystem dynamics, can also play an important role in recruitment to reproductive age. Connectivity between reefs can be determined directly using population genetics (Hedgecock et al. 2007), chemical markers (Jones et al. 2005), or through direct observation (Leis et al. 2006), but these methods are labor intensive and often tell us little about the large-scale patterns of a region. Indirect methods of studying connectivity often utilize a combination biological–physical model (Werner et al. 2007; Kool et al. 2011), where multiple spawning events over a large regional scale can be simulated and analyzed.

This study utilizes such a biological–physical model to examine connectivity at the scale of individual reefs of the Spratly Islands to determine (1) which are the most important source reefs to the Spratly Islands themselves, (2) which reefs of the greater South China Sea are dependent upon the Spratly Islands as a larval source, and (3) whether there are seasonal differences in connectivity and larval dispersal from the Spratly Islands. Given the lack of direct observations of connectivity in the Coral Triangle region, this reef-scale modeling approach provides practical information for guiding management of the Spratly Island archipelago.

Materials and methods

This study used output from the Regional Ocean Modeling System (ROMS) (Shchepetkin and McWilliams 2005; Haidvogel et al. 2008), configured for the Coral Triangle region, from a 1960–2005 hindcast simulation to drive a particle-tracking model. Particles were released from reef locations within the Spratly Islands as larvae of the species *Acropora millepora*, a common and well-studied broadcast spawning coral of the Spratly Islands (Latypov 2011, 2012; Zhao et al. 2013). The particles incorporated biological parameters for competency, mortality, and settling on coral substrate during their transport through the South China Sea and Coral Triangle region.

Coral reef data

Reef locations throughout the Coral Triangle and Spratly Islands were determined using coral coverage data from the Global Distribution of Coral Reefs (2010). The dataset was compiled by UNEP World Conservation Monitoring Centre (UNEP-WCMC) and the WorldFish Centre, in collaboration with World Resources Institute and The Nature Conservancy. Data were from the Millennium Coral Reef

Mapping Project (IMaRS-USF 2005; IMaRS-USF and IRD 2005) and the World Atlas of Coral Reefs (Spalding et al. 2001). The data were converted from ArcGIS shape files to 30-m resolution raster files and then upscaled to an approximately 1-km^2 grid. Each reef grid cell was assigned a percentage of reef area based on the data.

Biology of *Acropora millepora*

Biological parameters for the coral species *A. millepora* were derived from experimental work by Heyward and Negri (2010) and Connolly and Baird (2010). The percentage of the population that was competent and able to settle at any model time ($\mathrm{PC_T}$) was determined using Eq. (1), where C_A is the rate of acquisition of competency (0.18 d^{-1}), C_L is the rate of loss of competency (0.050 d^{-1}), T is the time since larval release, and T_{crit} is the pre-competency period (3.239 d). All parameters are mean values reported by Connolly and Baird (2010).

$$\mathrm{PC_T} = \frac{C_A\left(e^{(-C_L(T-T_{\mathrm{crit}}))} - e^{(-C_A(T-T_{\mathrm{crit}}))}\right)}{C_A - C_L} \quad (1)$$

Mortality rate (M; units = d^{-1}) of the population was determined using Eq. (2), derived from data presented in Connolly and Baird (2010), where T is the time since larval release (units = d).

$$M = 0.106T^{-0.46} \quad (2)$$

Probability of settlement for any individual in our model (S_I) at any location (i,j) was determined using Eq. (3) where S_{pop} is the general population settlement rate (0.25 h^{-1}) and $S_{\mathrm{coral}(i,j)}$ is the probability of settlement based on the amount of coral reef coverage at any location (i,j) (Table 1).

$$S_{I(i,j)} = S_{\mathrm{pop}} S_{\mathrm{coral}(i,j)} \quad (3)$$

Settlement of in situ larvae onto a reef is dependent on a myriad of settlement cues (Ritson-Williams et al. 2009) that occur on a much smaller scale (centimeter or meter scale) than our physical oceanographic model results (kilometer scale). Present-day knowledge of these processes is insufficient for deriving a specialized settlement routine within our model framework, and Eq. (3) was devised as a simple approximation of settlement and recruitment. In addition, the calculations do not consider post-settlement mortality, competition, and predation. We have chosen a settlement rate of 25 % h^{-1} so that some portion of larvae would transit a reef, as is likely to happen in the natural environment. Further, the threshold ranges of coral coverage (Table 1) were set to avoid "over prescribing" our model and to simplify settlement, as we have very little empirical knowledge of these factors.

