El Niño and coral larval dispersal across the Eastern Pacific marine Barrier

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Keywords: Larval dispersal, marine connectivity, coral reefs, coral biogeography, biophysical dispersal model, El Niño/Southern Oscillation (ENSO), Pacific oceanography

Abstract

More than 5000 km separates the frequently disturbed coral reefs of the Eastern Tropical Pacific (ETP) from western sources of population replenishment. It has been hypothesised that El Niño events facilitate eastward dispersal across this 'East Pacific Barrier' (EPB). Here we present a biophysical coral larval dispersal model driven by 14.5 years of high-resolution surface ocean current data including the extreme 1997-98 El Niño. We find no eastward cross-EPB connections over this period, which implies that ETP coral populations decimated by the 1998 bleaching event can only have recovered from eastern Pacific sources, in congruence with genetic data. Instead, rare connections between eastern and central Pacific reefs are simulated in a westward direction. Significant complexity and variability in the surface flows transporting larvae mean that generalised upper-ocean circulation patterns are poor descriptors of inter-regional connectivity, complicating the assessment of how climate change will impact coral gene flow Pacific-wide.

Coral populations of the Eastern Tropical Pacific (ETP) survive in some of the harshest conditions for reef development worldwide[1]. Limited shallow-water habitat, combined with frequent environmental disturbances and upwelling of cool, low pH waters that restrict skeletal calcium carbonate production results in small, patchy reefs prone to erosion[2-4]. Consequently, ETP reefs are considered modern-day analogues for future reefs under rising atmospheric CO_2[2], although cool upwelled waters may also buffer 21st century ETP reefs from the rising sea surface temperatures expected to devastate western Pacific populations[5]. This environmental setting makes ETP reefs an interesting case study, both as vulnerable marginal populations and as potential refuges for coral reef biodiversity under climate change.

The El Niño-Southern Oscillation (ENSO) dominates climatic variability across the tropical Pacific. Warm El Niño or cold La Niña phases, occurring every 2-7 years, cause wide-scale ecological disturbances in the region[3]. In particular, anomalously high temperatures associated with El Niño induce 'coral bleaching' – the expulsion of symbiotic photosynthetic algae that provide corals with energy for reef formation – in severe cases leading to the death of the host coral[6]. The extreme El Niño events of 1982-83 and 1997-98, considered the most intense of the past century[7,8], caused widespread severe bleaching, followed by coral mortality and local extinctions within the eastern Pacific[9-12]. While some reefs have since recovered[13-15], others have not[16], and East Pacific reef recovery is notably slower than other regions globally[17].

The delayed recovery of ETP reefs can be attributed, in part, to their extreme geographic isolation and therefore limited sources of population replenishment[17].

Broadcast spawning corals, in common with many benthic marine species, disperse via a pelagic larval life history stage that drifts with ocean currents over potentially vast distances[18]. However, barriers to dispersal exist where the oceanographic distance between habitats, driven by the speed and direction of the connecting ocean currents, exceeds larval lifetimes of the species in question. More than 5000 km of open ocean, the 'East Pacific Barrier' (EPB), separates eastern Pacific coral populations from their western counterparts, a distance historically considered impassable for many marine larvae[3,19,20] (Fig. 1) . Indeed, recent population genetic data for the trans-Pacific coral *Porites lobata* suggest that eastern Pacific populations have been isolated from those of the central Pacific for at least several generations[21] (considering the multi-century lifespans of massive poritid colonies[15] this equates to potentially thousands of years of separation). It follows that recovery of ETP reefs following disturbance may be highly reliant on survivors of affected populations[14,17] rather than being fuelled by more diverse central Pacific populations.

However, the presence of a number of trans-Pacific species in the ETP, such as *Porites lobata* and *Pocillopora damicornis,* implies that the EPB has, at least historically, been breached[3]. When and how frequently cross-EPB genetic exchange occurs has implications for both the origin of ETP reef faunas[3,19,22] and their resilience to continuing pressures such as warming and ocean acidification. Prevailing upper-ocean flow across the tropical Pacific is westward via the North and South Equatorial Currents (NEC/SEC, Fig. 1). However, inferred transport times across the EPB exceed the larval life span of most marine species[19,20,23]. Instead, it has commonly been proposed that El Niño events may facilitate cross-Pacific dispersal of marine larvae counter to the prevailing flow, via enhanced flow of the

eastward North Equatorial Counter-Current (NECC, Fig. 1)[3,14,19,20,23-27]. Because future climate change may potentially modulate the strength, frequency and 'type' of El Niño events[28,29], and thereby coral reef disturbance, connectivity and recovery rates, it is important to explore whether this hypothesis is correct.

It is impossible to measure larval dispersal directly over large distances. Instead, in this paper we test whether eastward dispersal across the EPB is more likely during El Niño events using a biophysical model of the dispersive larval stage of corals in the surface ocean. We model the oceanographic transport of larvae of a generic, ubiquitously-distributed broadcast spawning coral with high dispersal potential over 14.5 years (1997-2011), covering a full spectrum of ENSO conditions, including the extreme El Niño of 1997-98 (Fig. 2a), as well as other sources of variability in surface circulation. Despite maximising the potential for long distance dispersal in the model, no connections from the central Pacific to any eastern Pacific reefs are obtained for any of the 5.14 billion larval paths modelled over the entire study period. This implies that eastern Pacific broadcast spawning coral populations have been isolated from central Pacific sources of larval recruitment since at least 1997, a finding corroborated by genetic data for the widespread Pacific coral *Porites lobata*[21]. Instead, the EPB is breached in the opposite direction by larvae released from both the Galapagos archipelago and Clipperton Island in the model. However, whether these westward connections could be realised will depend on the timing of coral spawning and the negative reproductive impact of El Niño-linked temperature stress.

Results

Modelled potential larval connectivity

We released 1600 larvae daily from each of 636 reef locations in the model, grouped into 10 eastern and 10 central Pacific 'ecoregions'[30] (Fig. 1b), over a total of 14.5 years (1st January 1997 to 3rd July 2011). Model larvae were advected with high resolution, eddy-resolving ocean current reanalysis data for a maximum of 120 days - the maximum competency duration reported for any broadcast spawning coral species[31], and subjected to a daily probability of mortality in order to mimic inter-individual variability in survival durations[31] (see Methods). The number of model larvae successfully 'settling' (defined as arrival within a certain distance of suitable habitat at one of the 636 reef sites, see Methods) over the entire 14.5 year study period are plotted as a connectivity matrix (Fig. 3a), which defines potential connectivity between regions (Fig. 1b).

No eastward dispersal across the EPB was observed at any point over the entire study period (Fig. 3a). Contrary to the hypothesis of increased eastward cross-EPB dispersal during El Niño, rare connections instead occurred in the opposite direction at various points during the study period (Figs 2 and 3); a southerly route from the Galapagos (GAL) to the Marquesas (MAR), Line Islands (NLI/SLI) and Tuamotu (TUA) for releases during 11 of the 14.5 years modelled, in particular mid-1998 and early 2003 (Fig. 2b; taking >77 days) and a northerly route from Clipperton (CLI) to the Northern Line Islands (NLI) for larval releases during just 2 months (January-February) of the 1997-98 El Niño (taking >104 days).

Variability in potential connectivity outcomes

We also explore inter-annual variability in the potential connectivity output occurring under different ENSO conditions (Fig. 2a) by extracting the connectivity data for 5

representative annual periods (Fig. 3b-f): the extreme 1997-98 El Niño (an eastern Pacific event[32]), a weaker, central Pacific El Niño (2009-10), the extreme 2010-11 La Niña, a weaker La Niña (2008-09) and a neutral period (2005-06). As El Niño/La Niña events usually peak around December, releases for the period 1st June through 31st May were selected in order to encompass a full year of seasonal variability including both the build-up and decline of ENSO events.

