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Modelling dispersal and connectivity of broadcast spawning corals at the global scale

RESEARCH PAPER

S. Wood[1], C. B. Paris[2], A. Ridgwell[1] and E. J. Hendy[3,4]*

[1]*School of Geographical Sciences, University of Bristol, Bristol BS8 1SS, UK,* [2]*Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149-1098, USA,* [3]*School of Earth Sciences, University of Bristol, Queens Road, Bristol BS8 1RJ, UK,* [4]*School of Biological Sciences, University of Bristol, Bristol BS8 1UG, UK*

ABSTRACT

Aim We develop the first global model of connectivity for a generic broadcast spawning coral, and compare the results to connectivity estimates from genetic studies, general biogeographic patterns and theories. We also derive various 'connectivity indices' describing relative isolation and source potential between locations.

Location Modelled oceans 47° S–47° N.

Methods Dispersal of model coral 'larvae' was simulated over 8 years using an individual-based biophysical dispersal model driven by 1/12°-resolution surface ocean current data and incorporating individual trait variability (e.g. a phased pre-competency period). Source and arrival locations of modelled larvae on suitable reef habitat gave standardized dispersal paths and relative levels of connectivity.

Results In the model *c.* 50% of connections occurred within 50–100 km, with rarer dispersal between regions linking entire oceans in a 'stepping stone' fashion. The central Pacific was an almost complete barrier to dispersal, only rarely breached westward from the Galapagos to Marquesas Islands. Areas showing strong isolation also included Hawaii, Easter Island, the Red Sea and the eastern Atlantic. The Indo-West Pacific and Great Barrier Reef showed the highest levels of connectivity, with secondary peaks in the western Indian Ocean, corresponding to areas of enriched coral diversity. The central Indo-Pacific diversity hotspot was overall a greater source than sink for dispersal.

Conclusions This study provides a global view of connectivity that complements genetic and biogeographic work as well as providing a number of novel findings relevant to biogeographic theories (e.g. the central Indo-Pacific as a dispersal source; Johnston Atoll as the sole 'stepping-stone' into Hawaii). Discrepancies with proposed connectivity patterns (e.g. one-way, westward, connectivity across the central Pacific) present hypotheses for future research. The model represents an effective tool for exploring the factors controlling connectivity on this scale and the effects of climate change on future connectivity, and will also aid predictions of future reef distributions.

Keywords

Biophysical modelling, connectivity, coral biogeography, coral reefs, 'Coral Triangle', East Pacific Barrier, Hawaii, Indian Ocean, larval dispersal, tropical eastern Pacific.

*Correspondence: E. J. Hendy, School of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ, UK. E-mail: e.hendy@bristol.ac.uk

INTRODUCTION

Scleractinian corals, the key ecosystem engineers of tropical reefs, rely on dispersal of a larval stage by ocean currents for population replenishment and colonization of fragmented shallow marine habitats. The process of larval dispersal and subsequent recruitment of individuals into a receiving population, termed 'connectivity', therefore influences coral biogeogra-

phy, genetic structure and population dynamics (reviewed in Paris-Limouzy, 2011) and has for example been hypothesized as a main driver of patterns of coral species richness (Veron, 1995). Coral diversity peaks in the Indo-West Pacific (IWP), decreasing both latitudinally and longitudinally away from the area between the Philippines, Indonesia and the Solomon Islands (the 'Coral Triangle'; Veron *et al.*, 2009). This attenuation of species richness with distance across the Pacific runs counter to prevailing westward equatorial currents, suggesting that zonally biased dispersal into and out of this region contributes to the observed diversity gradient (e.g. Jokiel & Martinelli, 1992; Connolly *et al.*, 2003). Connectivity is therefore likely to be a determining factor in future reef persistence and distribution (Munday *et al.*, 2009).

Connectivity operates over a range of scales, from demographically relevant exchanges of individuals, generally over small spatial scales (e.g. Gilmour *et al.*, 2009), to rarer long-distance dispersal, influencing species distributions and patterns of genetic diversity (Trakhtenbrot *et al.*, 2005). Due to the difficulty in empirically measuring dispersal of larvae in the open ocean, two indirect methods are generally used to determine population connectivity. The first uses genetic markers to identify degrees of differentiation between populations, from which inferences regarding the scale of dispersal and levels of exchange can be derived (reviewed in Hellberg, 2007). The second approach uses numerical modelling to simulate the process of dispersal (e.g. Kool *et al.*, 2013) and hence allow the controls on, and consequences of, connectivity to be explored in a synthetic environment.

Connectivity models have previously been employed on local to regional scales (e.g. Paris *et al.*, 2005; Baums *et al.*, 2006; Cowen *et al.*, 2006; Treml *et al.*, 2008, 2012; Kool *et al.*, 2011; Foster *et al.*, 2012 for both corals and reef fish). In contrast, model studies investigating the link between connectivity and biogeography have tended to include relatively simplified circulation patterns or population dynamics (Jokiel & Martinelli, 1992; Gaylord & Gaines, 2000). Taking advantage of recent advances in biophysical modelling, here we present a modelling framework driven by eddy-resolving ocean current data and incorporating representations of coral larval development and reef habitat. Our study is conducted at the global scale to capture potential long-distance and multigenerational 'stepping-stone' dispersal beyond regional scales. We parameterize the model to represent a generic, broadcast spawning coral species with high dispersal potential, and compare the results with general biogeographic and genetic patterns in corals. The results allow us to examine how well present-day dispersal patterns reflect current global coral biogeography.