Table 1 Model parameters that are dependent upon coral reef coverage

Coral reef coverage (%)	0	1–25	25–50	50–75	75–100
S_{coral}	0.0	0.25	0.50	0.75	1.0
Released larvae	0	50	100	150	200

Settlement probability (S_{coral}) used in Eq. (3) and number of released larvae from Spratly Island reef locations

Physical and individual-based model

A ROMS implementation for the Coral Triangle provided the physical oceanographic currents for the South China Sea and Coral Triangle region (Castruccio et al. 2013). ROMS is a commonly used three-dimensional hydrostatic ocean model with a terrain-following coordinate system (http://www.myroms.org). Model resolution was approximately 5 km in the horizontal with 50 vertical levels. Surface forcing of the ROMS model is from the Modern-Era Retrospective Analysis for Research and Applications (MERRA) dataset (Rienecker et al. 2011). MERRA is a reanalysis product of empirical data that is temporally and spatially consistent to drive the ROMS model. Average ROMS output was saved daily for the years 1960 through 2005, and daily snapshots of oceanographic conditions were read and processed by the individual-based particle-tracking model.

The individual-based model (IBM) has previously been used to model other zooplankton including copepods (Batchelder and Miller 1989; Batchelder et al. 2002) and krill (Dorman et al. 2011). The IBM interpolates saved physical data both spatially (to the particle location within the grid) and temporally (between saved time-steps). For each time-step (180 s), coral larvae were transported within the South China Sea and Coral Triangle using current data (horizontal and vertical) and a classic fourth-order Runge–Kutta advection scheme (Butcher 2003). Vertical diffusion is incorporated via a non-naïve random walk (Visser 1997), and no swimming behavior was assigned to the particles. Larvae acquired/lost competency, died, and settled based on Eqs. 1–3.

Model runs to examine the connectivity of *A. millepora* were initiated 5 d after the spring and fall full moon that corresponded most closely with 1 April and 1 October, respectively, for the years 1960–2005. Particles were released from each grid cell within the Spratly Islands that contained some coral coverage (over 3000 coral grid cells). Particles were released into surface waters (between 0 and 10 m depth), and all particles were tracked for 90 d. The number of particles released from each coral grid cell corresponded to the percent coral coverage (Table 1), resulting in approximately 330,000 coral larvae released from the Spratly Islands per model run. *Acropora* *millepora* population biology (acquisition/loss of competency, settlement, mortality) was simulated using saved 90-d particle tracks. A total of ten simulations of the population biology of *A. millepora* were modeled for each season/year of larval dispersal trajectories to account for variability in individual biological state (competency, mortality) while traversing underlying reef coverage.

A comparison of particle density distributions (using linear correlation coefficient; see Simons et al. 2013) over a range of number of larvae released (50–40,000 larvae) was conducted to determine the minimum number of particles to release from each reef to realize the "true" particle density distribution of the population (defined as the particle density distribution at 40,000 particles). We found that the fraction of unexplained variance ($1 - r^2$) was less than 10 % when releasing more than 6000 particles from a reef site. Increasing the number of released particles to 6000 per location would have made 46 years' worth of simulations computationally prohibitive. Thus our results employ temporal averages and focus on spatial variability throughout the Spratly Islands. To verify that releasing only 50 larvae yr^{-1} (our minimum number released) was sufficient for results that used 46-yr averages, we conducted additional simulations that released 50 and 6000 larvae from a single reef for 20 yr. Comparison of the average percentage of settled larvae at each reef within the Spratly Islands using Pearson's correlation coefficient found significant correlation ($r(149) = 0.99$, $p < 0.001$) between the 50-larvae and 6000-larvae simulations.

Analysis

Individual reefs were defined by combining coral grid cells that were contiguous into a single reef. In the Spratly Islands archipelago, this condensed the approximately 3000 coral grid cells into 151 reefs (Fig. 1). The number of larvae released from each reef was thus based on its total area and percent coral coverage.

Connectivity ($C_{\text{so,si}}$) between each source reef (so) and sink reef (si) was calculated using Eq. (4) where $S_{(\text{so,si})}$ is the number settled from source to sink reef and R_{so} is the number released from the source reef. Normalizing connectivity in this fashion provides insight into the success of the larvae of each source reef.

$$C_{(\text{so,si})} = \frac{S_{(\text{so,si})}}{R_{\text{so}}} \tag{4}$$

The measure of isolation used in our analysis was computed as the percentage of area with reef coverage in a 100-km radius from the center of the reef (higher isolation index equates to more reef coverage). The 100-km distance generally agrees with findings that the majority of larvae that settle do so within 50–150 km of the releasing location (Kool et al. 2011; Treml et al. 2012; Wood et al. 2014).

