Connectivity between submerged and near-sea-surface coral reefs: can submerged reef populations act as refuges?

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ABSTRACT

Aim Connectivity is a key determinant of coral reef resilience. However, connectivity models rarely account for deep or submerged reefs, despite their widespread occurrence in many coral reef provinces. Here, we model coral larval connectivity among submerged and near-sea-surface (NSS) reefs, investigate differences in dispersal potential for coral larvae from these differing reef morphologies and estimate the potential for deeper reef habitats (> 10 m) to provide a source of larvae to shallower reef habitats (< 10 m).

Location Great Barrier Reef, Australia.

Methods We used two newly developed, high-resolution models to identify the location and spatial extent of submerged and NSS reefs and to simulate oceanographic currents ('SLIM') affecting larval dispersal. Dispersal patterns for five depth-generalist coral species with differing life histories and dispersal potential were modelled using an individual-based model (IBM).

Results Near-sea-surface reefs were the largest source of larvae successfully settling, but submerged reefs exported a greater proportion of larvae per unit area to other reefs. Larvae originating from submerged reefs also dispersed greater distances. Recruits on shallow-water reef habitats primarily originated from other shallow areas, but two-way connectivity did occur between deep and shallow habitats. Empirical data indicate that long-term coral cover has declined most steeply on the shallow habitats predicted by our model to be highly dependent on other shallow habitats for recruits.

Main conclusions Submerged reefs may contribute significantly to larval production and should therefore be considered in connectivity analyses. The hydrodynamic environment on submerged reefs results in larvae dispersing greater distances, potentially increasing their importance as source reefs following disturbances. Deep reef habitats are generally less exposed to disturbances and could therefore constitute an important larval source to some shallow habitats following disturbances. Given the importance of connectivity to coral reef resilience, greater attention should be afforded to identifying and protecting submerged reefs and other deeper habitats.

Keywords
Biophysical model, connectivity, coral larva, larval dispersal, near-sea-surface reef, submerged reef.

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INTRODUCTION

Reef-building corals are the key ecosystem engineers of tropical coral reefs, the most diverse marine ecosystems on Earth. Increasing disturbance frequency is causing declines in the abundance and shifts in the composition of coral assemblages (Loya et al., 2001; Hughes et al., 2003; Wakeford et al., 2007). Altered coral assemblages can affect many other taxa dependent on structurally complex reefs (e.g. reef-associated fishes), leading to altered ecosystem processes and impacting the provision of ecosystem services (Hughes et al., 2010; Graham & Nash, 2013; Pratchett et al., 2014). Consequently, the ability of reefs to recover from disturbance and maintain a coral-dominated state (termed 'resilience') is a key objective of coral reef management (Mumby & Hastings, 2008; Mumby & Steneck, 2008; Hughes et al., 2010).

Like many marine invertebrates, adult corals are sessile and rely on larval transport for dispersal and population persistence (Shanks et al., 2003; Burgess et al., 2014). Consequently, the recovery of coral populations following disturbance is often dependent on recruitment of larvae from elsewhere (Connell et al., 1997; Hughes & Tanner, 2000). Understanding the potential for larval dispersal between reefs is important for predicting reef resilience. Well-connected reefs will receive a greater number of larvae from many sources and may be more resilient to disturbances (Hughes et al., 2005; Cowen et al., 2006), but may also be more vulnerable to biological invasions (Johnston & Purkis, 2011; Hock et al., 2014). Identifying reefs that can potentially export larvae to many other reefs within the region of interest is therefore a key consideration when designing marine protected areas (MPAs) (Roberts, 1997; Palumbi, 2003; Almany et al., 2009). In addition, MPA networks can be made more resilient by ensuring that protected reefs are also well connected with each other (Christie et al., 2010; Kininmonth et al., 2011).

Despite the implied importance of pelagic larval dispersal, a growing body of research on marine benthic organisms suggests that a large proportion of larvae are retained locally, even in species with the potential for long-distance dispersal (Swearer et al., 2002; Cowen & Sponaugle, 2009; Shanks, 2009). For example, mark–recapture and parentage analysis of reef fishes indicate remarkably high levels (5–72%) of recruitment back to the natal population (Jones et al., 2009a). Corals also tend to exhibit high levels of local retention (fraction of offspring produced by a population that recruits back into that population) and therefore rely heavily on local sources of larvae for population replenishment (Gilmour et al., 2009; Figueiredo et al., 2013). Rising sea temperatures result in higher mortality and more rapid development of coral larvae, and therefore, climate change is predicted to further reduce dispersal capacity and reef connectivity (Figueiredo et al., 2014). Consequently, accurate knowledge of connectivity patterns is essential for effective implementation of marine reserve networks (Almany et al., 2009).

Despite widespread acknowledgement of its importance (McCook et al., 2010; Harrison et al., 2012), connectivity patterns remain poorly understood at regional scales relevant to management (Drew & Barber, 2012). For most marine species, it is practically impossible to empirically track a significant number of larvae during the dispersal stage. Measures of genetic similarity are often used to infer connectivity between different populations (Palumbi, 2003; Hedgecock et al., 2007; Burton, 2009). However, these tools can only infer genetic connectivity (the flow of genes between populations), and not demographic connectivity, which concerns the flow of individuals in sufficient numbers to influence population growth and persistence (Lowe & Allendorf, 2010; Leis et al., 2011).