Broad scale patterns of regional-scale connectivity, such as the isolation of the ETP and Easter Island from the central Pacific and relative isolation of Hawaii from the central Pacific and the northern (north of Honduras; CAM region, Fig. 1b) from the southern ETP, were persistent between years (Fig. 3). However, inter-regional connectivity within the eastern and central Pacific regions was sensitive to stochastic, daily to inter-annual variability as evident by changes in connections between matrices (Fig. 3). For example, connections within the southern ETP from the remote Columbia/Ecuador region (COL) region north to Costa Rica/Panama (CRP), Cocos (COC) and Malpelo (MAL) Islands and west to the Galapagos (GAL) were obtained in the 2009-10 central Pacific El Niño, both the 2008-09/2010-11 La Niñas and the 2005-06 neutral period, but not the stronger 1997-98 eastern Pacific El Niño, whereas a connection from the central American (CAM) to CRP region was obtained in both La Niñas, the 1997-98 El Niño and the neutral period but not the weaker 2009-10 central Pacific El Niño.

Biophysical model sensitivity

While we parameterise the model to maximise the potential for long-distance dispersal (e.g. applying the maximum larval competency duration values reported for

any broadcast spawning coral in the literature and releasing model larvae year round, see Methods), the ability to capture rare dispersal events may be affected by the biological parameters used. To test whether the result of solely westward dispersal across the EPB in the model is sensitive to model parameter choice, we further enhanced the potential for long distance dispersal over the strongest El Niño period in the model (June 1997 to May 1998), as the most likely period for eastward cross-EPB dispersal, by extending the larval duration and doubling the larval half-life (see Methods). Both changes increased inter-regional connectivity predominantly within the ETP and also to a lesser extent central Pacific regions, however, the outcome of no eastward connections across the EPB remained unchanged (Supplementary Fig. 1).

We also ran the model for the 5 representative annual periods detailed above (with reduced larval numbers due to computational constraints) excluding larval biology (mortality and settlement, i.e. advecting all larvae for the full 120 days), for releases from the Galapagos (Fig. 4a), Clipperton (Fig. 4b) and the northern Line Islands (Fig. 4c) as the most likely sources of dispersal across the EPB. Plotted larval trajectories from this model run show that although a few eastward larval trajectories from the northern Line Islands reach the longitude of Clipperton within 120 days (during the 1997-98 El Niño period; Fig. 4c.ii), they pass to the south of the island by ~1-2 degrees (~100-200 km).

Comparison of the biophysical model with genetic data

The model was not parameterised to represent a specific coral species – an aim that would be impossible given issues such as limited temporal and spatial data on

population sizes, timing of spawning, larval characteristics and recent recognition of the presence of cryptic species in the region. Instead, a species trait approach has been taken, with the model parameterised to represent a generic, broadcast-spawning coral with high dispersal potential. However, in order to explore how far the model results may be applicable for a specific species, and identify differences where research effort should be focused (in terms of modelling, biological observations and sensitive locations for additional genetic sampling), we compare connections generated by the biophysical model with recently published genetic differentiation data for the common trans-Pacific coral *Porites lobata*[21]. Mantel tests between the number of model larvae exchanged and the amount of genetic differentiation between each pair of populations (expressed as F'_{ST}) indicated that the biophysical model explained 15% of the variation in the genetic data. This value increased to 52% when the number of modelled larvae exchanged was expressed on a logarithmic scale, a common transformation used to highlight rare long-distance connections[33,34] (Supplementary Fig. 2). In comparison, Euclidian distance between reefs explained 26% of the genetic data, and 37% when converted to a log-10 scale.

We explore whether the patterns of realised connectivity seen in the genetic differentiation data for *P. lobata* are better reflected by dispersal conditions present under specific ENSO states by comparing the model-genetic correlation for the representative annual periods highlighted in Fig. 2a. Correlation between the biophysical model and the genetic data was highest for the strongest 2010-11 La Niña and weaker 2009-10 El Niño (both 47%) followed by the weaker 2008-09 La Niña (45%) and strongest 1997-98 El Niño (43%) periods compared to the neutral period (2005-06; 35%).

For the 1997-98 El Niño period, increasing the maximum larval duration and reducing mortality rate improved the model-genetic correlation from 43% to 51% and 50%, respectively. This increase in correlation was due to a greater number of inter-regional connections being made (Supplementary Fig. 1), predominantly within the ETP, which were otherwise significantly reduced during this El Niño event relative to other periods within the decade (Fig. 3). Of these additional connections, 2 were new intra-regional connections not previously simulated at any time during the full study period (from PIT to EAS, and REV to COC; Fig. 3a and Supplementary Fig. 1). However, sampling gaps in the genetics dataset (Supplementary Fig. 3) as well as limited distribution of *P. lobata* compared to the model coverage (*P. lobata* is replaced by *P. evermanni*, a previously unrecognized species, in the northern ETP[35]), limit the model-genetic comparison, and mean that the influence of the additional connections involving the Pitcairns, Easter and Revillagigedo Islands cannot be tested at present.

Discussion

It has been proposed that El Niño events enhance eastward dispersal across the vast expanse of the Eastern Pacific Barrier, thereby lessening the isolation of reefs in the Eastern Pacific[3,14,19,20,23-27]. Following the extreme 1982-83 El Niño, for example, the recording of a number of Indo-Pacific mollusc, echinoderm and fish colonists in the ETP was tentatively ascribed to dispersal from the central Pacific via the NECC[3] (Fig. 1). For the modelled broadcast spawning coral we find that although central Pacific larvae from the northern Line Islands (NLI) do reach their most easterly range of dispersal during the extreme 1997-98 El Niño when compared to 4 other

representative annual periods (Fig. 4c), no connections were made eastward from the central to eastern Pacific at any time over the study period (Fig. 3a). This failure to connect eastward across the EPB occurs despite maximising potential for long distance dispersal, and is also robust to variations in larval duration, mortality rate and numbers of larvae modelled. Significantly, this result suggests that ETP coral populations have been isolated from central Pacific sources of larval replenishment over the 14.5 years studied, implying that present ETP populations consist entirely of survivors of the extreme 1997-98 El Niño event and recruits from local sources. This hypothesis is supported by a recent survey of a dense *Pocillopora* reef in the Galapagos[36] which was found to consist entirely of a single clone propagated asexually from colony remnants following the 1997-98 El Niño-related mortality event.

The modelled dispersal paths demonstrate how, due to limited area for coral settlement in the ETP, subtle details in surface flow mean crucial east to west connections are missed (Fig. 4). They also highlight the value of biophysical dispersal modelling in providing additional detail on the complexity of surface flows not captured by generalised circulation patterns. For example, the timing of maximum eastward dispersal from the NLI (May-September 1997; Supplementary Movie 1), corresponds to the early development stage of El Niño, when easterly surface flow intensifies as the easterly trade winds weaken and westerly wind bursts develop[8,37]. However, modelled dispersal paths during this period pass ~100-200km to the south of Clipperton Island, the key stepping stone for onward connections into the ETP (Fig. 3), and fall short of reaching reefs further within the ETP (Fig. 4c(iii)). A southerly shift in the position of the NECC at the longitude of Clipperton (~110°W) is

a persistent feature of eastern-Pacific type El Niños[37] ('EP'-El Niño in Fig 3a). In contrast, no enhanced eastward dispersal from the NLI occurs during the 2009-10 El Niño (Fig. 3iv), instead dispersal is even more curtailed than that seen during neutral (Fig. 4ii) or La Niña conditions (Fig. 4 v, vi). This outcome is consistent with the observation that central Pacific El Niños ('CP'-El Niño in Fig 3a) have a negligible influence on the NECC, particularly in the ETP[37].

Breaking the model dispersal paths down by release month (Supplementary Movies 1-3) shows significant seasonal variation in dispersal direction. While dispersal paths from the NLI reached their most easterly longitudes in May to October 1997, more easterly dispersal was a persistent pattern of the boreal summer in other years (May/June to August; Supplementary Movie 1). This corresponds to seasonal strengthening of the NECC, beginning in the eastern Pacific from August and propagating west across the central Pacific during October-December[38] (note that the effect on dispersal is integrated over the 4 month larval transport period, e.g. larvae released in August could be transported into November). This seasonality in the NECC intensity can also be seen in the trajectories from Clipperton, which extend eastward into the ETP between May and September.