Diversity of larval sources for each reef was calculated using the Simpson index of diversity, Eq. (5), which includes both source richness (number of source reefs) and evenness (number of larvae from each source reef). $D_{(\text{si})}$ is the diversity index for each sink reef, $n_{(i)}$ is the number of larvae from each source reef, and N is the total number of larvae that settled on the sink reef. An index of diversity measurement was calculated for every reef and every year modeled. The yearly diversity values were averaged together for analysis and presentation.

$$D_{(\text{si})} = 1 - \left(\frac{\sum_{i=1}^{\text{so}} n_i (n_i - 1)}{N(N-1)} \right) \tag{5}$$

Results

ROMS average currents

Circulation patterns from the ROMS simulation confirm the observations of Hu et al. (2000) that surface circulation in the South China Sea is driven by seasonal differences in the state of monsoonal winds. Average (30 d) seasonal surface currents of the region differ in two primary ways. During the fall, the seasonal southward-flowing current along the Vietnam coastline is much stronger than in spring (Fig. 2). South China Sea surface currents generally flow out of the Sulu Sea during spring and into the Sulu Sea in the fall through the Mindoro Strait (north of Palawan) and Balabac Strait (south of Palawan) (Fig. 2).

Within the Spratly Island archipelago, currents tend to be stronger during the spring, especially in the southern islands. Spring currents in the western Spratly Islands (west of 115°E) tend to flow to the north (and slightly westward), while the eastern Spratly Islands are influenced by southerly flow leaving the Mindoro Strait which turns clockwise and joins the northerly flow leaving the Spratly Islands. Those reefs closest to the southern end of Palawan experience the weakest surface currents. Fall surface currents are more consistently northward (and slightly eastward) throughout the Spratly Islands.

Connectivity within the Spratly Islands

Self-retention of *A. millepora*, i.e., the percentage of larvae that settled on the reef they were released from, was evident at all locations in the Spratly Islands and was significantly greater during the fall (1.52 % of larvae released) than during spring (0.52 %; $t(300) = 7.23$, $p < 0.001$; Fig. 3, diagonal of matrices). Reefs of the western Spratly

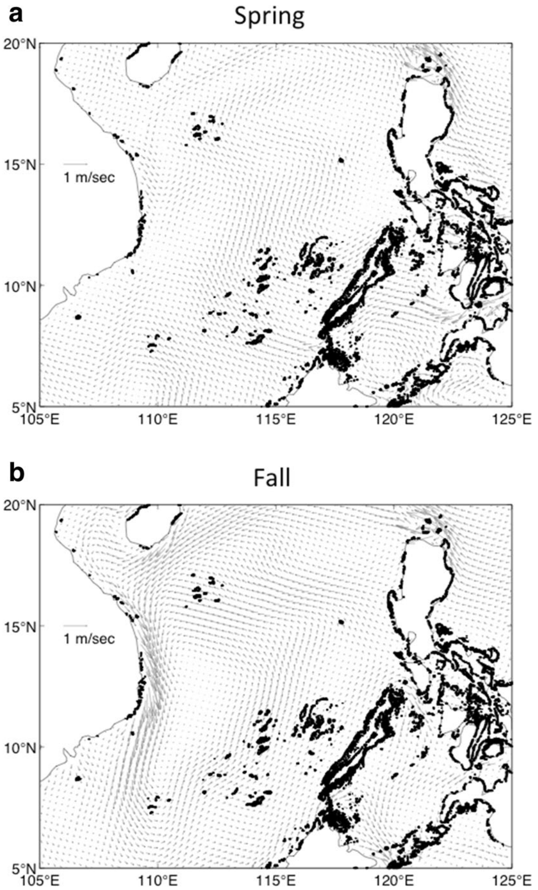

Fig. 2 Mean simulated (ROMS) surface currents of the South China Sea from 1960 to 2005 during **a** spring and **b** fall. Yearly means of the 30 d post-release of larvae (release date varied based on lunar cycle) were averaged over the 46 yr of simulations

Islands (reef numbers 1–48) were not well connected with the rest of the Spratly Islands. These reefs were rarely a strong source of larvae to the more easterly reefs of the Spratly Islands and were not a strong sink of larvae from other Spratly Island reefs (Fig. 3). The reefs of the eastern Spratly Islands are in close proximity to one another, and greater connectivity among many reefs is evident. Throughout the islands, the larger reefs tended to be strong sinks of larvae from many reefs (Figs. 1, 3; see reefs 27 and 31).

Reef isolation was significantly correlated with success of settlement of spawned larvae for both spring and fall ($r(149) = 0.86$, $p < 0.001$ (spring); $r(149) = 0.77$, $p < 0.001$ (fall); Fig. 4). The reefs that were the strongest sources for other Spratly Island reefs were located in the eastern Spratly Islands where reef density is greater; conversely, the weakest sources were located in the western Spratly Islands where reefs are more isolated (Fig. 5).