In the light of these limitations, numerical modelling has become an important tool for estimating patterns of larval dispersal and connectivity (Werner et al., 2007). For example, individual-based models (IBMs) coupled with hydrodynamic models have successfully been used to explicitly model larval dispersal (North et al., 2009). However, accurately modelling water circulation at the spatial scales that affect larval dispersal remains a key challenge. For example, small-scale circulation features close to reefs and islands increases local retention of larvae on their natal reef (Burgess et al., 2007; Figueiredo et al., 2013) and can also influence large-scale circulation patterns in reef-dense regions (Wolanski & Spagnol, 2000; Andutta et al., 2012). Consequently, hydrodynamic models must resolve circulation down to the scale of reefs and reef passages, typically in the order of 100–1000 m in regions with complex topography. To date, very few regional-scale models exist at this resolution, due to both the paucity of data at this level of detail and the large computational resources required. Recent advances in hydrodynamic models using unstructured meshes offer a potential solution to the latter problem by allowing for spatially variable model resolution (Pietrzak et al., 2005; Bernard et al., 2007; Hanert et al., 2009). Unstructured meshes allow the model resolution to be increased close to reefs and coastlines while keeping computational costs manageable, making them particularly useful in areas of complex topography such as Australia's Great Barrier Reef (GBR), where grid nesting is impractical (Lambrechts et al., 2008). A further challenge lies in obtaining accurate, high-resolution data to force such models, such as high-resolution bathymetry of topographically complex reef ecosystems, or sufficient hydrodynamic time series data to calibrate model paramaterizations. Even relatively small inaccuracies in forcings or parameters can lead to considerable inaccuracies in model predictions, potentially nullifying the gains in precision, for both the hydrodynamic model (e.g. see Camacho et al., 2014) and the coupled IBM (e.g. see Hrycik et al., 2013).

Technological advances in recent years (e.g. multibeam sonar, autonomous imaging systems and mixed-gas diving) have facilitated research in remote and/or deeper habitats that were previously inaccessible or prohibitively expensive (Kahng et al., 2014). Submerged banks, defined as isolated

elevations of the sea floor over which the depth of water is relatively shallow but sufficient for safe surface navigation (IHO 2008), are common features of continental shelves, oceanic islands and seamounts world-wide (Abbey & Webster, 2011). Many submerged banks provide habitat for reef-building corals, but their location and spatial extent is poorly known in many parts of the world (Heyward *et al.*, 1997; Harris *et al.*, 2013). Submerged banks composed of reef carbonates (hereafter 'submerged reefs') are common on the continental shelf of the GBR (Harris *et al.*, 2013), and are known to support diverse coral assemblages (Bridge *et al.*, 2011; Roberts *et al.*, 2015). Despite many submerged reefs rising to within 10 m of the surface at their shallowest points, the location of most submerged reefs in the GBR has been delineated only recently with the use of new remote sensing technology (Bridge *et al.*, 2012; Harris *et al.*, 2013). In this study, we define reefs as being either 'submerged' if they are at least 10 m deep at their shallowest point or 'near-sea-surface' (NSS) if they are shallower than 10 m at their shallowest point (and potentially subaerially exposed at low tide). It is important to note that NSS reefs may also support substantial areas of coral habitat in deeper waters on their lower slopes.

Deeper reefs have been proposed as potential refuges for coral reef taxa from environmental stress (Riegl & Piller, 2003; Bongaerts *et al.*, 2010a; Bridge *et al.*, 2013) because disturbance impacts are often most severe in shallow waters (Sheppard & Obura, 2005; Bridge *et al.*, 2014; Smith *et al.*, 2014). Recent observations have confirmed that deep populations can mitigate local extinction following severe disturbance (Sinniger *et al.*, 2013; Smith *et al.*, 2014). Many corals can occur over a depth range of at least 30 m (Bridge *et al.*, 2013), indicating potential for movement of propagules between deep and shallow coral populations (defined here as occurring deeper or shallower than 10 m). However, connectivity among deep and shallow populations appears variable both geographically and among species (van Oppen *et al.*, 2011; Serrano *et al.*, 2014), and the true extent of demographic connectivity between deep- and shallow-water coral populations remains unclear.

Here, we use a newly developed high-resolution model to estimate larval dispersal and potential connectivity patterns among deep and shallow coral populations on two reef types (submerged and near-sea-surface) in the central Great Barrier Reef, Australia. Our model identifies the relative contribution of submerged reefs to larval supply in the central GBR, allowing us to estimate their capacity to act as a source of larval recruits. Specifically, we will (1) compare patterns of connectivity between reefs of differing morphologies (submerged and NSS); (2) investigate the potential for connectivity between areas of reefs at different depths (shallower than 10 m and deeper than 10 m); and (3) identify regions in the central GBR most vulnerable to depth-dependent disturbances (e.g. storms or bleaching events) based on their potential connectivity to other deep reef habitats and identify the morphology and depth of the source reefs that potentially contribute recruits to the most vulnerable areas.

METHODS

Study site

The Great Barrier Reef Marine Park (GBRMP) is located off north-eastern Australia and covers an area of 344 000 km^2. Until recently, coral reefs were thought to occupy ~20,000 km^2 within the GBRMP; however, recent studies have shown that submerged reefs may provide an additional ~20,000 km^2 of coral habitat (Harris *et al.*, 2013). Consequently, previous studies examining connectivity patterns and source-sink dynamics among reefs in the GBR (e.g. Caley *et al.*, 1996; Bode *et al.*, 2006; Thomas *et al.*, 2014) have not accounted for submerged and deep reefs.

Over the 14° of latitudinal extent of the GBR, there are substantial changes in the geomorphic and environmental characteristics of the continental shelf which strongly affect the development and morphology of reefs (Hopley, 2006; Hopley *et al.*, 2007). To account for potential confounding effects of this variability, our study focused on a subset of the GBRMP (central GBR, 16.3–20.4°S, Fig. S1 in Supporting Information) where the shelf morphology is relatively uniform, reefs are well mapped and water circulation patterns are relatively well known. NSS reefs are well spaced and set back from the shelf-edge, while submerged reefs occur on the shelf-edge approximately 70 km from the coast (Hopley, 2006). Additional submerged reefs occur on the mid-shelf throughout the lagoon (Harris *et al.*, 2013). Few reefs occur within ~30 km of the coast, primarily because of turbidity from several large rivers in the region. The study area contained a total of 1023 reefs, 607 of which were NSS reefs.