Conditions during the 1997-98 El Niño event also promoted the most westward dispersal of larvae across the EPB compared to the other representative annual periods (from both the Galapagos and Clipperton from November 1997 to the end of the releases in August 1998; Fig. 2b/c(ii), Supplementary Movie 1/2) and the largest number of larvae from the ETP successfully reaching reefs in the central Pacific occurred for releases following the 1998 and to a lesser extent 2003 El Niño events

(Figs 2a, 3c). However, this was not a unique situation; westward cross-EPB connections from the Galapagos to central Pacific were simulated in 11 out of the 14.5 years of the study (Fig. 2). Releases in the middle to latter half of the year (June/July onwards, excluding the end of the 2002-03 El Niño in early 2003) appeared more likely to make westward cross-EPB connections (Fig. 2b, Supplementary Movie 2), possibly partially corresponding to strengthening of the SEC during the Austral winter when the southeasterly trades are at their strongest[39]. However, the dispersal paths from the Galapagos were extremely complex, possibly confounded by seasonal shearing between the westward-flowing SEC and eastward-flowing NECC and eddies generated by Tropical Instability Waves[40].

These rare westward cross-EPB connections identified by the biophysical model (Fig. 2) are not supported by the only available genetic data for a broadcast-spawning coral species across the region, which suggest no gene flow between the central and eastern Pacific in either direction by the coral *P. lobata* for potentially hundreds to thousands of years[21]. There are a number of reasons why the westward connections suggested by the model may not be realised for this species. In particular, westward-EPB connections will likely be overestimated in the model because larvae were released daily all year round, while in reality coral spawn over discrete periods that are species-dependent but at the most a few months per year[41]. As discussed above, the model demonstrates marked variability in direction of dispersal pathways depending on month of release. These results are intentionally unconstrained due to our aim to model the maximum possible dispersal potential for a generic, ubiquitous species (see Methods). Observations of coral spawning in the eastern Pacific are almost non-existent. However, in the case of *P. lobata*, indirect

evidence from the Galapagos points to larval releases occurring during at least May to June[42]. Consequently, for example, the peaks in cross-EPB connections via the Galapagos occurring for releases from November-December 1997, July-August 1998 and March 2003 in the model (Fig. 2) would not be realised for this species.

A further consideration is that while the biophysical model provides predictions of the pre-settlement distribution of larvae, genetic data also integrate over post-settlement processes, including mortality, predation and competition, which will reduce the population evidence of dispersal connections[43]. After the long journey across the EPB, settling larvae face very different conditions in the arrival location compared to their origin, likely resulting in post-settlement selection against migrants[44]. Of further significance is the probable impact of El Niño conditions. Widespread El Niño-related mortality in the central and eastern Pacific[9-12] would open up settlement habitat for new recruits, but any migrants would then also have to survive the elevated temperatures and subsequent secondary stresses caused by the event[9]. Further, immediate and long-term reductions in coral fecundity following bleaching stress[45], reduced adult spawning populations due to bleaching-related mortality[10] and direct impact of elevated temperatures on larval development[46], would significantly reduce larval dispersal potential during and following El Niño. Since reefs across the central and eastern Pacific were exposed to bleaching–level thermal stress starting in April 1997 through to June 1998[47] it is, therefore, highly unlikely that any of the modelled cross-EPB connections via the Galapagos archipelago or Clipperton Island were realised in 1997-98.

Despite the caveats discussed above - the different aspects of the dispersal process captured by the two approaches (i.e. differences in temporal resolution and pre- versus post-settlement) as well as lack of model parameterisation for any single species, a surprisingly large amount of the reported genetic variation between populations of *P. lobata*, up to 52%, can be explained by the modelled connections for a generic broadcast spawning coral over the 14.5 year period. This has a number of potential implications. Firstly, that pre-settlement dispersal patterns, set primarily by the oceanographic conditions, are roughly as important in driving genetic patterns as post-settlement selection. Secondly, that these oceanographic controls appear to have been relatively persistent over time, considering that genetic data integrate over multiple generations (amounting to centennial-millennial timescales), whereas the model covers only a 14.5 year period. Finally, the correlation also implies that the generic model may be generally applicable to specific species. Further testing is currently limited by a lack of data (both genetics and field observations) across the region, both to compare the model with other species, or to parameterise the model for a specific species (e.g. population sizes, larval characteristics, timing of spawning). This has, however, been done for coral species in other regions; *Orbicella* (previously *Montastraea*) *annularis* in the Caribbean[48] (46% correlation) and *Acropora hyacinthus* (75-89%) and *A. digitifera* (48-83%) in Micronesia[49].

Returning to the hypothesised importance of El Niño events for gene flow in the eastern Pacific – are the patterns of genetic connectivity for *P. lobata* better reflected by the dispersal conditions present during El Niño? Comparing the model-genetic correlation between years indicates that ENSO events of both signs do have a larger influence on the realised connectivity captured in the genetic data when compared to

neutral conditions (8-12% increase in the variation in the genetic data explained). However, it is difficult to determine specifically what about the La Niña/El Niño periods compared to the neutral period, such as changes in the strength and/or number of connections within the eastern and/or central Pacific, is driving the improvement in the correlation with the genetic data. Regarding potential cross-EPB dispersal, while there is some correlation between modelled cross-EPB connections from the Galapagos and the genetic data (~6% for the full model time period), the genetic data indicate that such connections were not recent, although increased samples would be needed to strengthen this conclusion. Novel genotyping-by-sequencing approaches promise to provide higher resolution of population genetic structure in non-model organisms and could yield additional insights with regards to the timing and direction of any gene flow across the EPB in reef-building corals.

Areas where the model differs from the available genetic data suggest prudent sites for further empirical research - particularly significant given the ongoing strong El Niño event in the Pacific. These areas include Clipperton, the Galapagos, Northern Line Islands, Marquesas Islands and Tuamoto, as well as locations currently missing in existing datasets such as the Revillagigedos Islands. Importantly, the model is able to suggest specific sites within these regions where connections may occur in order to focus field efforts. For example, connections from the Galapagos to Marquesas regions in the model occurred predominantly into the northernmost Marquesas Islands, which were not sampled in the genetic data (Supplementary Fig. 3, Supplementary Table 1). Further, improved modelling incorporating field and laboratory data, particularly timing of spawning, for specific species at the key locations mentioned above is required to make more accurate predictions of

dispersal patterns. However, in the absence of such data, an alternative approach would be to conduct sensitivity analyses of the model output to biologically realistic variations in the timing of spawning and other biological parameters, in order to quantify uncertainty and guide future empirical work.

Finally, genetic data for non-coral species (e.g. the gastropods *Conus ebraeus*[50] and *C. chaldaeus*[51], sea urchin *Echinothrix diadema*[52], and boxfish *Ostraceon meleagris*[25]) have provided evidence for connections across the EPB, including from west to east[25] and between Hawaii and the ETP. Our model suggests that both easterly cross-EPB dispersal, as well as connections in either direction between Hawaii and the ETP, are highly unlikely to have occurred at any time over the previous decade for surface-dwelling larvae. This does not, however, exclude this possibility for species with differing dispersal modes, such as lower buoyancy or vertical swimming behaviour and consequently a greater depth in the water column. Due to occasionally marked differences in flow with depth, especially in areas of strong surface heating, such organisms could follow different dispersal paths to those presented here. Our results also do not consider the potential for longer-distance dispersal by rafting of adult corals on drifting materials, observed for colonies at least 1 year old[53]. For example, reports of pumice arriving at Hawaii and Christmas Island (NLI) originating from the Revillagigedos Islands (REV; Fig. 1) in the ETP[54] suggest that westward dispersal across the EPB by rafting of adult corals on drifting material beyond the 4 month larval duration limit set in our model could be possible. Indeed, model larvae trajectories from Clipperton Island did approach within ~200-300km of the southern tip of Hawaii within the 120 day larval duration when mortality and larval settlement were excluded (Fig. 3b). In contrast, dispersal

paths from Hawaii are swept rapidly to the west by the NEC (data not shown), excluding the possibility of eastward dispersal into the ETP via this route.