METHODS

Oceanographic and habitat parameterization

Reef habitat for particle release and settlement was obtained by combining global coral reef distributions from the Ocean Data Viewer (UNEP-WCMC 2010, downloaded from http://data.unep-wcmc.org/datasets/13) with those from ReefBase (version 2000, http://www.reefbase.org/gis_maps/datasets.aspx; Vergara *et al.*, 2000) in order to capture all potential reef and non-reef coral locations (J. McManus, Rosenstiel School of Marine and Atmospheric Science, Miami, pers. comm.). The combined coral reef distribution data were re-gridded onto 1/6° (*c.* 18 km^2) cells in ESRI ArcMap10, creating 12,397 habitat cells which define the release and settlement locations in the model (see Fig. S1 in Supporting Information).

We used a Lagrangian dispersal model (the Connectivity Modelling System; Paris *et al.*, 2013) which tracks the paths of individual particles in a three-dimensional flow field, incorporating stochastic mortality, turbulent motion, variable particle attributes and representation of habitat for settlement. Model particles, which can be parameterized to represent any dispersing object, are released at a time/location specified by the user and advected using velocity fields from inputted oceanographic data. Daily average surface ocean currents from the hybrid coordinate ocean model (HYCOM; Chassignet *et al.*, 2007) were used, covering global marine waters from 47° N to 47° S at 1/12° spatial resolution and the time period 3 November 2003 to 9 November 2011. To account for turbulent motion not captured at the resolution of the oceanographic data, particles were given a 'random walk' impulse at 4-hourly time steps using a diffusion coefficient of 7 m^2 s^{-1} (after Okubo, 1971).

Biological parameterization

Particles were parameterized to represent the larvae of a generic broadcast spawning coral species, in order to focus the study on general patterns of connectivity driven by oceanographic circulation and the influence of basic biology (Siegel *et al.*, 2003).

Larval release

One hundred model larvae were released from each of the 12,397 habitat locations per month (93 spawning events; in total > 115 million particles). Note that we did not attempt to model realistic numbers of dispersing larvae or specific spawning timings, but rather give a representation of potential dispersal paths and relative levels of connectivity between locations.

Pre-competency period

Coral larvae must undergo a period of development before they are able to settle out of the water column and begin metamorphosis into a coral polyp (termed 'competency'). We phased the acquisition of competency within each release cohort (100 particles), with 10% of the cohort becoming capable of settling per day from day 1 to 10 following release, approximating the curves of Connolly & Baird (2010; see Fig. S2), allowing for retention of larvae within the release reef as well as longer-distance transport.

Competency duration and mortality

Larvae spend a finite time in this 'competent' phase, beyond which their energy reserves become too depleted for them to

Figure 1 Map of the 115.29×10^{-6} simulated coral 'larvae' trajectories aggregated over the 8-year model period (2003–11). The colour scale shows the log number of individual particles passing through each cell on a $1 \times 1°$ grid. Projection: Mollweide.
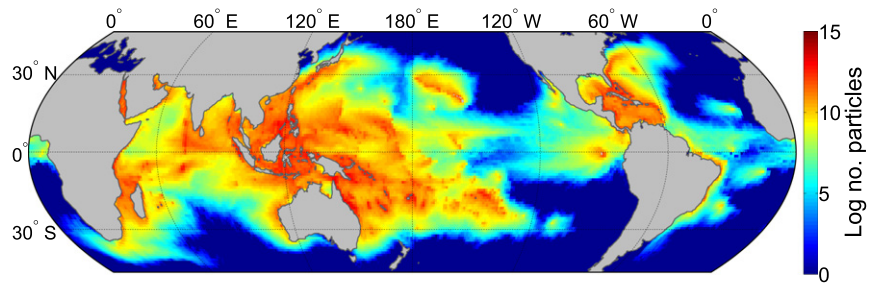
complete settlement and metamorphosis (Richmond, 1987; Connolly & Baird, 2010). Larval durations were therefore parameterized to represent the loss of competency by subjecting particles from a single release 'cohort' to an exponential decay curve:

$$S^{t+1} = S^t e^{-\lambda t}$$

where S^{t+1} is the proportion of larvae surviving (competent) at time $t+1$ and λ is the mortality rate or decay constant calculated as

$$\lambda = \ln(2)/(\text{PLD}/2)$$

where PLD is the pelagic larval duration or maximum competency period. The 'half-life' for decay (PLD/2) was set at 35 days, and particles terminated if not already 'settled' or 'dead' after 120 days, the maximum competency duration published for broadcast spawning corals (Connolly & Baird, 2010).

Larval behaviour

The swimming capabilities of coral larvae are limited, and orientation and active settling behaviours are likely to only play a significant role at the settlement phase on scales of metres at most (e.g. Pizarro & Thomason, 2008). At the scale of this study, therefore, particles were considered passive and confined to the surface layer in the model.