Distribution of reefs

The locations of submerged and NSS reefs in the central GBR were delineated using a newly developed feature layer for the Great Barrier Reef, which represents an updated version of the GBR Reef Features GIS Database (GBRMPA 2013). The incorporation of satellite-derived bathymetry allowed delineation of many submerged reefs shallower than depths of 20–30 m that had not been identified in previous versions of GBR features, which missed many reefs greater than 5–10 m in depth at their shallowest points. Although extensive reef habitat also occurs in mesophotic depths > 30 m (Bridge *et al.*, 2011, 2012), this study considered only habitat shallower than ~30 m likely to support the common shallow-water coral species used in our model. Field surveys of coral assemblages occupying submerged reef in the central GBR (Beaman *et al.*, 2011; Roberts *et al.*, 2015) confirmed the accuracy of the new feature layer for delineating previously unidentified submerged coral reef habitat.

Larval dispersal model

Larval dispersal patterns were simulated for five coral species: *Platygyra daedalea*, *Acropora humilis*, *Acropora valida*,

Seriotopora hystrix and *Stylophora pistillata*. These species were chosen because (1) they are common in the study region (Done, 1982; DeVantier *et al.*, 2006); (2) they exhibit relatively broad depth distributions (at least 20 m; Bridge *et al.*, 2013; Roberts *et al.*, 2015); and (3) they represent different reproductive modes (Baird *et al.*, 2009). Most importantly, empirical larval competence and mortality data are available for these species (see below), enabling greater accuracy in predictions of demographic connectivity, as even small differences in competence and/or mortality rates can have large effects on estimates of larval dispersal (Connolly & Baird, 2010).

Larval dispersal was modelled using the biophysical model of Thomas *et al.* (2014), which couples the unstructured-mesh, depth-integrated hydrodynamic model SLIM[1] with an individual-based model to simulate particle transport and behaviour. SLIM's multiscale capabilities make it ideally suited to modelling water circulation in complex environments such as the GBR (e.g. see Lambrechts *et al.*, 2008; Andutta *et al.*, 2011; Wolanski *et al.*, 2013). The model mesh covered the entire GBR shelf and the size of the mesh elements was kept proportional to their distance from the nearest reef or coastline and inversely proportional to water depth (see Legrand *et al.*, 2006). The model resolution ranged from 200 m close to reefs to 5 km in open-sea areas and therefore captured small-scale features such as reef wake eddies which can strongly affect particle dispersal. Additional details and validation of the hydrodynamic model are provided in Appendix S1.

We simulated water circulation in the GBR for the 35 days following coral spawning in 4 years for which hydrodynamic data were available to calibrate and validate the model (2007, 2008, 2010 and 2012). Analysis of wind and tide data over several years indicated that these years exhibited typical flow patterns in the central GBR during the spawning season. Dispersal and settlement of larvae through the region were then modelled with the IBM presented in Thomas *et al.* (2014). 'Virtual larvae' were gradually released over all reefs in the domain over 48 h following the observed initiation of spawning. Coral larvae are poor swimmers and were assumed to disperse passively in the model. We also assumed that corals were equally abundant among reefs throughout the domain; therefore, the number of larvae released over each reef was proportional to the reef's surface area.

Larval mortality and competence acquisition were modelled using the parameters reported in Figueiredo *et al.* (2013). Larvae were considered to acquire competence at a fixed rate following an initial delay after spawning (tc) and to die off at a constant mortality rate. Mortality rates and competence acquisition delay times were different for each species, meaning that the mean time-to-competence (mtc) was species-specific (the observed values of mtc for the species studied are given in Table S5 in the Supplementary

Information). Larvae that died or strayed outside the model domain were removed from the remainder of the simulation. Larvae were assumed to settle on the first reef they travelled over after acquiring competence and were subsequently removed from the simulation. At the end of each simulation, a connectivity matrix was produced, with each element recording the number of larvae released over the source reef identified by the row index which had settled onto the destination reef identified by the column index, over the course of the simulation. All larvae settling on reefs which were inside a 30 km 'buffer zone' from the northern and southern domain boundaries were disregarded from the connectivity analysis, to account for the fact that upstream sources north or south of the domain can contribute larvae inside the domain. Larval dispersal statistics such as self-recruitment and mean dispersal distance were calculated separately for each year's simulation and then averaged over the 4 years, to obtain a single value for each species.

Connectivity among reef morphologies and depths

Connectivity matrices were used to examine the extent of the connectivity between reefs of different morphologies (submerged versus NSS) and depths ('shallow': < 10 m; and 'deep': > 10 m). Ten metres was considered as a suitable cut-off between 'deep' and 'shallow' reefs, as reefs deeper than 10 m are often less affected by depth-dependent disturbances such as warm-water coral bleaching (Bridge *et al.*, 2014; Smith *et al.*, 2014). Although disturbances can clearly extend into deeper waters, reefs on the GBR deeper than 10 m likely experience less frequent disturbances than those in shallower waters (e.g. Marshall & Baird, 2000; Roberts *et al.*, 2015). Using this cut-off value meant that all submerged reefs in the domain were entirely classed as 'deep' areas (as, by their definition, their shallowest points were deeper than 10 m), whereas NSS reefs could have both deep and shallow areas. We identified the proportion of larvae settling at < 10 m depth on each reef originating from (1) < 10 m depth on the same reef; (2) > 10 m depth on the same reef; (3) < 10 m depth on another reef; and (4) > 10 m depth on another reef. This allowed examination of both the potential for deep to shallow connectivity, and also the importance of self-recruitment in the recovery of shallow and deep habitats.