Our results demonstrate the sensitivity of dispersal patterns across the equatorial Pacific to surface oceanographic conditions. These patterns show significant complexity on intra- and inter-annual scales, indicating that variations on decadal (e.g. Pacific Decadal Oscillation) and longer timescales must also be considered. Our results suggest that future changes in the frequency, intensity and dynamics of ENSO events[28,29] are likely to have implications for coral connectivity, and therefore the resilience of reefs Pacific-wide to climate change. However, predictions of how these changes will impact connectivity patterns based on generalised circulation patterns are too simplistic. Biophysical dispersal modelling, incorporating high resolution oceanographic data and incorporating more detailed empirical data on a greater range of species, is required to make more accurate forecasts.

Methods

Biophysical dispersal model

Following the methods of Wood *et al*.[55], we modelled the dispersal of coral larvae using the Connectivity Modelling System (CMS), an open source program developed to model the dispersal of large numbers of biotic or abiotic particles in the marine environment[56]. CMS is a stochastic Lagrangian (water parcel following) Individual Based Model which uses inputted oceanographic data to advect and track particles in a 3D ocean, incorporating individual variability in particle attributes and representation of habitat for larval release and settlement.

Model larvae were ‘released’ from 636 reef release sites across the central and eastern Pacific (Fig. 1 and see ‘Biological parameterisation, below) over a 14.5-year period: 1st January 1997 to 3rd July 2011. This represents the longest time period of any coral dispersal modelling study to date, encompassing a decade and a half of oceanographic variability including a full spectrum of ENSO conditions; both the extreme 1997-98 El Niño and 2010-11 La Niña, as well as a number of smaller ENSO events and ‘neutral’ and transitional periods, and includes both ‘types’ of El Niño: Central Pacific (2004-05 and 2009-10) and Eastern Pacific types (1997-98 and 2006-07; Fig. 2a)[32].

The model larvae were advected using daily (at 00Z) surface ocean current data from the HYbrid Coordinate Ocean Model (HYCOM[57]; GLBu0.08/expt_19.1). At 1/12° (~9km), the spatial and temporal resolution of HYCOM is sufficient to capture transient features such as eddies which may act to entrain or transport larvae in the open ocean[58-60]. To account for smaller scale diffusive turbulent motion not captured at this resolution, a stochastic ‘random walk’ impulse was applied to each model larva at each 4-hour time step, using a horizontal diffusion coefficient of $7 m^2 s^{-1}$ based on the relationship between model resolution and diffusion defined by Okubo (1971). Note that the model time period from 1st Jan 2004 to the last release on the 7th November 2011 was run using an earlier release of the HYCOM global reanalysis data than the earlier period 1st January 1997 to 31st December 2003, due to the release of new HYCOM reanalysis data extending back to 1992 mid-way through the study in late 2014. While the horizontal resolution remained constant between the 2 datasets, the depth of the surface layer over which the currents used to drive the

dispersal models were averaged reduced slightly from 3m to 1m in the newer data (see Sensitivity analysis', below).

Biological parameterisation

As the focus of this study was to test the hypothesis of increased probability of rare long-distance dispersal across the EPB during El Niño events, our approach was to maximise the potential for rare long-distance dispersal, within realistic limits of dispersal parameters reported in the literature for broadcast spawning coral species. Due to significant variability in the biological factors influencing dispersal both between and within species, as well as a lack of empirical data for parameterisation across the study region, we did not attempt to recreate dispersal patterns for any specific species. As such, we do not claim to attempt to recreate biological realism in the model. Model larvae were instead parameterised to represent the positively buoyant larvae of a generic, ubiquitously distributed broadcast spawning coral with high dispersal potential.

Field observations of positively buoyant coral larvae report aggregates restricted to the top few cm's of the water column, even under moderate winds ($<8 ms^{-1}$)[61,62]. It is only during strong winds that some larvae could potentially be mixed deeper into sub-surface currents (~20m)[62], conditions which concurrently homogenise flow depth profiles. Model larvae were therefore restricted to the surface layer in the model (i.e. the model was run in 2D only).

Reef habitat for larval release and settlement was defined using combined global reef and non-reef forming coral community distribution data from ReefBase v.2000[63] and UNEP-WCMC 2010[64]. Due to computational constraints, this combined reef data

was re-gridded onto a 1/6° grid, giving 636 ~17x17 km reef habitat ‘cells’ (Fig. 1, and see below). 1600 model larvae (see ‘Larval release numbers, below) were released daily from the centre of each habitat cell year-round, giving 5054 release events and over 5.1 billion larvae modelled. Whilst this represents a highly unrealistic spawning scenario (see Discussion), in line with our aim this allows us to capture the maximum amount of variation in dispersal paths driven by seasonal variability in ocean currents, providing an oceanographically driven ‘baseline’ over which inter-species, geographical and temporal variability in spawning times will reduce the modelled dispersal estimations. As equal numbers of larvae were released from each habitat cell, larger numbers of habitat cells in areas of higher reef cover approximates for larger adult population sizes in these areas.

To obtain estimates of potential connectivity (exchange of individuals between populations via dispersal), model larvae passing within a reef cell within a prescribed ‘competency window’ (see below) were considered ‘settled’, their advection stopped and their source and arrival location recorded. This information was then summed for all habitat cells within each region, see Fig. 1, to build the regional connectivity matrix, Fig. 3). Due to the gridding method used to transform the reef distribution data into a manageable number of release sites for the model, some cells extended further from the land mask of the oceanographic data than others (due simply to how the grid lay in relation to the land mask). This meant that the distance a larva could get to the coast before being considered ‘settled’ varied from cell to cell. As the habitat grid was created at half the resolution of the HYCOM fields (1/6°) and aligned to this grid, the maximum distance a habitat cell could extend from the model ‘coast’ was 1/6° (~18.5 km at the equator) and the minimum ½ of a cell or 1/12° (~9 km at

the equator). This also meant that the habitat area for settlement varied by cell and by region, with again the maximum area per cell being a whole cell (~18.5 x 18.5 km at the equator) and the minimum being ¼ of a cell (~9 x 9 km at the equator). This method differs from smaller scale dispersal modelling approaches, where a uniform buffer (a 'sensory zone' for larvae) is applied around known reef extents, and should be noted as a caveat to our results.

The inclusion of larval behaviour was not considered appropriate given the scale of this study and size of the habitat settlement cells, as coral larvae are weak swimmers and active seeking and orientation behaviour is likely to play a role at scale of meters at most[65]. However, the size of the habitat cells, whilst computationally-driven, could be considered to compensate for near-shore processes not captured at the resolution of the oceanographic fields which may entrain larvae near coastlines[62], maximising the potential to capture rare connections. As we are not concerned with the actual numbers of dispersers (see 'Larval release numbers', below), but rather relative levels of connectivity between locations and the potential for long-distance dispersal, individual particles in the model can be thought of as 'packages' of larvae, which, if transported near enough to a reef have at least some probability of some individuals being entrained and reaching it.

Whilst we parameterise the model to maximise dispersal potential in order to capture 'extreme' dispersal events, we incorporate basic biological parameters as well as inter-individual variability in these parameters known to be an important factor driving connectivity patterns[66]. This gives a realistic shape to the dispersal 'kernel', whereby

the majority of larvae settle close to their natal reef and a relatively small proportion are transported longer distances[67], allowing for both local retention and rarer long-distance dispersal and giving estimates of relative levels of connectivity between locations. Following fertilisation (which for broadcast spawning corals occurs in the water column), larvae must firstly undergo a period of development before they are able (competent) to detect and settle onto suitable reef habitat and undertake metamorphosis to the adult coral stage. To approximate variation in this 'pre-competency' duration in the model, 10% of each release 'cohort' became competent to settle from day 1 to 10 following release, within the range of values reported from laboratory studies[31]. Once developed, larvae have a finite amount of time over which they can survive in the plankton and still be competent to settle and complete metamorphosis into an adult coral polyp. To achieve variability in this larval duration, larvae were subjected to a constant mortality probability value of 0.02 day^{-1}, corresponding to a half-life of 35 days. This value was not based on experimental data, but rather chosen in order to give an exponentially-decreasing number of particles competent to settle over time within our specified maximum competency duration. In this case, larvae were transported to a maximum of 120 days, the maximum competency duration reported in the literature for any broadcast spawning coral[31], and terminated at that point if not already settled or dead. In this way we cover both between-species (maximum possible values: 120 day larval duration, 10 day maximum pre-competency period, ubiquitous distribution) and within-species (a full range within the above) variability. Therefore, for some species for example, short pre-competency durations of 1-2 days may overestimate the amount of local

retention, while the long maximum competency of 120 days may overestimate long-distance dispersal.