The diversity of sources of larvae was significantly greater ($t(300) = 4.65$, $p < 0.001$) during spring (mean $D_{(si)} = 0.65$) than during fall (mean $D_{(si)} = 0.59$) for reefs of the Spratly Islands. During both spring and fall model runs, reefs in the western half of the Spratly Islands generally had the lowest $D_{(si)}$ values (Fig. 6).

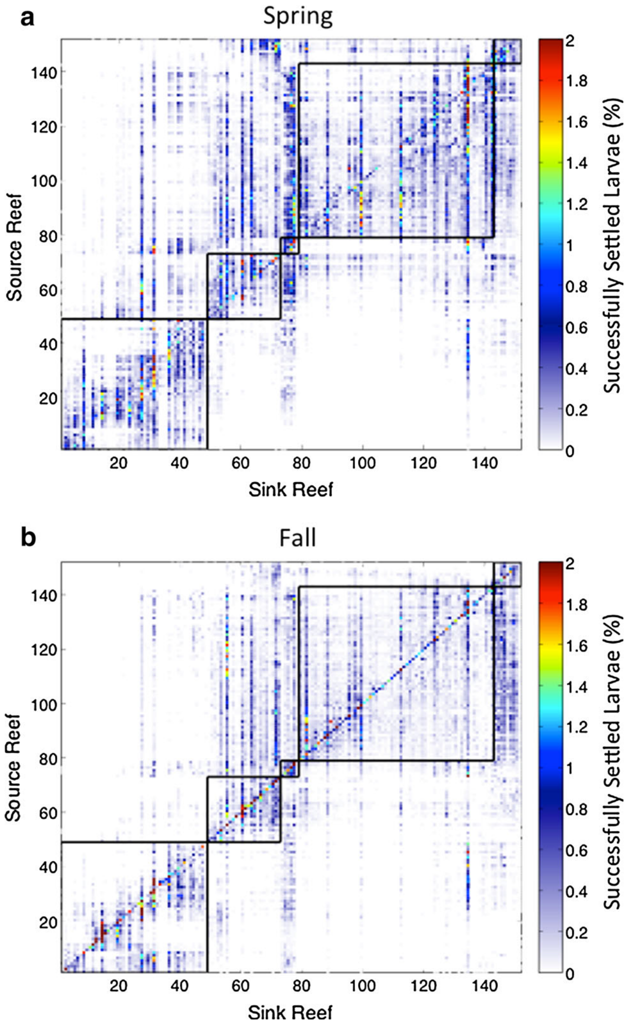

Fig. 3 Mean connectivity between of reefs of the Spratly Islands during **a** spring and **b** fall model simulations. *Black lines* represent geographic break points between regions (reef numbers are plotted in Fig. 1a)

Settlement beyond the Spratly Islands

Palawan (Philippines) was the location of the greatest settlement of larvae from the Spratly Islands (Fig. 7). Mean settlement was less than 1 % of larvae released, but connectivity between the Spratly Islands and Palawan was realized in over 50 % of our model runs. Settlement was concentrated to the southern Palawan reefs during spring and to the northern Palawan reefs during fall (Figs. 7, 8).

Several isolated reefs of the South China Sea were locations of settlement for Spratly Island coral larvae.

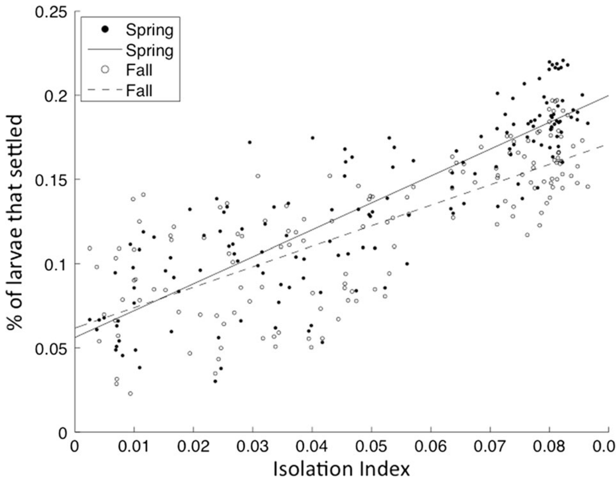

Fig. 4 Effect of reef isolation on successful settlement of spawned larvae during spring (*filled circles* and *solid line*) and fall (*open circles* and *dashed line*) model simulations. The isolation index for any individual reef is defined here as the percentage of reef area within a 100-km radius; thus a lower isolation index indicates more isolation