Identification of vulnerable shallow-water reef habitats

Larval dispersal models can provide insight into the vulnerability or resilience of reefs to disturbance based on the extent of connectivity to potential larval sources. Reefs that can potentially receive many larvae from other reefs, and therefore do not rely only on locally retained larvae for persistence, are likely to recover more rapidly from localized disturbances by having a more stable supply of recruits (Mumby & Hastings, 2008; Jones *et al.*, 2009b; Burgess *et al.*, 2014). Furthermore, reefs which rely heavily only on

other shallow reef habitats for larval recruits would be expected to be more vulnerable to coral decline associated with depth-dependent disturbances, whereas reefs receiving a demographically significant quantity of larvae from deeper populations (where demographically significant means enough to contribute significantly to the size and persistence of the population) could be expected to show greater resilience.

We assessed the predicted vulnerability of shallow-water reef habitats in 16 subregions in the central GBR by qualitatively categorizing the subregions as either 'low', 'medium' or 'high' vulnerability, depending on the proportion of shallow-water reefs dependent on other shallow reef habitats for larval replenishment. Vulnerability was estimated by qualitatively assessing the number of reefs within a subregion that rely heavily on recruitment from habitats shallower than 10 m. Subregions were derived from the Australian Institute of Marine Science's Long-term Monitoring Program (LTMP) (Sweatman *et al.*, 2011), which assesses coral cover trends on ~200 shallow reefs (6–9 m depth) in 29 subregions of the GBR. Each subregion was defined by its position across and along the GBR shelf (11 sectors comprising approximately equal bands of latitude, and three cross-shelf zones: inner-, mid- and outer-shelf). Sixteen of the 29 subregions examined by the LTMP occur within the domain covered by our model. We compared vulnerability within each subregion predicted by our model to the observed linear trend (in % coral cover yr^{-1}) for the period 1986–2004 (Sweatman *et al.*, 2011).

RESULTS

The model revealed clear cross-shelf differences in connectivity, with inshore reefs consistently having higher rates of self-recruitment (Fig. 1) and exporting fewer larvae (Fig. 2a) than mid- and outer-shelf reefs. Mid- and outer-shelf reefs in the southern part of the domain also exported greater numbers of larvae than reefs in the north.

Connectivity variables, such as self-recruitment and dispersal distances, also varied considerably between species due to differences in mean time-to-competence and mortality rates. As expected, the three broadcast-spawning species (*P. daedalea*, *A. humilis* and *A. valida*) dispersed further and were less reliant on self-recruitment than the two brooding species (*S. hystrix* and *S. pistillata*) (Table 1), due to their much lower mtc (Table S5). Among the three broadcasters, the species with lower mtc showed higher rates of self-recruitment and smaller mean dispersal distances. Despite these differences, all three broadcast spawners had similar geographical dispersal patterns. Therefore, below we present data for *A. humilis* only (except where explicitly indicated), which has an intermediate mtc and is considered representative of broadcast-spawning species. Both brooding species also exhibited almost identical dispersal patterns.

Connectivity between submerged and near-sea surface reefs

Significant differences in connectivity patterns were found between larvae released from NSS and submerged reefs (Table 1). For broadcast spawners, self-recruitment rates were three to five times higher for NSS reefs than for submerged reefs, and larvae released over submerged reefs dispersed 40% to 83% further.

The number of larvae produced on each reef was assumed to be proportional to its size, so larger reefs exported greater numbers of larvae to other reefs, in absolute terms, than smaller reefs (Fig. 2b). The largest reefs were all NSS reefs, so NSS reefs contributed most to the total larval production. However, submerged reefs exported a greater number of larvae per unit area than NSS reefs (Fig. 2b). The connectivity matrix (Fig. 3) shows that connections occurred, in both directions, between both reef types, although NSS-to-NSS connections were most common. For broadcast-spawning coral, 79% of larvae released on NSS reefs which settled somewhere settled on other NSS reefs, with the remaining 21% settling on submerged reefs. Of the larvae released from submerged reefs, however, only 52% of those that settled somewhere settled on submerged reefs, with the remaining 48% instead settling on NSS reefs. As more larvae were released over NSS reefs than submerged reefs (due to the greater extent of NSS reefs in the domain), NSS reefs provided 90% and 70% of settlers to NSS and submerged reefs, respectively. Brooders showed lower connectivity between submerged and NSS reefs: 91% of brooder larvae released from NSS reefs settled on NSS reefs, and 73% from submerged reefs also settled on submerged reefs.