Finally, an additional run was conducted excluding larval biology (mortality and settlement), in which model particles were simply advected to a maximum of 120 days, incorporating stochastic turbulent motion only, and their trajectories plotted (Fig. 4). This gives an idea of the maximum 'oceanographic range' for the study period, excluding the influence of biology. As this run was more computationally demanding, 20 larvae were released daily from Clipperton Island (CLI; 1 reef cell), the Galapagos (GAL; 43 reef cells) and northern Line Islands (NLI; 22 reef cells) over 5 representative annual periods (see below) only.

It must be noted that we only model 'potential' connectivity - arrival of a larvae at a reef site does not imply successful settlement of the larvae onto the reef or recruitment into the host population. This process, which defines true population connectivity, is controlled by a host of further factors, such as predation and competition, which are not possible to include in the model.

Inter-annual analysis

Five representative annual periods were extracted from the full model output in order to compare between different years experiencing different ENSO conditions (Figs 3 and 4); the extreme 1997-98 El Niño (an eastern Pacific event[32]), a weaker, central Pacific El Niño (2009-10), the extreme 2010-11 La Niña, a weaker La Niña (2008-09) and a neutral period (2005-06). Releases from 1st June to 31st May the following year were selected, in order to cover a full annual cycle of seasonal variability in

circulation, centred around the peak of typical El Niño/La Niña events (December) in order to capture both the build-up and tail of these events.

Sensitivity analysis

Sensitivity of the model output to the maximum competency duration and mortality rate was tested over the 1997-1998 El Niño period, as the most likely period for eastward cross-Pacific dispersal. Two additional runs, attempting to further maximise the potential for long-distance dispersal, were conducted for this period; 1) 130 instead of 120 day maximum larval duration and 2) 70 instead of 35 day half-life (Biophysical model S1). 1600 larvae were released daily from all 636 locations from the 1st June 1997 to 31st May 1998. All other conditions remained constant.

The number of larvae released per event was primarily computationally constrained. However, in the absence of empirical data on the size of adult populations or their reproductive output across the region, biologically realistic parametrisation for larval release numbers was not considered feasible or applicable for this study. Instead, sensitivity of model output on the scale of interest (inter-regional connections) to larval numbers was tested to determine the appropriate number of larval releases per site. For this, the model was run multiple times with releases from 3rd November 2003 to 3rd July 2011 with an increasing number of larvae per daily release (N); from N=90 to N=1600, and the total number of inter-regional connections (regions defined as in Fig. 1) obtained calculated for each run (Supplementary Fig. 4). Individual runs at each value of N were also repeated in order to gain an idea of the spread in the number of connections obtained due to model stochasticity (Supplementary Table 2). At 1600 larvae per release, the number of connections between regions levels off at

(Supplementary Fig. 4), suggesting that the model system (given the 8 years of oceanographic data and biological parameters used) is ‘saturated’ with respect to the number of inter-regional connections at this scale. However, the overall number of connections likely reflects a balance of both losses and gains in connectivity due to model stochasticity, i.e. specific connections may vary even as the total number of connections levels off. To test whether this was the case, runs of incrementally increasing larval numbers were created by summing the output of smaller runs (see Supplementary Table 2). Difference matrices between each run were then plotted, showing connections lost or gained between runs (Supplementary Fig. 5). Up to N=800, a small number (1-2) of inter-regional connections were gained by increasing the number of larvae modelled. At N>800, no differences in specific inter-regional connections occurred within the study area, although 1 connection was gained between N=1400 and N=1600. In summary, model stochasticity does not impact large scale connections, but will introduce local level variability between runs.

The implications of a slightly different depth of surface layer in the HYCOM data between the 1997-2003 (0-1m, downloaded in 2014) and 2004-11 (0-3m, downloaded in 2013) periods used to drive the model was tested by repeating the 2010-11 La Niña period (releases from 1st June 2010 to 31st May 2011) using both the original and new HYCOM data. The result was a small overall decrease in the number of regional connections with the 1m compared to 3m surface layer depth data, totalling 7 losses and 5 gains, and all, with one exception, within the ETP (Supplementary Fig. 6). However, there was no change to the key model result of rare westward and no eastward dispersal across the EPB for this period.

Model-genetic comparison

We quantitatively compared the model output for a generic broadcast spawning coral with recently published microsatellite genetic data across the region for the common Pacific species *Porites lobata*[21]. Model connectivity output for the locations where genetic data were available (Supplementary Fig. 3) was extracted from the full matrix, giving 21 sub-regional groups (152 cells; Supplementary Table 1). Note that only the following regions used in the connectivity matrices were represented by genetic data: NHW, EHW, NLI, MAR, CLI, GAL, COC, CRP and COL (Supplementary Fig. 3). The distribution of *P. lobata* does not extend to the northern ETP, where it is instead replaced by *P. evermanni*[35], limiting the extent of the model domain that could be compared with genetic data.

A number of transformations were made to the model output before it could be compared to the empirical data. Firstly, as genetic data integrate over connections operating in both directions between two populations, they therefore give triangular 'half' matrices of the level of differentiation between each population pair. In contrast, the model output is expressed as a two-way matrix giving the number of larvae exchanged between each pair of populations in each direction. The raw model connectivity matrix was therefore firstly converted into a directionless half matrix by summing along the diagonal, i.e. summing the number of particles exchanged in both directions between each pair of populations. Values along the diagonal (retention within the release location; 'self-seeding'), not present in the genetic data, were excluded from the analysis. The resulting 'triangular' connectivity matrix was then normalised to the total number of particles released, effectively converting the

values into a probability of successful dispersal between each pair of locations (as we consider relative levels of connectivity, absolute values are not required). Secondly, genetic data are expressed as the level of differentiation between populations (F'st[68]) on a scale of 0 to 1, with 0 being no differentiation (maximum connectivity) and 1 being maximum differentiation. Large values in the model output, conversely, correspond to high levels of connectivity. The half matrix was therefore inverted in order to be directly comparable with the F'st data. A Mantel test (again using GenAlEx) was then performed to compare the measure of standardised genetic distance between locations (F'st) with both the transformed model data and approximate Euclidian geographic distance (both raw and converted to a logarithmic scale) between each pair of location (Supplementary Fig.

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Code availability

The biophysical model presented uses the open-source Connectivity Modelling System[56]. The source code is freely available to download and customise at https://github.com/beatrixparis/connectivity-modeling-system.

Data availability

The model output data presented in this manuscript are available from the corresponding author on request. The reef distribution data used to create the habitat cells was taken from UNEP-WCMC (2010)[64] available at http://data.unep-wcmc.org/datasets/1, and ReefBase 2000[63] available at http://reefgis.reefbase.org/. The oceanographic data (surface u and v current velocities) used to drive the biophysical dispersal model was downloaded from the HYCOM + NCODA Global 1/12° Reanalysis data server at https://hycom.org/dataserver/glb-reanalysis. The genetic data for *Porites lobata* used in the model-genetic comparison is presented in Baums *et al*.[21] and available on DRYAD (doi:10.5061/dryad.7gp1f).

Author contributions

S.W. conducted all modelling and analysis/plotting of output and wrote the manuscript. I.B.B. provided the genetic data and devised the model-genetic comparison. E.J.H., A.R, and C.B.P co-conceived (with S.W.) and supervised the project. E.J.H., A.R, I.B.B and C.B.P. discussed the results and commented on/edited the manuscript. W.S.K commented on and co-wrote the oceanographic section of the manuscript discussion.