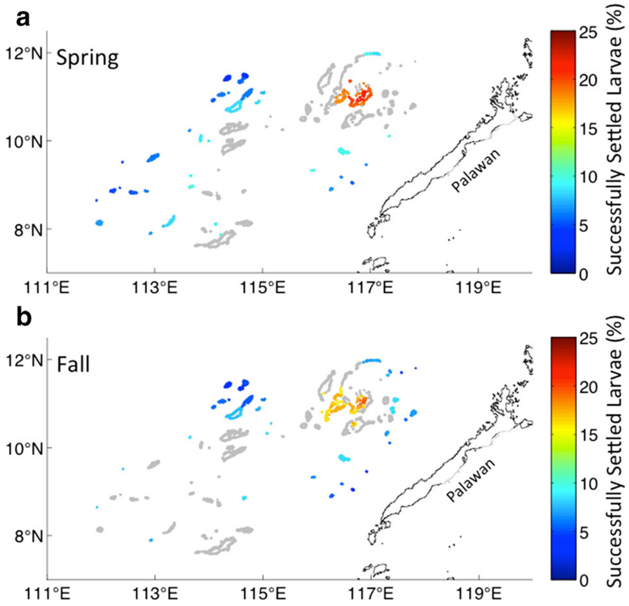

Fig. 5 Average spawned larvae settlement success (% of released larvae) of Spratly Island reefs during **a** spring and **b** fall model simulations. The upper and lower quartile are plotted to show the most and least successful reefs, respectively. Reefs plotted in *gray* are from the middle quartiles

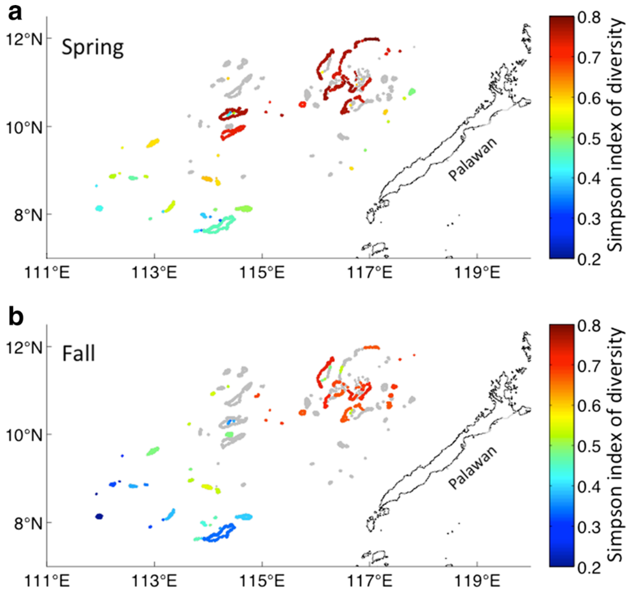

Fig. 6 Simpson index of diversity of source reefs supplying Spratly Islands reefs during **a** spring and **b** fall model simulations. The upper and lower quartile are plotted to show reefs with the most and least number of reefs that supply larvae, respectively. Reefs plotted in *gray* are from the middle quartiles of the data

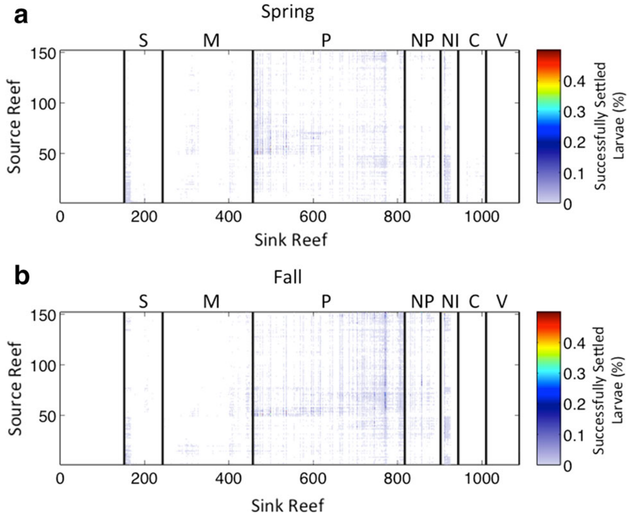

Fig. 7 Average settlement during **a** spring and **b** fall model simulations from reefs of the Spratly Islands (source reefs) to reefs of the South China Sea and greater Coral Triangle region (sink reefs). Raw numbers of settled larvae were converted to a percentage by dividing by total number released from the source reef. *S* southern islands, *M* Malaysia, *P* Palawan, *NP* northern Philippines, *NI* northern islands, *C* China, *V* Vietnam. Settlement on the Spratly Islands (reefs 1–151) is not plotted

Acropora millepora larvae settled on Scarborough Reef (15.1°N, 117.2°E) in over 20 % of our model runs during both spring and fall seasons. During the spring, settlement was realized more than 20 % of the time to the south (Grainger Bank, 7.8°N, 110.4°E) and during fall, settlement was realized more than 20 % of the time to the Paracel Island reefs (16.0°N, 112.5°E) and scattered reefs through the northern Philippines. Spratly Island reefs that realized connectivity in more than 20 % of model runs were distributed more southerly during spring releases and more northerly during fall releases (Fig. 8).