Connectivity among deep and shallow reef habitats

Horizontal connectivity (dispersal of larvae among habitats of the same depth) was more common than vertical connectivity (dispersal from deep to shallow, or vice-versa; note that vertical connectivity requires horizontal movement of larvae between habitats of different depths) (Fig. 4). Only 24% of reef habitat in the domain was shallower than 10 m, but 52% of larvae recruiting to shallow habitats originated from other shallow habitats. Of this 52%, the majority (75%) originated from the same reef. However, deeper reef habitats still provided 48% of all recruits to shallow-water habitats, suggesting potential for demographically significant connectivity from deep to shallow habitats. A higher proportion of recruits to deep reef habitats originated from deep water, regardless of whether these habitats are on NSS (82%) or submerged (86%) reefs. Deep habitats on NSS reefs had higher self-recruitment than those on submerged reefs (28% against 2%), a reflection of the greater spatial extent of NSS reefs, and the different current regimes present around them, as described in the Discussion.
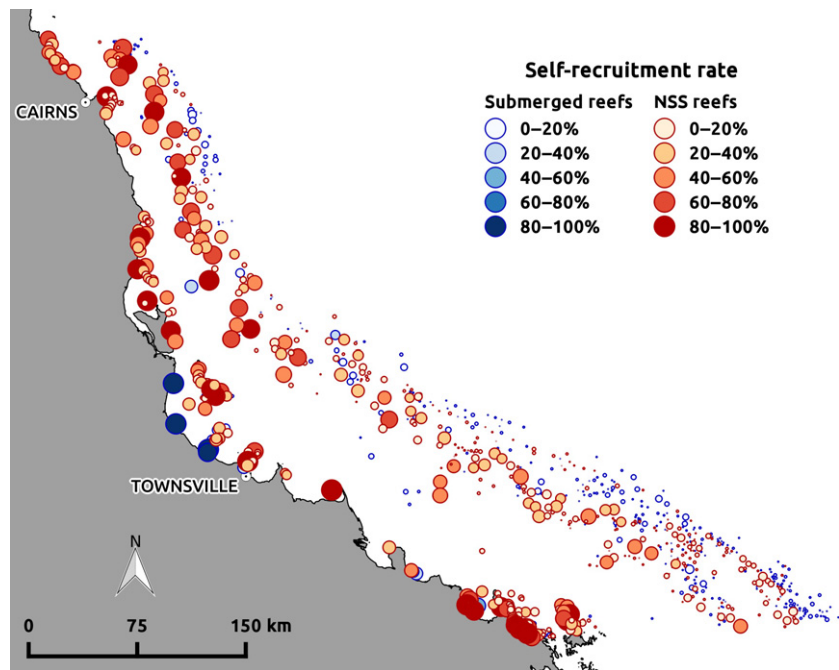
Figure 1 Map of self-recruitment in the central GBR predicted by the SLIM model. Coloured dots represent NSS (red scale) and submerged (blue scale) reefs, with the colour scale showing the self-recruitment rate on each reef, from white (0%) to dark red or blue (100%), for *Acropora humilis*. Reef size is also scaled by self-recruitment rate, so larger reefs have the highest self-recruitment.
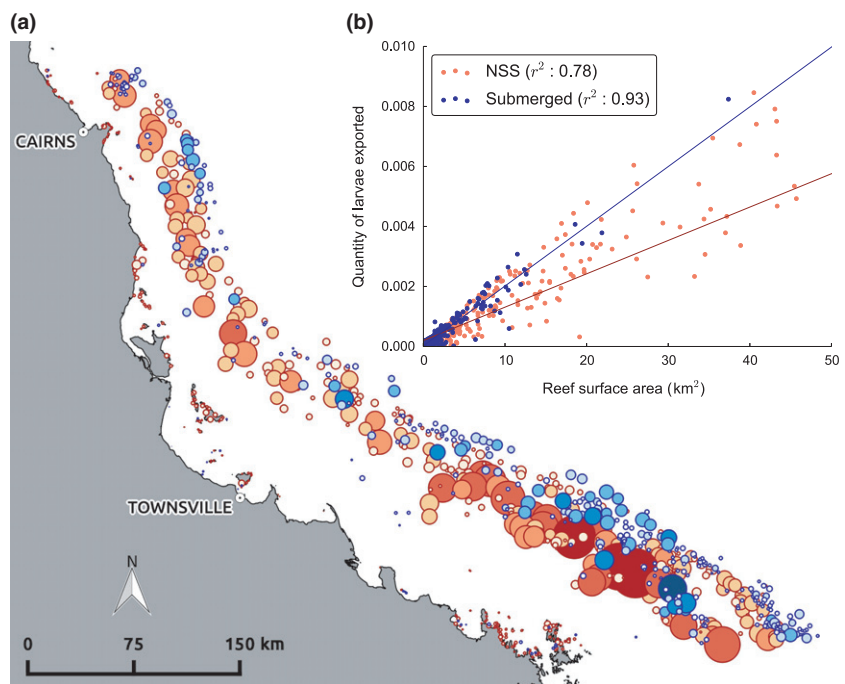

Figure 2 (a) Map showing the number of larvae exported by each reef in the central GBR as predicted by the SLIM model. Dots represent NSS (red scale) and submerged (blue scale) reefs, with size and colour scale indicating the number of larvae exported, from white (0) to red or blue (highest), for *Acropora humilis*. (b) Inset scatter graph shows the relationship between the number of larvae exported (normalized by the total number of recruited larvae) and reef surface area.

Predicted versus observed vulnerability of shallow-water reef habitats

Our model indicated that the most vulnerable subregions occur inshore and in the north of the domain (Fig. 5). In contrast, shallow reef habitats on the mid- and outer-shelf in the southern half of the domain can receive larvae from a large number of sources, including a substantial proportion of larvae from adjacent deep habitats. Comparing our predicted vulnerability for shallow-water coral habitats to

observed trends in coral cover from 1986–2004, we found that subregions with high predicted vulnerability corresponded to those that exhibited the steepest rate of coral cover decline (Fig. 6). In contrast, subregions with low predicted vulnerability showed no negative trend in coral cover trajectories. In total, 43% of subregions predicted to have high vulnerability based on their reliance on shallow-water habitats for recruits showed substantial linear changes in coral cover over 18 years (Sweatman *et al.*, 2011), compared to no subregions where vulnerability was predicted to be low.

Table 1 Table showing larval dispersal statistics averaged over four spawning seasons as predicted by the SLIM model. The statistics describe all larvae released over the reef type specified in the first column and settling on any reef. Self-Rec. is the proportion of larvae which self-recruited and Av. Dispersal Distance is the mean distance from their natal reef at which larvae settled (including zero-distance connections), given with its standard deviation.