Acknowledgements

S.W. was funded through a NERC postgraduate research grant (NERC/GEOG.SN1604.6525) and also acknowledges post-doctoral funding kindly provided by Alex Willmot-Sitwell through the University of Bristol Alumni Foundation. A.R. acknowledges funding from NERC NE/H017453/1. I.B. was supported by the

Alexander von Humboldt Foundation. The model-genetics comparison element of this work was funded through a WUN Researcher Mobility Grant awarded to S.W. to visit the Baums Laboratory. We would like to thank Jonty Rougier and Mark Beaumont (U. Bristol Department of Mathematics) and Naomi Altman (Department of Statistics, PSU) for informative discussions regarding the model-genetic comparison. The modelling work was carried out using the computational facilities of the Advanced Computing Research Centre, University of Bristol (www.bris.ac.uk/acrc/). Funding for development of the Connectivity Modelling System came from NSF grants NSF-RAPID 1048697 and NSF-OCE 1260424. This is contribution number 4301 of the Pacific Marine Environmental Laboratory/NOAA.

Figure legends

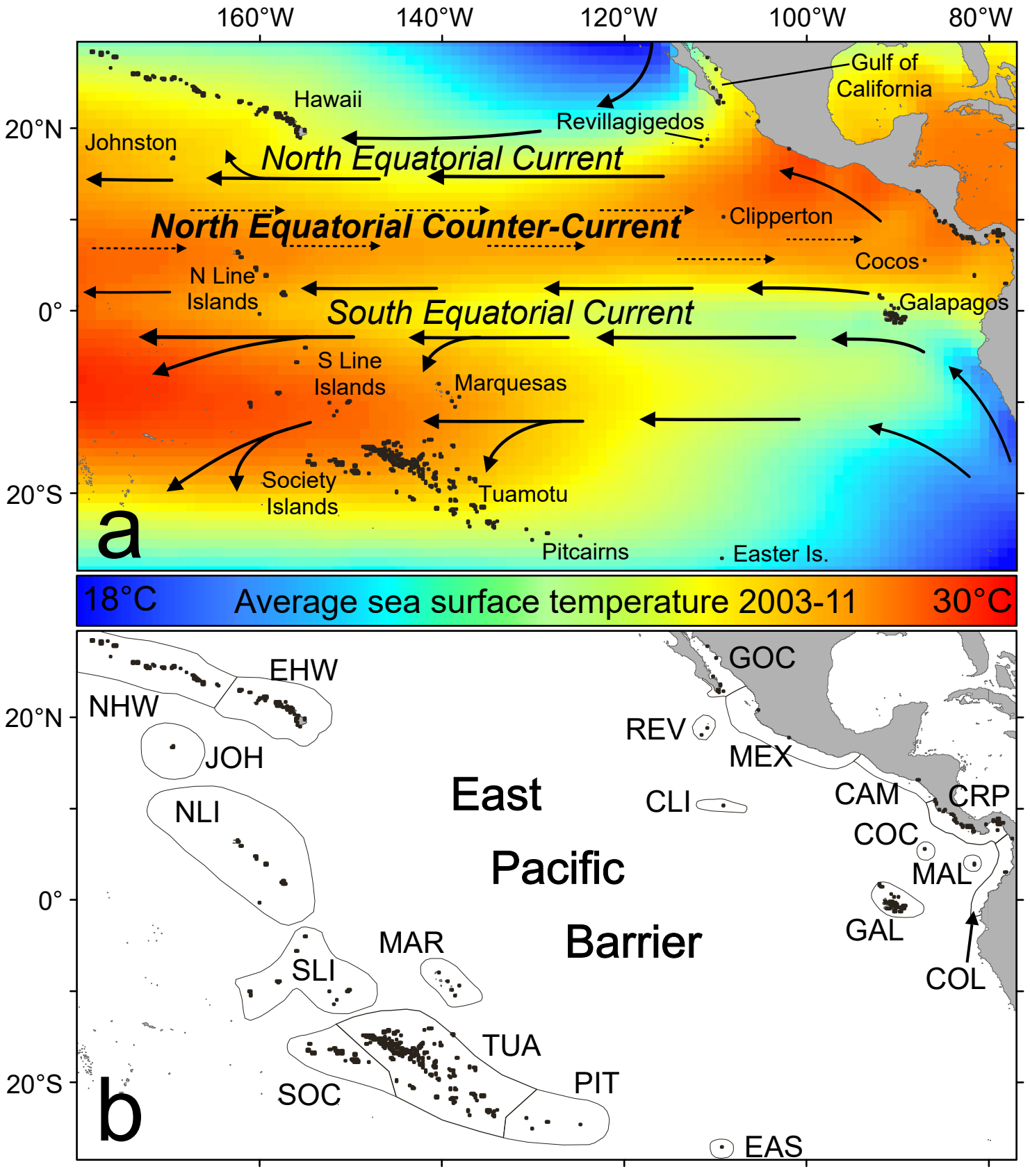
Figure 1 | Model domain. (a) Central and eastern Pacific model reef cells (black squares), observed sea surface temperatures (average of HadISST monthly means for the period 2003-2011), and schematic of large-scale surface currents (black arrows). **(b)** Regional reef delimitations (grey outlines, adapted from multispecies coral 'ecoregions'[30]) and codes used throughout the manuscript; EHW: Eastern Hawaiian Islands, NHW: northern Hawaiian Islands, JOH: Johnston Atoll, NLI: northern Line Islands, SLI: Southern Line Islands, SOC: Society Islands, TUA: Tuamoto Archipelago, PIT: Pitcairn Islands, EAS: Easter Island, MAR: Marquesas Islands, CLI: Clipperton Island, REV: Revillagigedo Islands, GOC: Gulf of California, MEX: Pacific Mexico, CAM: Pacific Central America (Guatemala, El Salvador, Honduras, Nicaragua), CRP: Pacific Costa Rica and Panama, COC: Cocos Island MAL: Malpelo Island, GAL: Galapagos Islands, COL: Columbia and Ecuador.

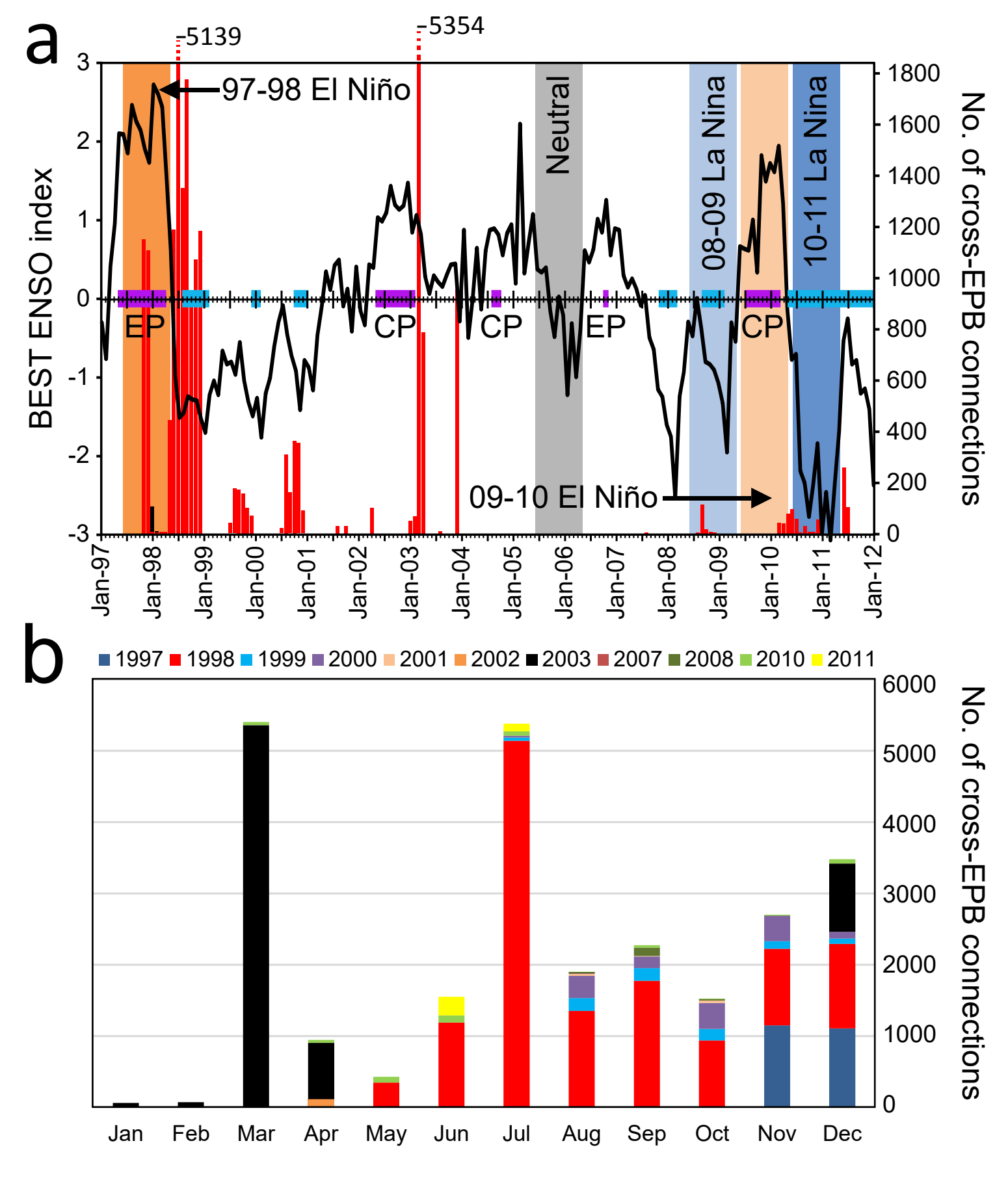
Figure 2 | Cross-EPB connections. (a) The number of successful cross EPB connections (right axis) westward from the ETP to the central Pacific over the model period (releases from 1st January 1997 to 3rd July 2011) shown by month of release (x-axis) from the Galapagos (GAL; red vertical bars) and Clipperton (CLI; black bars). The thick black line shows corresponding monthly ENSO phase and strength (Bivariate EnSo Timeseries 'BEST'[69], left axis). El Niño (purple; identified by type as eastern Pacific, 'EP', or central Pacific, 'CP'[32,70]) and La Niña (blue) events are marked along the central axis (defined by the BEST index, relaxed criteria; www.esrl.noaa.gov/psd/people/cathy.smith/best/table33.txt). The representative annual periods (June through May) used in the comparison of dispersal variability under different ENSO conditions are highlighted as vertical bars; 1997-98 (dark orange) and 2009-10 (light orange) El Niño, 2008-09 (light blue) and 2010-11 (dark blue) La Niña and 2005-06 neutral period (grey). **(b)** Number of successful cross-EPB connections from the Galapagos only by release month for the 11 years over which such connections occurred.