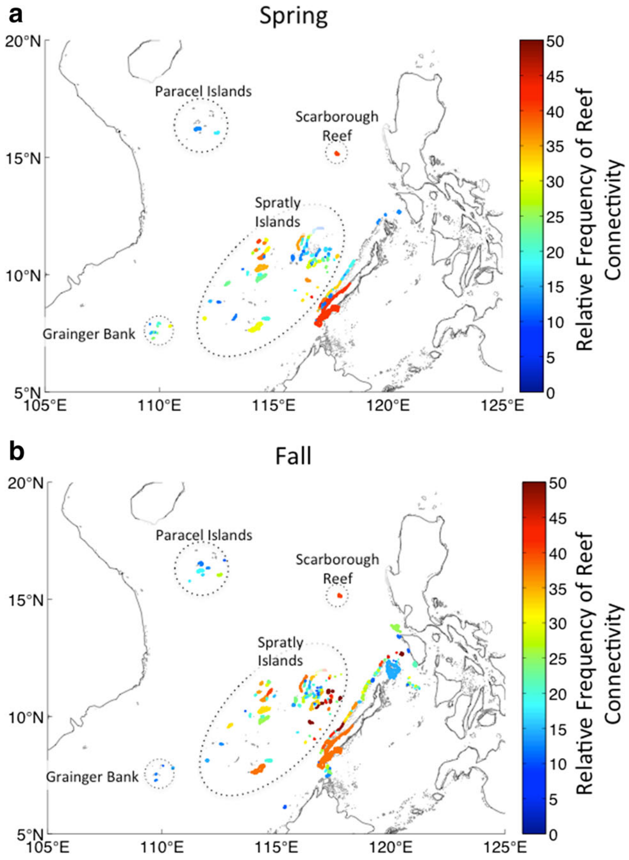

Fig. 8 Relative frequency of connectivity (i.e., percentage of model simulations where any level of connectivity is achieved) between the Spratly Islands and reefs of the South China Sea and greater Coral Triangle region in **a** spring and **b** fall. Each Spratly Island reef may have multiple connections with other reefs; only the greatest relative frequency of connectivity is plotted

Dispersal of larvae without settlement

The physical dispersal of particles, disregarding biological traits (competency, mortality, settlement), from the Spratly Islands to the greater South China Sea was examined at 30 and 60 model days. Results indicate that transport pathways exist between the Spratly Islands and reefs of northwestern Philippines, Malaysia, and Brunei (in addition to Scarborough Reef, Grainger Bank, and the Paracel Islands) in over 20 % of our model runs during both spring and fall (Fig. 9). During spring releases, more particles were dispersed in a westerly direction toward Vietnam. During fall releases, more particles were found near reefs of western Malaysia and Brunei, eastern Indonesia, the northern Philippines, and the Paracel Islands (Fig. 9).

Discussion

This modeling study provides a detailed look at the connectivity of the reefs of the Spratly Islands over 46 yr. Due to the remote nature of this archipelago, there is little empirical data on corals of the region and nothing known regarding connectivity patterns between individual reefs. Therefore, our model results should be considered potential results until further data become available and allow verification. Considering the lack of empirical data in the region, these results should be an important tool to inform any future management of the Spratly Islands.

Connectivity within the Spratly Islands

Our model results suggest that within the Spratly Islands, ocean currents, reef isolation, and positioning relative to other reefs are all important factors in understanding the degree to which any one reef acts as a larval source to other Spratly Island reefs. Modeled larvae released from the large cluster of reefs in the eastern Spratly Islands, for example, were the most likely to successfully settle on other reefs within the Spratly Islands (Fig. 5). Based on calculations of a settlement radius that takes into account when the majority of *A. millepora* larvae are competent, these reefs appear to be the best connected within the Spratly Islands. Reefs that had the lowest percentage of their larvae settle within the Spratly Islands tended to be isolated on the edges of the archipelago, especially to the north (Fig. 5). The majority of larvae released from these reefs were generally transported by northward-flowing currents away from Spratly Island settlement locations and toward hundreds of kilometers of open ocean (Fig. 2). Most of the larvae from these reefs did not encounter reef substrate while competent, but these same reefs were the strongest sources of Spratly Island larvae to reefs external to the Spratly Islands (see below).