Data analysis and visualization

For visualization of results, due to the large number/small size of the habitat cells the values obtained for each 1/6° cell were processed by summing or averaging onto a larger-scale 2° grid. For analysis of levels of larval exchange between locations on a regional scale, these cells were then grouped into geographic regions (Fig. 3), using the 'ecoregions' defined by Veron *et al.* (2009; J.E.N. Veron, Townsville, pers. comm.) from distinct multispecies coral assemblages. These ecoregions were further grouped into larger (purely geographical) regional areas for global scale visualization (Fig. 2).

RESULTS

Dispersal paths

The aggregated trajectories of all (> 115 million) modelled particles over the entire 8-year model period, including those

unable to reach reef habitat, highlight dominant 'highways' and major barriers to dispersal (Fig. 1; e.g. the central Pacific barrier and isolation of Hawaii and Easter Island). Whilst higher dispersal path densities naturally corresponded to areas of high reef density, coral larvae reached currently unpopulated areas, such as mainland Japan, the south-western tip of Africa and the western coasts of central Africa and South America. The maximum distance travelled in the model was almost 10,000 km (roughly the entire width of the Pacific).

The settlement/potential connectivity matrix

The number of particles released from each release location i reaching a habitat cell j (i.e. potential connectivity, denoted $S_{(i \rightarrow j)}$), were recorded in the settlement matrix, S. In order to examine the strength and direction of potential connections on a regional scale, the settlement information was summed on a 2° grid and plotted as a connectivity matrix (Figs 2 & 3), showing the number of particles exchanged between each release and settlement location. Self-seeding, i.e. particles settling within their release location ($S_{(i \rightarrow i)}$), plots along the diagonal.

We found that potential connectivity was mainly limited to subregional scales (Fig. 2); 44% of particles 'settled' within 50 km, 63% within 100 km, 79% within 200 km and 89% within 4000 km of release. Much lower levels of exchange occurred between geographical regions, linking entire ocean basins over multiple release events in a stepping-stone fashion. For example, the regions of the IWP (SIWP and NIWP in Fig. 2) supplied particles to Micronesia (NWP), which in turn supplied the islands of the central Pacific Ocean (CPAC), but almost no direct recruitment occurred from the IWP to the central Pacific. Likewise the IWP supplied recruits westward into the east Indian Ocean (EIO), which in turn supplied the central Indian Ocean (CIO), and from here the western Indian Ocean (SEY and EAFR regions). In this way, almost the entire Indo-Pacific was linked by low levels of connectivity over the 8-year time period. Inter-regional dispersal events were generally an order of magnitude lower (i.e. 8–10 times fewer particles) than local-scale settlement.