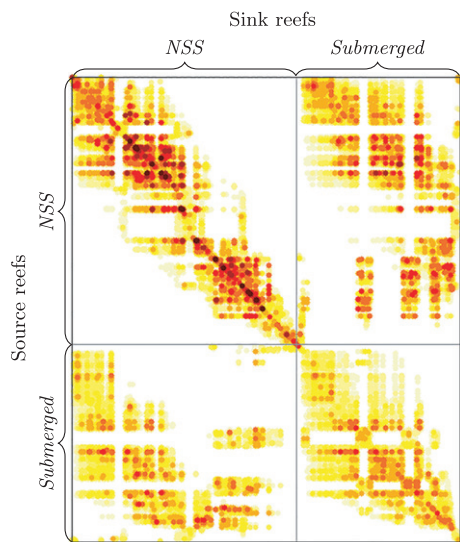| Coral species	Reef type	Self-rec. (%)	Av. dispersal distance (km)
Platygyra daedalea	NSS	21.8	26.2 ± 5.8
	Submerged	3.9	36.7 ± 11.8
Acropora humilis	NSS	30.9	16.2 ± 2.9
	Submerged	5.8	28.1 ± 7.8
Acropora valida	NSS	42.8	11.0 ± 1.1
	Submerged	11.6	20.7 ± 3.8
Seriatopora hystrix	NSS	70.2	3.3 ± 0.3
	Submerged	34.7	8.9 ± 1.3
Stylophora pistillata	NSS	71.9	3.1 ± 0.3
	Submerged	34.5	9.2 ± 1.3

Figure 3 Connectivity matrix for *Acropora humilis*, averaged over four spawning seasons, as predicted by the SLIM model. Each matrix element represents an exchange of larvae from the source reef (row) to the sink reef (column). The strength of the larval exchange ranges from white (no larvae exchanged) to dark red (highest number of larvae). The matrix is rectangular as there are more sources than sinks, as reefs located in the 30 km buffer zones at the northern and southern domain boundaries are not included as sinks, as described in the main text.

DISCUSSION

Variability among submerged and NSS reefs

NSS reefs were the largest sources of larvae due to their greater spatial extent; however, larvae from submerged reefs dispersed further and were more likely to settle onto NSS reefs than vice-versa. If corals are equally abundant on all reefs in the domain, as assumed in the model, then larger reefs supporting more corals would export a greater number of larvae. In this case, our results support the hypothesis that reef size is a key indicator of the importance of a reef as a larval source (James *et al.*, 2002). However, our model also indicated that submerged reefs also represent important larval source reefs, exporting a greater number of larvae per unit area due to differences in water circulation patterns over submerged and NSS reefs. A submerged reef presents less of an obstacle to water flow compared with an NSS reef, so the turbulent features formed in the reef's wake will tend to be less pronounced than for an NSS reef. Reef wake eddies can be responsible for trapping significant numbers of larvae close to the reef, resulting in high self-recruitment rates on NSS reefs (Wolanski *et al.*, 1989; Burgess *et al.*, 2007; Figueiredo *et al.*, 2013). Submerged reefs also tend to be found in slightly deeper water, where net water flow is stronger due to the smaller overall influence of friction with the rough reef surface, increasing the likelihood that larvae will be rapidly flushed from the reef. In addition to exporting a greater proportion of their larvae, our model indicated that submerged reefs are less reliant on other submerged reefs for their recruits. Most recruits on submerged reefs were predicted to originate from NSS reefs.

Influence of coral reproductive mode

As expected, larvae of broadcast-spawning species dispersed greater distances than larvae of brooding species due to the significantly shorter mtc in brooders. Nonetheless, this finding highlights the importance of considering reproductive biology in connectivity models and emphasizes the challenges posed by incorporating larval connectivity in planning MPA networks. Our results demonstrate the influence of life-history traits on potential connectivity, a finding broadly applicable to any species with a pelagic larval dispersal stage. Managers must account for corals (and other taxa) with vastly different reproductive biology inhabiting the same reef. Accounting for additional factors that may influence dispersal potential (e.g. larval buoyancy and behaviour) could further accentuate the estimated differences in dispersal potential between broadcast spawners and brooders and would provide additional information on intraspecific differences in dispersal potential.

Connectivity between deep and shallow habitats

Our results indicate that vertical connectivity is less common than horizontal connectivity. The majority (52%) of recruits on shallow reef habitats originate from other shallow habitats, despite deeper habitats accounting for 76% of the total available coral reef habitat. This finding supports empirical studies of genetic connectivity in corals (Bongaerts *et al.*, 2010b; Serrano *et al.*, 2014) and suggests that