One consideration in determining the resilience of a reef to environmental perturbations is the number of other reefs that are potential sources of recruits. High diversity in larval sources and even distribution of supply from those sources protects against loss of connectivity from any one particular source and may provide a greater level of genetic diversity at the species level (Palumbi 1994). Reefs with the lowest diversity of sources in the Spratly Islands were found primarily in the western part of the archipelago (Fig. 6). As we only released larvae from Spratly Island reefs and currents were generally northward (Fig. 2), some of the limited diversity is likely an artifact of our study method (i.e., no reef sources upstream). In our model results, reefs that were surrounded on most sides by other reefs, such as the central reefs of the eastern Spratly Islands, also had a low diversity of sources. This reflects possible “rain out” of larvae settling on other reefs before coming in contact with “interior” reefs. The degree to which this occurs would be sensitive to the parameters determining larval settlement rate (S_I) in Eq. (3). As these same reefs were in the upper quartile of successful source

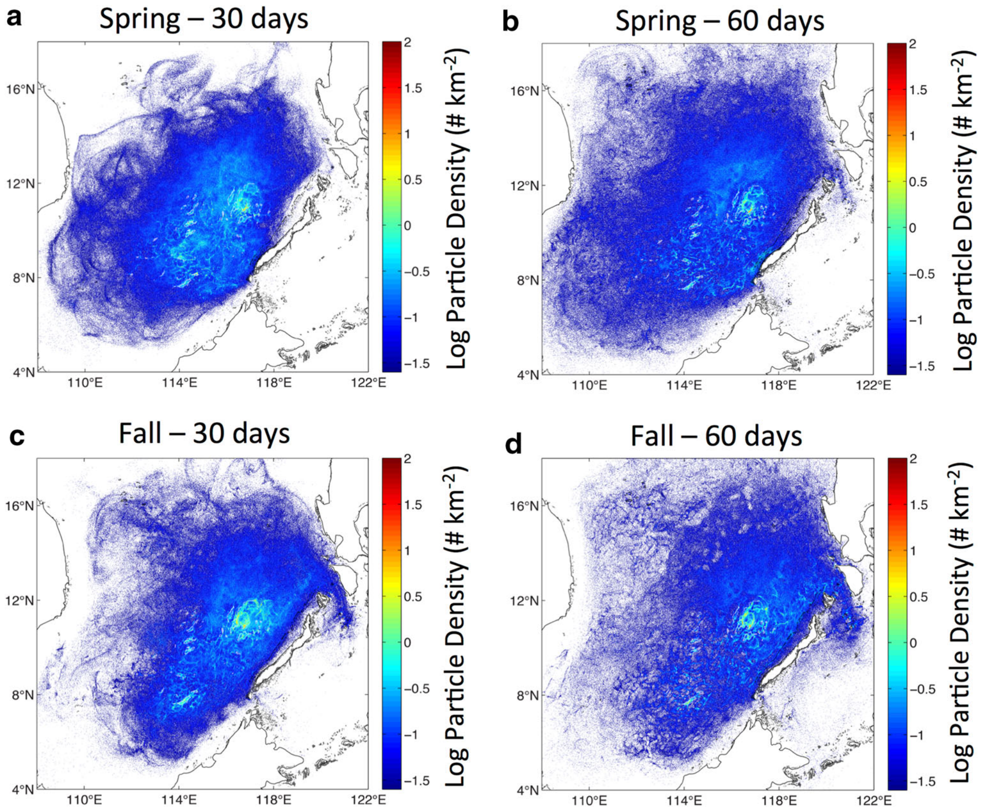

Fig. 9 Log of particle densities in the South China Sea at **a**, **c** 30 d and **b**, **d** 60 d post-release from the Spratly Islands during **a**, **b** spring and **c**, **d** fall model simulations

reefs of the Spratly Islands, the potential lack of diversity of their sources of larvae should be of concern from a management perspective.

Settlement beyond the Spratly Islands

The Spratly Islands, despite their isolation, appear to be a source of *A. millepora* larvae to the more isolated reefs of the South China Sea (Paracel Islands, Scarborough Reef, and Grainger Bank). Larvae from the Spratly Islands settled on these reefs in over 20 % of our model simulations (Fig. 8). Isolated reefs are generally thought to recover more slowly from disturbance events (Ayre and Hughes 2004; Graham et al. 2006) due to lower recruitment, which is considered to be an important factor in recovery from such events (McClanahan et al. 2012). Larval supply to isolated reefs is also especially important for genetic diversity of reef corals (Planes and Fauvelot 2002), and thus resilience of those reefs to changing environmental conditions (Munday et al. 2009). The reefs of the Spratly Islands that are sources to external reefs tend to be on the northern and southern edges of the archipelago and have been identified as not contributing much as a local source population to the Spratly Islands. This result highlights the need to approach management of these reef resources from as broad a perspective as possible as management strategies that encompass solely the Spratly Islands might not recognize the importance of these reefs to reefs beyond the archipelago.