Subregional scale plots (Fig. 3) allow more detailed analysis of rarer inter-regional dispersal events. For example, the eastern Pacific was almost entirely isolated from the central Pacific in our model except for extremely rare (four particles in 8 years) westward dispersal from the Galapagos (GAL) to the Marquesas Islands (MARQ). The Hawaiian Islands (NHW and EHW) were also extremely isolated, with Johnston Atoll (JOH) providing the
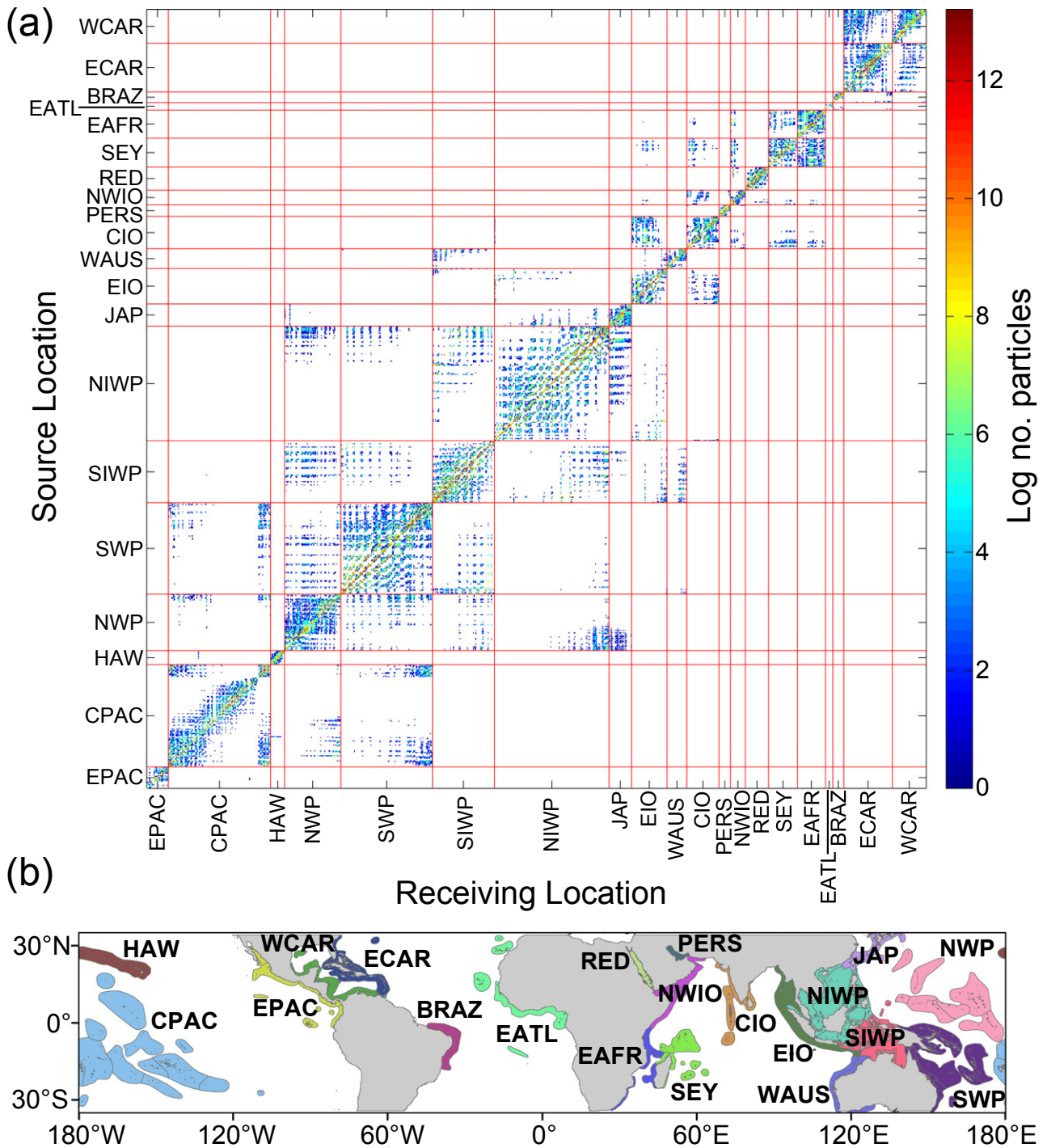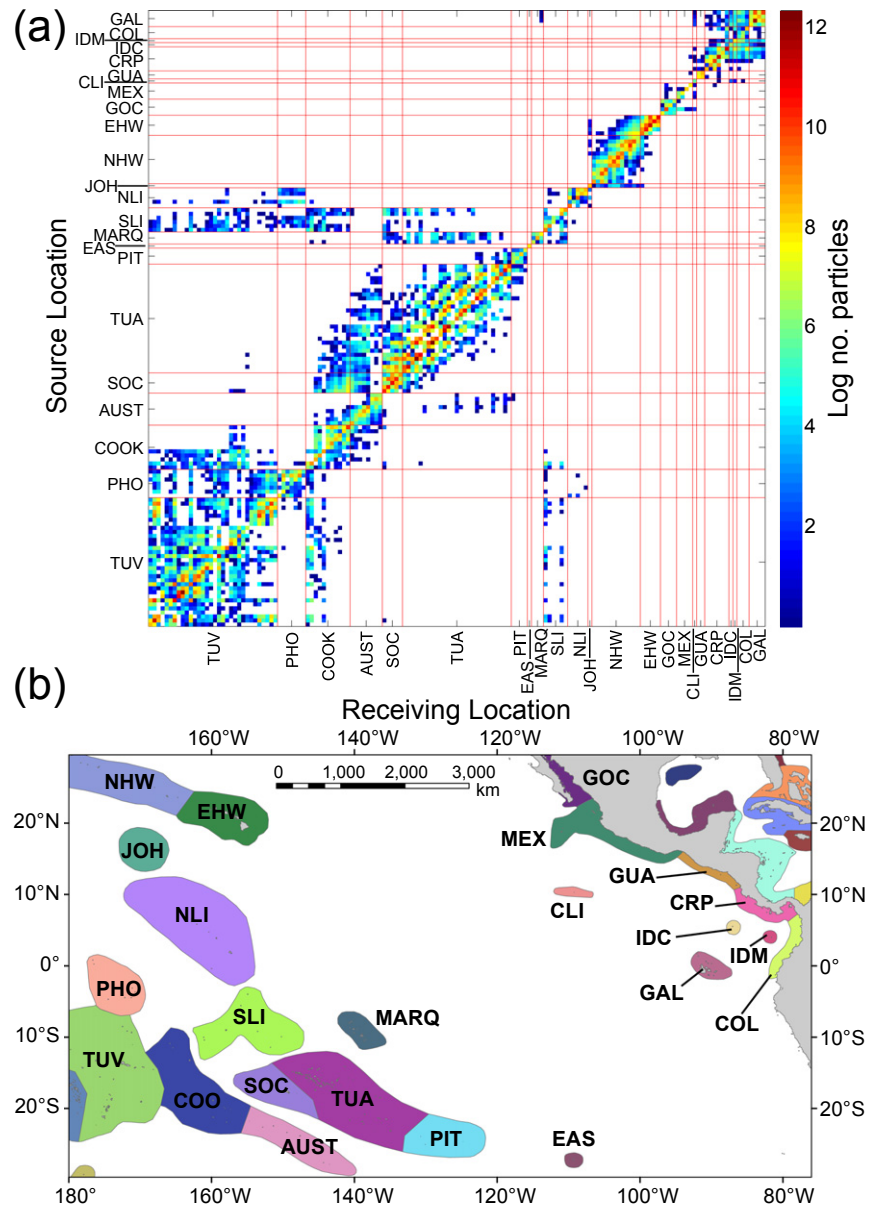
Figure 2 (a) Global potential connectivity matrix. The scale shows the log number of particles exchanged between each release (*y*-axis) and settlement (*x*-axis) location in the model, including settlement of a particle within its release region (along the diagonal). Due to the large number of habitat locations in the model, for visualization purposes these were overlain by a 2° grid and results summed on this scale, giving the individual points on the plot, and grouped into geographical regions (b), created by merging the ecoregions defined by Veron *et al.* (2009) onto an appropriate sub-basin scale.

only stepping stone for one-way dispersal into Hawaii, from the Northern Line Islands (NLI). Easter Island (EAS) was completely isolated with no external larvae exchanged over the whole 8-year period.