Figure 4 Bar charts showing the provenance of larvae settling on the shallowest parts (where depth < 10 m) and deeper parts (where depth > 10 m) of NSS and submerged reefs as predicted by the SLIM model. The labels 'shallow' and 'deep' in the figure refer to larvae seeded in areas shallower and deeper than 10 m, respectively. 'Same reef' refers to larvae that settle on the same reef they are seeded over; 'other reef' refers to larvae that settle outside their natal reef. Note that most NSS reefs in the domain straddle the shallow/deep threshold, with their upper reaches in 'shallow' water and their lower banks in 'deep' water, while submerged reefs, by their definition, are all entirely located in 'deep' water.
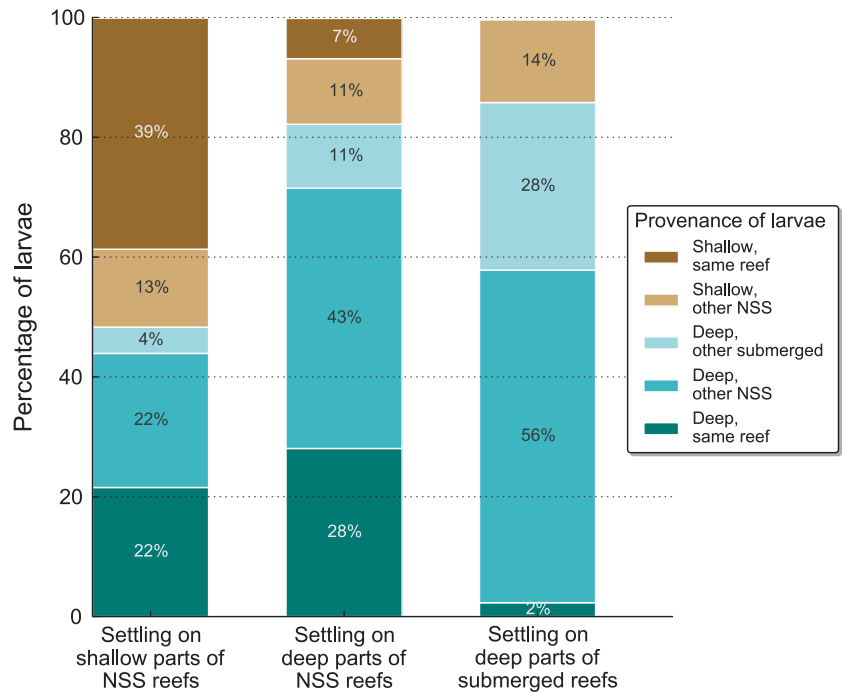

Figure 5 Map showing shallow reef areas in the domain (where depth < 10 m), with reef size and colour showing the proportion of recruits which come from other shallow reef areas, as predicted by the model. Only reefs with at least part of their surface area in water shallower than 10 m are shown. Black lines delineate sector boundaries used by Sweatman *et al.* (2011), and red boxes identify the subregions classed as most vulnerable by our numerical model.
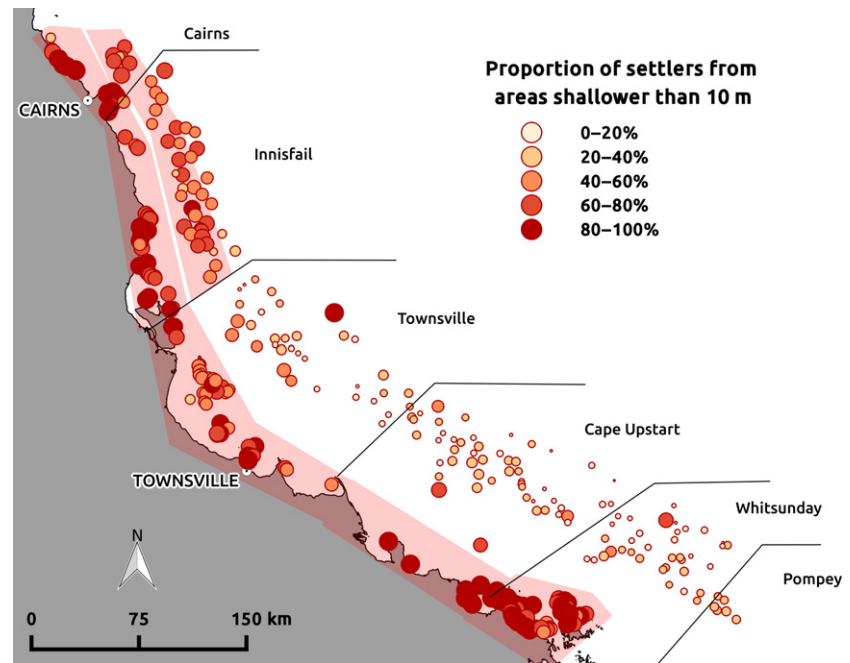
dispersal limitation may play a role in population partitioning among reef habitats. However, the model also indicated that demographically significant two-way connectivity between deep and shallow habitats could constitute an important source of larvae to shallow habitats. The extent of connectivity between deep and shallow habitats was geographically variable (Fig. 5): inner-shelf reefs were highly dependent on recruits from shallow water, and reefs in the north of the domain were also more reliant on larvae from shallow water than those further south. This is primarily due to spatial differences in current strength: inner-shelf reefs are mainly found in shallow water and experience weaker currents than offshore reefs, reducing larval dispersal. Meanwhile in the southern half of the domain, the wider continental shelf amplifies the tidal currents (Andrews & Bode, 1988) leading to greater dispersal distances and more connections between reefs, enhancing deep to shallow connectivity.
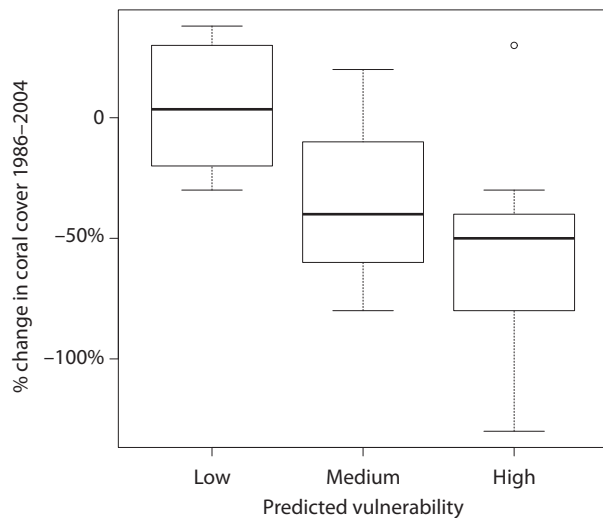
Figure 6 Vulnerability of shallow-water reefs predicted by our model versus the 19-year linear trend (in % coral cover yr^{-1}). Each point used in the analysis represents a value for one of 16 subregions reported in the Australian Institute of Marine Science Long-Term Monitoring Program (Sweatman *et al.*, 2011). Seven subregions were classified as high predicted vulnerability, three 'medium' and six 'low'.