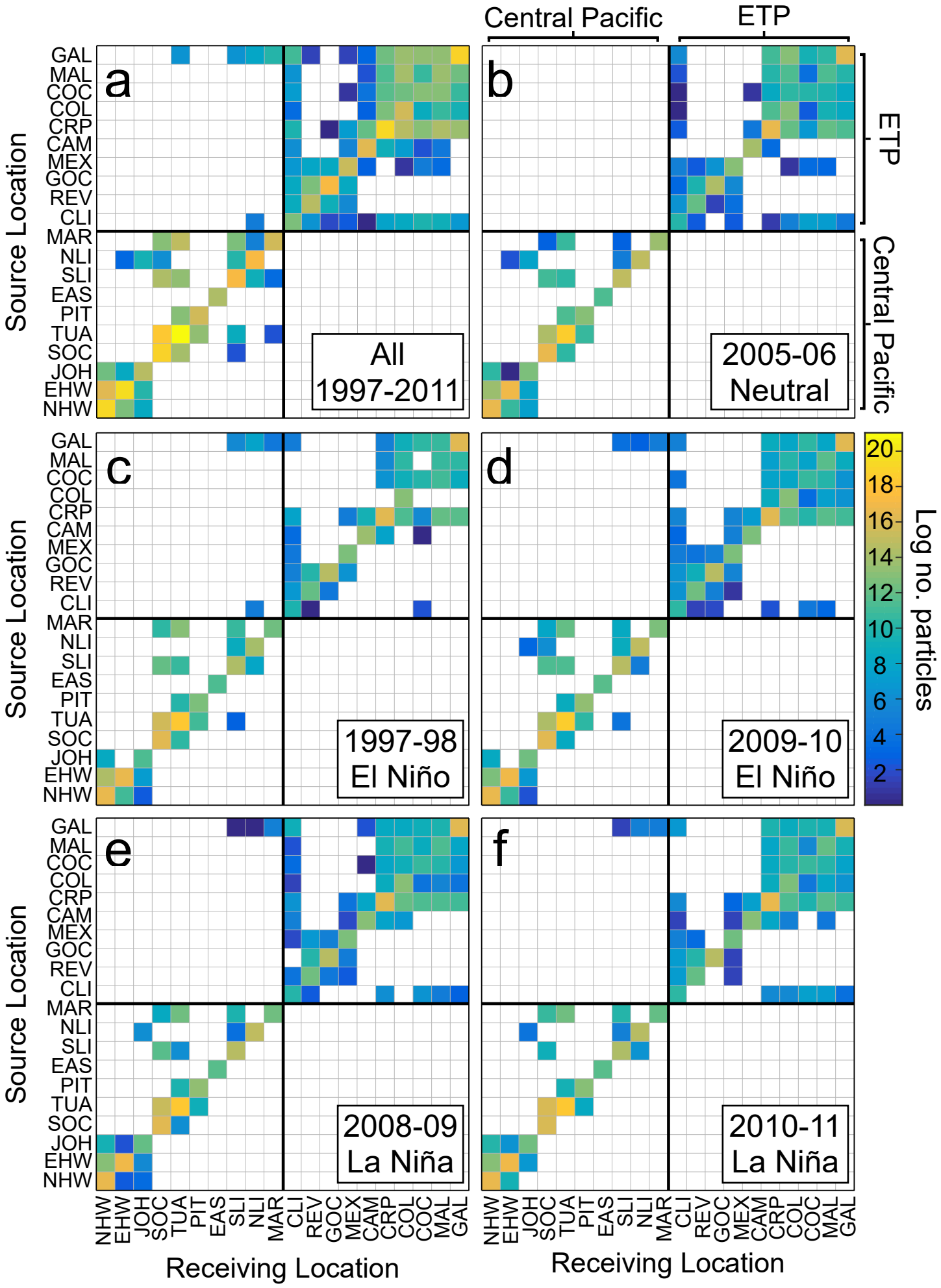
Figure 3 | Potential connectivity matrices. Connectivity matrices showing the number of model larvae exchanged between each release (y-axis) and receiving (x-axis) region for **(a)** the entire study period (releases from 1st January 1997 to 3rd July 2011), and representative annual periods (releases from 1st June to 31st May) for **(b)** the 2005-06 neutral period, **(c)** 1997-98 El Niño, **(d)** 2009-10 El Niño, **(e)** 2008-09 La Niña and **(f)** 2010-11 La Niña, (shown in Fig. 2a). Region delimitations used in the matrices are given in Fig. 1b. The central and eastern tropical Pacific (ETP) regions