Potential connectivity indices

The settlement data were used to derive relative potential connectivity indices (Figs 4 & 5) at the scale of the habitat cells and

Figure 3 (a) Central/East Pacific regional potential connectivity matrix (as in Fig. 2) and (b) corresponding 'ecoregion' groupings (coloured), relating to distinct multispecies coral assemblages described in Veron *et al.* (2009).

above, giving information on both source (outgoing) and sink (incoming) potential for each location.
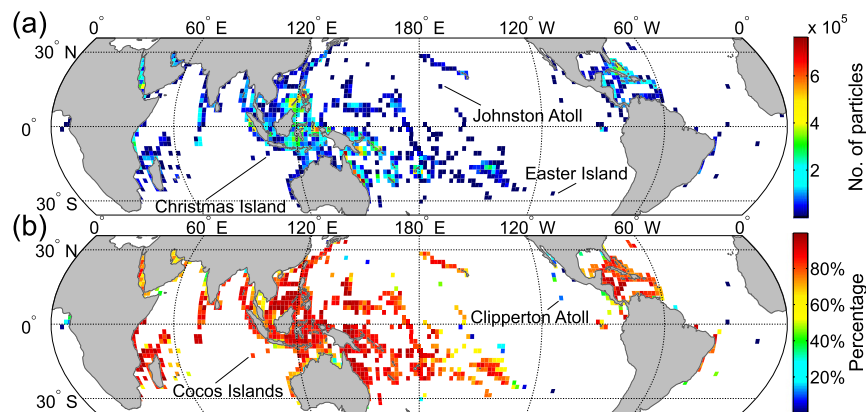
Isolation indices

Figure 4 shows indices for relative levels of isolation from incoming larval sources. The number of larvae that arrived within each habitat cell from any source location (including the settlement location itself) was recorded as 'total incoming settlement' ($S_{(\Sigma i \to j)}$). The highest levels of total incoming settlement were found in the IWP region and Great Barrier Reef (GBR), Australia (Fig. 4a). There were also additional peaks in incoming settlement around Sumatra and East Africa/the Red Sea. Even at the 2° grid scale used in the figures, local-scale patterns can be discerned, such as the inshore GBR receiving higher levels of incoming settlement than offshore GBR reefs.

To highlight locations which may be isolated from external larval sources, despite showing potentially high total incoming settlement (Fig. 4a), self-seeding was subtracted from total incoming settlement to give import, reported as a percentage of total incoming settlement (Fig. 4b):

$$\% \text{ import} = [(S_{(\Sigma i \to j)} - S_{(i \to i)})/S_{(\Sigma i \to j)}] \times 100.$$

The majority of reef locations exhibited high levels of % import (Fig. 4b), indicating that dispersal predominantly occurred at distances greater than the *c.* 10 km scale of the habitat cells in the model (model larvae were released from the centre point of each 1/6° cell). However, extremely isolated areas such as some central Pacific islands showed low levels of % import (< 15%). Many of these locations also showed low levels of total incoming settlement (e.g. Easter Island; Fig. 4b). Other isolated islands (e.g.

Figure 4 Isolation indices based on the number of incoming particles to a habitat cell (*j*). (a) Total incoming settlement ($S_{(\Sigma i \to j)}$): the sum of particles arriving at all habitat cells within the display cell, including self-seeding. (b) Percentage import, $[(S_{(\Sigma i \to j)} - S_{(i \to i)})/S_{(\Sigma i \to j)}] \times 100$: the number of incoming particles that originated from outside of the habitat cell (*i*) as a percentage of its total incoming. The plotted value is the average of the values of habitat cells within each 2° display cell. Locations mentioned in text are labelled. Projection: Mollweide.
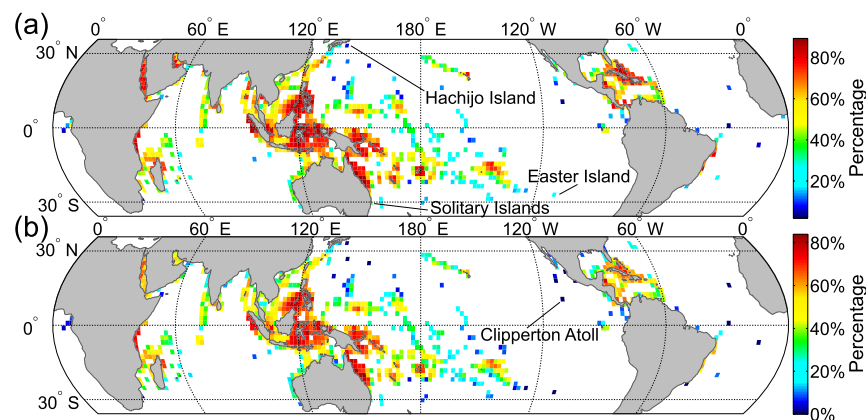
Figure 5 Source potential indices. (a) Percentage outgoing settlement, the percentage of the total number of particles released from a site (N_i) that successfully reach a settlement cell (*j*), including self-seeding, ($S_{(i \to \Sigma j)}/N_i) \times 100$. (b) Percentage export, the percentage of the total number of particles released from a site that reach a habitat cell outside of their release cell, $(S_{(i \to \Sigma j)} - S_{(i \to i)}/N_i) \times 100$. Both indices are plotted as an average of the values for the habitat cells within each 2° display cell. Projection: Mollweide.