Ascertaining the true extent of vertical connectivity requires empirical testing, but our model suggests that the horizontal currents present no obvious barrier to connectivity between deep and shallow reef habitats in the region, assuming the water column is well mixed. Spatial variability in the extent of vertical connectivity has been previously reported using genetic techniques (van Oppen *et al.*, 2011; Serrano *et al.*, 2014), and our results support the hypothesis that oceanography may provide a mechanism to explain this variation. If connectivity between deep and shallow habitats promotes resilience in shallow-water reef habitats, then determining the spatial location, extent and biodiversity of deep reefs should be afforded greater importance by marine resource managers

Reef habitats in deeper waters are not immune from disturbance, but many disturbances are less frequent and/or severe at greater depths (Woodley *et al.*, 1981; Marshall & Baird, 2000; Riegl & Piller, 2003). Consequently, deeper reefs often exhibit greater long-term stability than adjacent shallow habitats (Bak & Nieuwland, 1995; Lesser *et al.*, 2009). Our results indicate that most recruits on deep reef habitats originate from other deep habitats; therefore, depth-dependent disturbances would have little influence on larval supply to deep habitats. Lower self-recruitment rates also suggest that deeper habitat may have greater capacity to recover than shallows if they are affected by a reef-scale disturbance. However, these factors may also result in slower recovery of deeper reefs if coral declines in deeper waters were widespread.

Assessing vulnerability of shallow-water habitats

Subregions where shallow-water reef habitats are predicted to source a greater proportion of recruits from deeper habitats

showed no significant trends in coral cover from 1986 to 2004 (Fig. 6). In contrast, subregions heavily reliant on shallow-water reef habitats for larval recruitment have shown much steeper declines in coral cover. However, the response of vulnerable subregions was also highly variable. We propose two potential causes of variability, which are not mutually exclusive. Firstly, coral decline requires a cause, and it is possible that some highly vulnerable habitats may have escaped disturbance over the study period. However, the frequency and spatial scale of disturbance events in the central GBR over the study period (Sweatman *et al.*, 2011; De'ath *et al.*, 2012) would indicate that this pattern cannot be attributed entirely to differences in exposure to disturbance. Alternatively, it is possible that some reefs with low connectivity are actually relatively resilient to disturbances if: (1) the disturbance is not too severe and some breeding adults survive; and (2) local retention of larvae is high (e.g. Botsford *et al.*, 2009). Whatever the cause of variability in coral cover trajectories on vulnerable reefs, it is clear that shallow habitats with high predicted vulnerability have, on average, showed much steeper declines in coral cover than the shallow habitats with low predicted vulnerability. This finding supports the hypothesis that reefs receiving larvae from deeper sources may be more resilient than those reliant entirely on shallow sources.

The capacity for reefs to maintain coral-dominated states or return to coral-dominated states following disturbances is influenced by the types of stressors to which the reef is exposed. Chronic 'press' type stressors (e.g. pollution, overfishing) reduce overall capacity to recover, whereas reefs can recover from acute 'pulse' disturbances (e.g. storms and bleaching events) if reef resilience is maintained (Anthony *et al.*, 2015). For corals, connectivity is most beneficial against 'pulse' disturbances, where deeper areas that have avoided significant coral loss can provide propagules to repopulate shallower areas. It is important to consider that our model shows only potential connections between reefs based on hydrodynamics, larval survival and competence dynamics and does not account for important factors such as adaptive divergence among habitat types or post-settlement processes affecting recruitment success (Mundy & Babcock, 2000; Bongaerts *et al.*, 2011). Some coral species are habitat specialists, restricted to either very shallow or very deep habitats; such species will not colonize new habitats even if physically connected by larval dispersal. Nevertheless, our model suggests that deep habitats may constitute a source of larvae for depth-generalist species. Our predictions support empirical findings that while genetic connectivity between deep and shallow populations is not as common as horizontal connectivity (Serrano *et al.*, 2014), demographically significant connectivity can occur between deep and shallow habitats. The concordance between our predicted vulnerability and observed trends in coral cover suggests that deep to shallow connectivity may be important for post-disturbance recovery in coral communities. This reinforces the need to consider deeper reef habitats when assessing the

impacts of disturbances, trajectories of coral communities and planning conservation measures.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Bathymetric map of the study region.

Appendix S1 Setup and validation of the hydrodynamic model.

Table S1 Validation data for the 2007 simulation.

Table S2 Validation data for the 2008 simulation.

Table S3 Validation data for the 2010 simulation.

Table S4 Validation data for the 2012 simulation.

Table S5 Mean times to competence (mtc) for the five species modelled. Data reproduced from Figueiredo *et al.* (2013).

BIOSKETCHES

Christopher J. Thomas is interested in biophysical modelling of larval dispersal in coastal oceans and studying their connectivity patterns.

Tom C.L. Bridge is interested in biodiversity of mesophotic coral reef ecosystems, the ecological relationship between deep and shallow-water reefs, and their potential to act as refugia for corals and associated species from stressors associated with climate change and other human impacts.

Author contributions: T.C.L.B and C.J.T. conceived the ideas with input from J.F.; C.J.T. developed and carried out numerical hydrodynamic and IBM simulations with input from E.H. and E.D.; C.J.T., T.C.L.B. and J.F. analysed the data; C.J.T. and T.C.L.B. co-wrote the manuscript, with contributions from all authors.

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