Our results agree with those of Kool et al. (2011) that the Spratly Island reefs are a likely source of larvae for the western Coral Triangle region. If the Spratly Islands are a significant source of larvae into the Sulu Sea, the lack of management (McManus et al. 2010) and more recent destruction of coral habitat (Rapp-Hooper 2015) in the region should be of concern to management efforts within the western Coral Triangle. Over multiple generations of coral spawning, these reefs likely contribute to genetic diversity throughout the Coral Triangle (Kool et al. 2011), further highlighting the importance of the Spratly Islands to the greater region. Finally, about 50 % of the Spratly Island reefs that were found to contribute larvae to the Coral Triangle region (southern Palawan Island or into the Sulu Sea) are those with the least amount of diversity of source reefs (Figs. 6, 7), perhaps making them more susceptible to changing environmental conditions or anthropogenic impacts.

The seasonal difference in modeled connectivity between reefs is most prevalent in settlement to reefs external to the Spratly Islands. Settlement is greatest at the southern end of Palawan during the spring model simulations and at the northern end of Palawan during the fall simulations. There is a corresponding seasonal northerly shift in the Spratly Island source reefs to Palawan as well (Fig. 7). Given these differences, understanding the seasonal patterns in coral spawning in the Spratly Islands is critical for effective management. Due to their remote nature, there are very few data on the timing of coral spawning in the Spratly Islands or the surrounding region. The geographically closest study we know of that observed coral spawning was to the north of the Spratly Island in northwestern Luzon, Philippines (Vicentuan et al. 2008). Spawning was observed during March through May for the region, but sampling was not conducted during the fall months. Other studies have found fall spawning of *Acropora* species (Baird et al. 2000) and both spring and fall spawning for a multitude of corals (Penland et al. 2004) at similar latitudes. Mass spawning of coral and other invertebrate larvae is influenced by a variety of external factors including sea surface temperature (Penland et al. 2004), solar radiation and lunar phase (Sweeney et al. 2010), and time of year (Guest et al. 2005). In tropical regions, where there is little variation in sea surface temperature throughout the year, mass spawning is more likely controlled by solar and lunar spectral dynamics. As the Spratly Islands are between latitude 7 and 12 degrees North and experience two separate peaks in solar radiation over the course of a year, we think it is likely that this region experiences two distinct seasonal spawning events. If this is true, then our model results suggest that the seasonal differences in connectivity between the Spratly Islands and external reefs are an important factor in understanding reef connectivity patterns within the South China Sea.

Dispersal of larvae without settlement

Particle densities at 30 and 60 d after release from Spratly Island reefs indicate that larvae from these reefs can be transported throughout the South China Sea and well into the Sulu Sea (Fig. 9). There are seasonal differences in the particle densities as spring particles are advected closer to the coast of Vietnam, while during the fall a strong south-flowing current prevents the particles from reaching the Vietnam coast. Fall densities show particles being advected much further into the straits to the north and south of Palawan and into the Sulu Sea, as well as being transported further north toward the Paracel Islands and the northern Philippines. This provides insight into the potential for connectivity between reef populations of other species of coral or other reef organisms with a longer planktonic larval stage including other coral species (Connolly and Baird 2010), reef fishes (Wellington and Victor 1992) and invertebrates (echinoderms—Lucas 1982; crustaceans—Booth and Phillips 1994; Kough et al. 2013; gastropods—Kano 2006). In most cases, the magnitude and frequency of connectivity to distant reefs was small, but these types of connections may still have an important influence on genetic make-up and influence populations over multiple generations (Kool et al. 2011) and on evolutionary timescales (Slatkin 1993).

It should also be noted that the greatest particle densities at both 30 and 60 d are adjacent to or surrounded by reefs of the Spratly Islands (Fig. 9). This illustrates how the small-scale flow around the reef bathymetry itself influences retention within the Spratly Island archipelago.

The results of this study further our understanding of connectivity of the Spratly Island reefs and their importance as a larval source of *A. millepora* within the archipelago and to reefs of the South China Sea and Coral Triangle region. While these results are based on modeling efforts and await validation with empirical data, they represent the most comprehensive information available on connectivity in this region to date. Understanding the relationship between reefs is critical for managing these important reef ecosystems at multiple spatial scales and for predicting their vulnerability to climate perturbations. Model simulations have demonstrated that the cluster of reefs in the eastern Spratly Islands are potentially important source reefs for the region and that reefs in the western Spratly Islands are the least successful sources with most larvae being transported to the north into the South China Sea. Due to prevailing currents, the reefs of the western Spratly Islands may also have limited connectivity to other reefs of the region and should be considered the most susceptible to large climate perturbations or disturbance events. The Spratly Islands are a potential source of larvae to Philippine reefs (primarily Palawan), as well as isolated South China Sea reefs. Seasonal differences in settlement patterns to these reefs make understanding the spawning patterns of reef organisms of the Spratly Islands a priority.

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