Cocos and Christmas Islands in the eastern Indian Ocean, Johnston Atoll in the central Pacific) showed relatively low levels of total incoming settlement but relatively high % import. For example, while Easter Island and Johnston Atoll appear equally isolated in Fig. 4(a), a comparison of the two in Fig. 4(b) shows Easter Island to be completely reliant on locally sourced recruits.

Source potential indices

Figure 5 displays two indices of source potential; the effectiveness of each site as a source for recruits. Percentage outgoing settlement (Fig. 5a) was calculated as the percentage of particles released from a site (N_i) that successfully reach a settlement cell (*j*), including self-seeding:

% outgoing settlement $= (S_{(i \to \Sigma j)}/N_i) \times 100$.

Trends seen in the plots of incoming particles (Fig. 4) were also apparent in the outgoing settlement success (Fig. 5a). Geo-

graphically isolated areas were less effective in supplying recruits, especially those lying 'downstream' of persistent unidirectional currents. For example, the Solitary and Hachijo Islands, at the high-latitudinal limits for coral in the East Australian and Kuroshio currents, respectively, show relatively low outward settlement success (Fig. 5a).

The % export (Fig. 5b) measures the supply of particles to locations outside of the release cell (i.e. total outgoing settlement minus self-seeding), calculated as the percentage of the total number of particles released from a site:

% export $= (S_{(i \to \Sigma j)} - S_{(i \to i)}/N_i) \times 100$.

A comparison of Easter Island and Clipperton Atoll shows that while Easter Island appeared the stronger larval source according to total outgoing settlement (Fig. 5a), again this was entirely due to self-seeding (0% export, c.f. 6% for Clipperton; Fig. 5b).

DISCUSSION

With global coverage and relatively high resolution, the model output provides data that can be analysed at a wide range of scales. Here we pick out examples of how the model can (1) be compared against connectivity estimates from empirical genetic studies, (2) fill in gaps between existing local- to regional-scale studies, and (3) provide supplementary evidence regarding various hypotheses developed to explain large-scale patterns in coral biogeography.

Model validation and scales of dispersal

The model reproduces dispersal patterns consistent with genetic studies of broadcast spawning coral species. Despite the high dispersal potential (maximum 120-day dispersal period), recruitment in the model occurred predominantly within 100 km, consistent with other studies and reflecting the influence of pre-competency and mortality on the main body of the dispersal kernel (e.g. Cowen *et al.*, 2006; Treml *et al.*, 2012). Levels of self-seeding (or local retention, occurring within *c.* 10 km at the scale of the habitat cells) were of the order of 15–100%, again consistent with other studies (e.g. Figueiredo *et al.*, 2013). However, much rarer connections also occurred between regions, connecting entire ocean basins in a 'stepping-stone' fashion along habitat corridors, and maximum dispersal distances reached thousands of kilometres, demonstrating the potential for extreme long-distance dispersal given the right oceanographic conditions. Genetic studies support similar high levels of recruitment on scales of tens to hundreds of kilometres, leading to high genetic structure on local scales (Ayre & Hughes, 2000; Gilmour *et al.*, 2009), with rarer long-distance dispersal resulting in the wide geographic ranges and genetic linkages observed in many coral species (Glynn & Ault, 2000; van Oppen *et al.*, 2011; and see Figueiredo *et al.*, 2013). This combination of dispersal scales is clearly replicated in our model.

At regional scales, a number of parallels exist between model results and field-based observations. For example, westward exchange between the Indian Ocean (IO) and IWP via the Singapore Strait in the model agrees with various regional genetic studies (reviewed in Kool *et al.*, 2011) as well as local modelling results suggesting that larvae are unable to pass eastwards along this path (Kool *et al.*, 2011). In a second example, relatively low but significant levels of connectivity are modelled along the entire GBR, operating mainly southerly in a stepping-stone manner that matches genetic findings (Ayre & Hughes, 2000; Rodriguez-Lanetty & Hoegh-Guldberg, 2002; van Oppen *et al.*, 2011), and the relative isolation of Lord Howe Island in the model fits observations of Ayre & Hughes (2004). The model results also match genetic findings suggesting that connectivity decreases in the southern/offshore GBR compared with the northern GBR (Ayre & Hughes, 2004; van Oppen *et al.*, 2011). However, the fact that the relatively isolated Lord Howe, Middleton and Elizabeth reefs are still connected to the GBR is in agreement with the genetic study of Miller & Ayre (2008).

Coral connectivity and global biogeography

Longitudinal species richness gradients

Although coral species richness declines with distance both east and west away from the central Indo-Pacific 'Coral Triangle', the rate of attenuation of diversity is lower in the Indian Ocean than across the Pacific, and a secondary peak in diversity is found along the western Indian Ocean (Veron, 1995). Explanations for areas of enriched diversity can be categorized simply into 'accumulation' or 'origination' theories: The former attributes higher species richness in western ocean basins to biased dispersal by prevailing westward equatorial currents (e.g. Jokiel & Martinelli, 1992). Theories based around species originating or increasing in number through, for example, low extinction rates (reviewed in Connolly *et al.*, 2003) also incorporate the subsequent difficulty in dispersal away from western boundary areas counter to the same equatorial currents.

While the two theories are therefore not mutually exclusive, whether prevailing circulation patterns lead to accumulation in certain areas can be explored using the model by considering the relative number of particles leaving versus arriving in different regions. Regarding the Indian Ocean, dispersal was biased into the west with the East African coastline (EAFR region, Fig. 2) receiving more import from the central Indian Ocean (SEY and CIO regions, Fig. 2) than it exported back. However, in the northern and eastern Indian Ocean, dispersal was biased towards the east (e.g. larval transport occurs from SEY and NWIO into EIO, but not vice versa, and exchange from CIO to EIO exceeds that in the reverse direction). The eastern Indian Ocean also received imports from the IWP to the west, at levels greater than it supplied in return. Therefore, larvae accumulated in both the western (EAFR) and eastern (EIO) Indian Ocean regions in the model. Peaks in incoming settlement were also observed for western Sumatra and the East African coast in the connectivity index plots (Fig. 4).

The IWP centre of diversity (NIWP + SIWP regions in Fig. 2) was overall a source region (with 9127, or 0.03%, more particles exported than imported), and provided larvae to the eastern Indian Ocean, GBR/Coral Sea region and Japanese islands. It did not, however, supply the central Pacific (CPAC, Fig. 2), counter to the westerly Pacific equatorial currents. This source dominance is also calculated for the 'Coral Triangle' (as defined by Veron *et al.*, 2009; 300,141, or 1.1%, more particles exported than imported), although this geographic cluster of reef habitats does demonstrate connectivity with the central Pacific. Relative to other locations, the IWP region also experiences high incoming (Fig. 4) and outgoing (Fig. 5) settlement, indicating strong connectivity within the region.

These results correspond to general diversity patterns (Veron, 1995), and specifically positive deviations in species richness and accumulations of species range endpoints reported in Connolly *et al.* (2003) for the IWP, western Indian Ocean and Sumatra. The results, therefore, support a correlation between dispersal/connectivity and general species richness patterns. With regards to accumulation versus origination theories of biodiversity, the

results reflect both the accumulation of particles at the western margins of the major ocean basins due to prevailing westerly equatorial currents, but also higher habitat areas and close spatial arrangement of habitat patches in these locations (see Fig. S3), leading to higher incoming settlement and, for the IWP, also greater source potential. The level of interconnectivity, including the number of connections made with different locations, is conceivably a more important determinant of diversity than simple source/sink relationships.

Isolation and endemism

Low species richness and high levels of endemism have been attributed to isolation from larval sources for a number of locations, including the Hawaiian Island group (Jokiel, 1987), the central Atlantic (Nunes *et al.*, 2011), Japanese mainland (Veron & Minchin, 1992) and eastern Pacific regions (Glynn & Ault, 2000). The isolation of these locations is apparent in the simulated trajectory (Fig. 1), connectivity matrix (Figs 2 & 3) and index results (Figs 4 & 5). For example, Hawaii is almost completely isolated (see Fig. 3), with only the Johnston Atoll providing a critical stepping stone into the region from the Line Islands to the south.

As well as isolation by oceanographic distance (geographic distance plus current speeds and direction), persistent unidirectional currents can also create one-way barriers to dispersal, 'locking up' species in 'downstream' locations. For example, dispersal along the northern IWP/Ryukyu Island chain region is predominantly northwards in our model, corresponding to positive deviations in the northern ranges of coral species between 25 and 30° N reported by Connolly *et al.* (2003) and attributable to the persistent northerly Kuroshio Current. However, occasional dispersal southwards from the islands south of Kyushu is modelled, corresponding to latitudes below which the Kuroshio forms mesoscale eddies (reviewed in Veron & Minchin, 1992).

Geographic differences in recruitment, isolation and self-seeding

It has been proposed that populations are maintained in isolated sites by high levels of self-seeding (e.g. Gilmour *et al.*, 2009). Our results suggest that this characteristic can be explained by physical (oceanographic) controls without necessarily invoking biological adaptation to isolation. For example, comparing Easter Island with Clipperton Atoll in the index plots shows that while both are equally isolated, Easter Island exhibits higher levels of self-seeding (Figs 4a,b & 5a,b; discussed in detail in Results). This probably reflects the position of Easter Island within the South Pacific gyre, an area of sluggish surface ocean currents, compared with Clipperton, lying in the stronger North Equatorial Current (NEC).

The Eastern Pacific dispersal barrier

Numerical models can be particularly useful when model predictions do not match observations or conform to prevailing hypotheses. For example, the poor diversity and high endemism of tropical eastern Pacific (TEP) coral faunas has been attributed, along with suboptimal environmental conditions, to isolation from western sources by over 5000 km of open water (the East Pacific Barrier, EPB), and this is clearly visible in our model results (Fig. 1). However, genetic affinities between eastern and central Pacific populations suggest that the EPB is breached, at least occasionally, in both directions (reviewed in Glynn & Ault, 2000; Lessios & Robertson, 2006). This has been hypothesized to occur predominantly west to east, due to a marked increase in speed of the eastward North Equatorial Counter Current (NECC) during El Niño events, with implications for the origin of TEP coral faunas (reviewed in Grigg & Hey, 1992). However, we observed only one-way dispersal in our study, occurring westward from the Galapagos to Marquesas Islands via the South Equatorial Current (SEC). The results, therefore, do not corroborate either westward dispersal via the North Equatorial Current (NEC) (Jokiel & Martinelli, 1992; Jokiel & Cox, 2003) or eastward via the NECC, and also conflict with genetic data showing Clipperton Atoll in the east Pacific region to be more closely related to central than eastern Pacific coral populations (Baums *et al.*, 2012). The model results do, however, correspond to findings of biased east to west dispersal in reef fishes with high dispersal potential (Lessios & Robertson, 2006). Long-distance dispersal events are sensitive to model parameterization; dispersal from the Northern Line Islands to Clipperton Atoll (via the NECC) was simulated in an earlier model run (unpublished) conducted at coarser habitat resolution (1°) and with longer larval competency (maximum 244 days), a finding which may more closely represent rafting of adult corals on drifting material, reported for the central Pacific (Jokiel & Cox, 2003). Overall, our results demonstrate that the EPB is a strong barrier to anything other than very rare dispersal, corresponding to the low diversity and high endemism in the TEP (Glynn & Ault, 2000), as well as a paucity of species range endpoints east of Polynesia identified by Connolly *et al.* (2003).

Model limitations

We parameterized the model to represent a potentially widely dispersing broadcast spawning coral in order to identify general connectivity patterns driven by oceanographic circulation and basic biology. Further model exploration is necessary to quantify the implications of the biological simplifications, particularly sensitivity to species-specific parameterizations. For example, assuming monthly spawning enhances the variability observed in dispersal paths (e.g. Carson *et al.*, 2010), and the mortality/competency profile may affect the potential for both local retention and long-distance dispersal (Graham *et al.*, 2008; Connolly & Baird, 2010). Constraints on the number of spawning locations and larvae will also affect simulation of rare connectivity events (Siegel *et al.*, 2003; Paris *et al.*, 2013), and the resolution and spatial relationships of the habitat cells should be considered when interpreting the results.

Although at the highest resolution available for the global scale (1/12°), the oceanographic data used in this study will not

resolve smaller-scale turbulent motion affecting transport and could fail to capture near-shore processes that entrain larvae along coastlines (e.g. Black, 1993; Andutta *et al.*, 2012). These issues are minimized by the inclusion of a random walk impulse and the scale of the habitat polygons (*c.* 18 km^2), which encapsulate onshore retention processes. Furthermore, while our study captures almost a decade of variability in ocean currents (2003–11) it lacks any strong El Niño–Southern Oscillation (ENSO) events, which are known to affect both current speed and direction, and consequently patterns of connectivity (e.g. Glynn & Ault, 2000; Treml *et al.*, 2008). The results, therefore, represent a 'baseline' condition of general dispersal against which the impact of phenomena like ENSO events can be compared. Finally, arrival on suitable reef habitat does not automatically translate into successful recruitment into a population, which is determined by a host of post-settlement factors (Penin *et al.*, 2010). This will affect how well model results can be validated using genetic data.

CONCLUSIONS AND FUTURE WORK

We present the first global model of dispersal and connectivity for a generic broadcast spawning coral species. The results both augment and fill in the gaps of genetic studies and regional-scale connectivity models. We demonstrate the potential of the global-scale model for establishing how surface ocean circulation affects coral biogeography on scales relevant to current rapid climate change. For example, our model supports evidence for the extreme isolation of TEP coral communities, with the simulation of rare dispersal events operating in a one-way (westerly) direction across the EPB having implications for the origin of eastern Pacific coral faunas and highlighting how model results provide testable hypotheses for future research.

Relative connectivity indices were developed to identify locations vulnerable to disturbance due to isolation from larval sources and key source, stepping-stone and sink locations for the transfer of genetic material, important in influencing resilience and adaptive potential (Munday *et al.*, 2009). These indices should be incorporated into models predicting reef distribution (e.g. Couce *et al.*, 2012). The indices support hypotheses of relationships between connectivity and species diversity gradients. For example, the central Indo-Pacific, GBR and western Indian Ocean all showed peaks in connectivity in the model, reflecting a combination of biased westerly dispersal in major ocean currents as well as high habitat density. Our ultimate aim is a model framework able to assess dispersal control on coral distribution shifts under coming decadal to century environmental change (e.g. Yamano *et al.*, 2011) as well as the effect of changes in ocean temperature and chemistry on dispersal and connectivity. Future work includes improving model representation of the physical controls on larval release, dispersal and settlement success.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Reef locations in the model and example of model habitat.
Figure S2 Competency curve for a single release cohort (100 larvae).
Figure S3 Habitat area for each 2° display cell in km^2.

BIOSKETCH

Sally Wood is a PhD student at the University of Bristol with a background in earth, atmospheric and life sciences, Sally's research interests are in ecological responses to environmental change, focusing on coral reefs, with the goal of informing appropriate management and protection of marine ecosystems in an uncertain future.

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