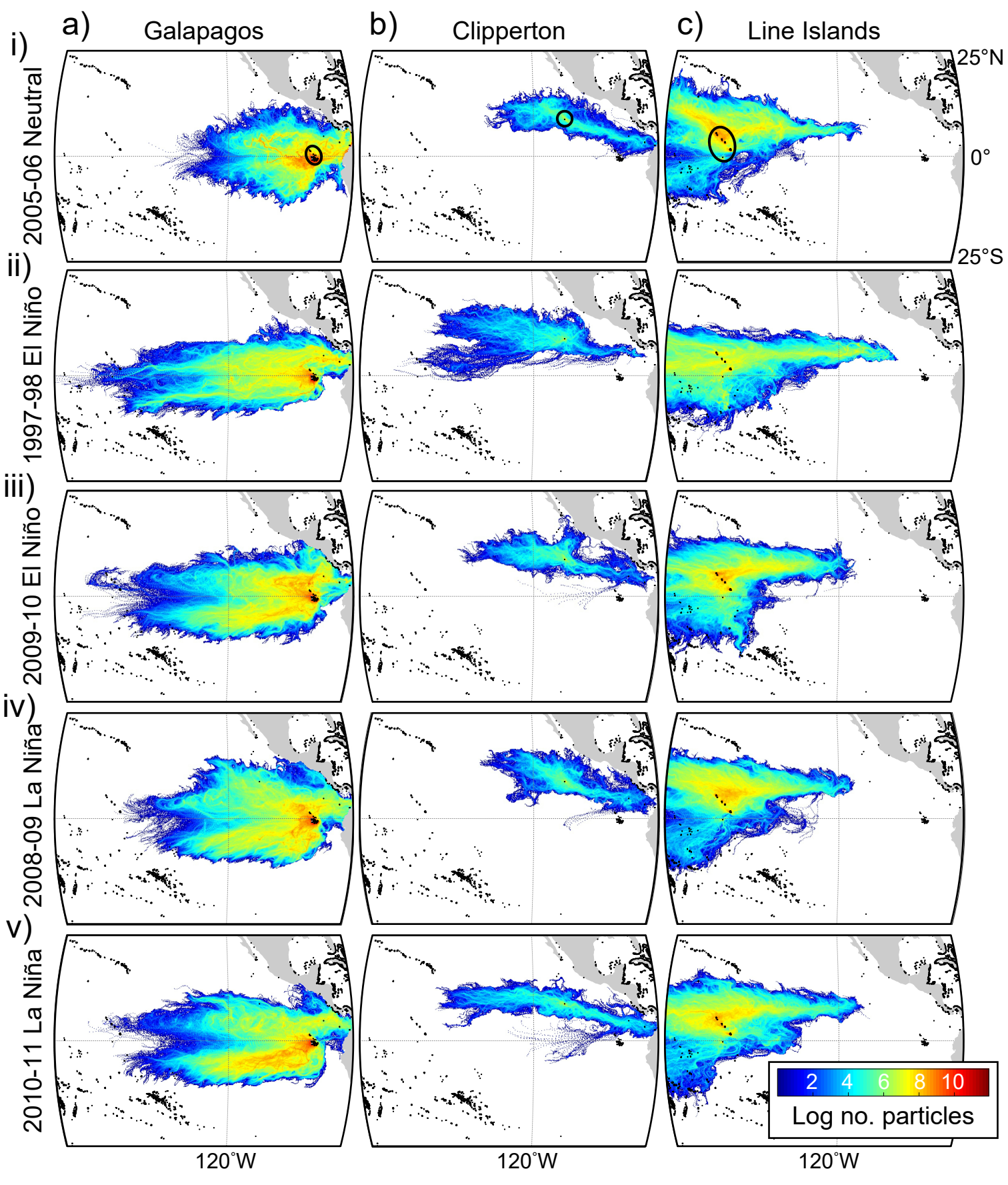
have been divided by a thick black line, representing the eastern Pacific barrier (EPB).

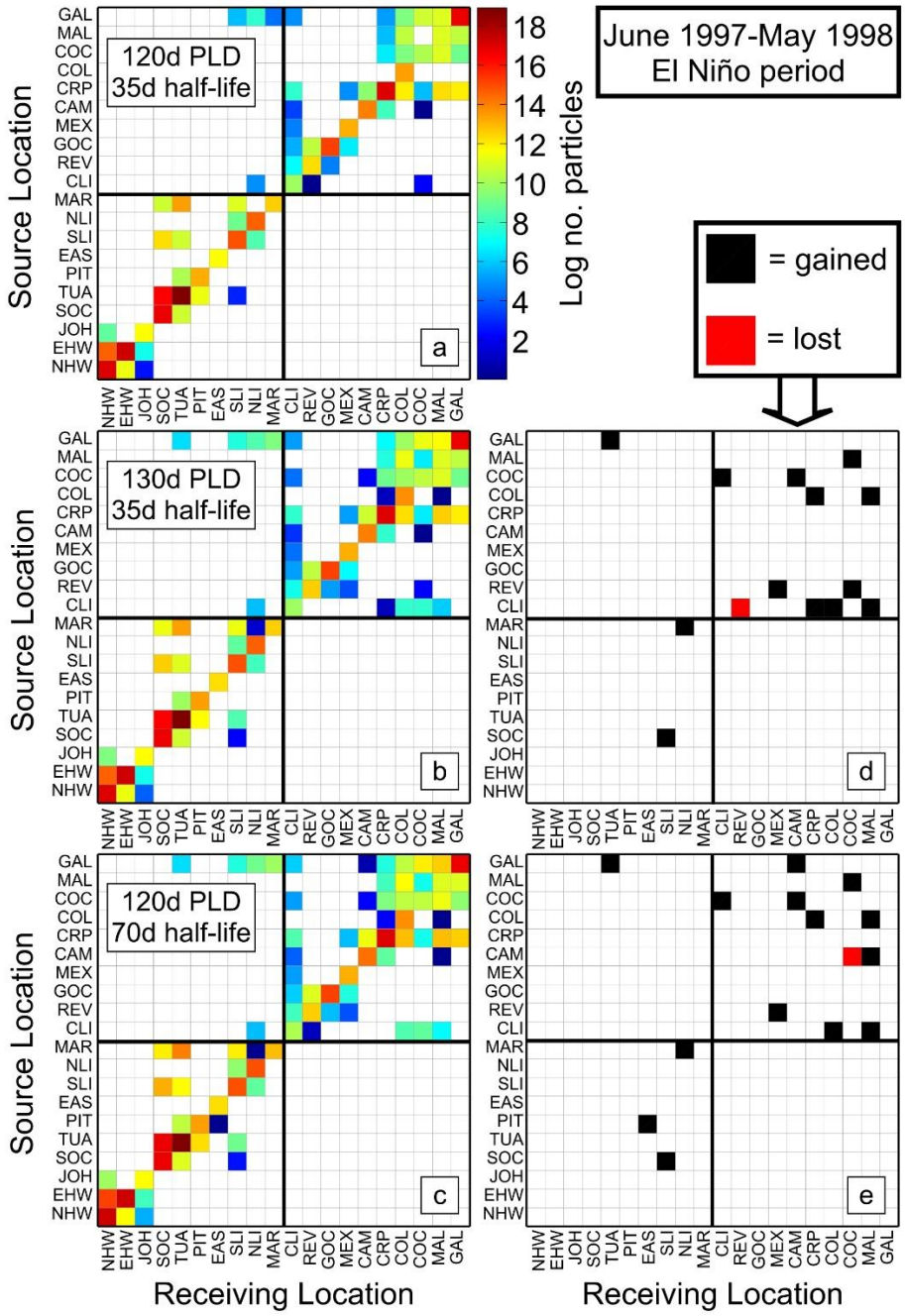
Figure 4 | 'Oceanography only' larval paths. Modelled dispersal paths conducted with a larval duration of 120 days, excluding mortality or settlement. 20 larvae were released from each habitat cell per day for a full annual period (1st June to 31st May), from **(a)** the Galapagos (43 release cells), **(b)** Clipperton (1 cell) and **(c)** Northern Line Islands (22 cells) over **(i)** the 2005-06 neutral period, **(ii)** 1997-98 eastern Pacific El Niño, **(iii)** 2009-10 central Pacific El Niño, **(iv)** 2008-09 La Niña and **(v)** 2010-11 La Niña (highlighted in Fig. 2a). Paths are plotted as larval densities, calculated as the number of particles passing through each cell on a 1/6 degree grid. Animations of these plots by release month can be viewed in Supplementary Movies 1 (Northern Line Islands), 2 (Galapagos) and 3 (Clipperton).


160°W
140°W
120°W
100°W
80°W
20°N
0°
20°S
Hawaii
Johnston
Revillagigedos
Gulf of California
North Equatorial Current
North Equatorial Counter-Current
Clipperton
Cocos
N Line Islands
South Equatorial Current
Galapagos
S Line Islands
Marquesas
Society Islands
Tuamotu
Pitcairns
Easter Is.
a
18°C
Average sea surface temperature 2003-11
30°C
EHW
NHW
JOH
NLI
SLI
MAR
TUA
PIT
SOC
East
Pacific
Barrier
GOC
REV
MEX
CLI
CAM
CRP
COC
MAL
GAL
COL
EAS
b

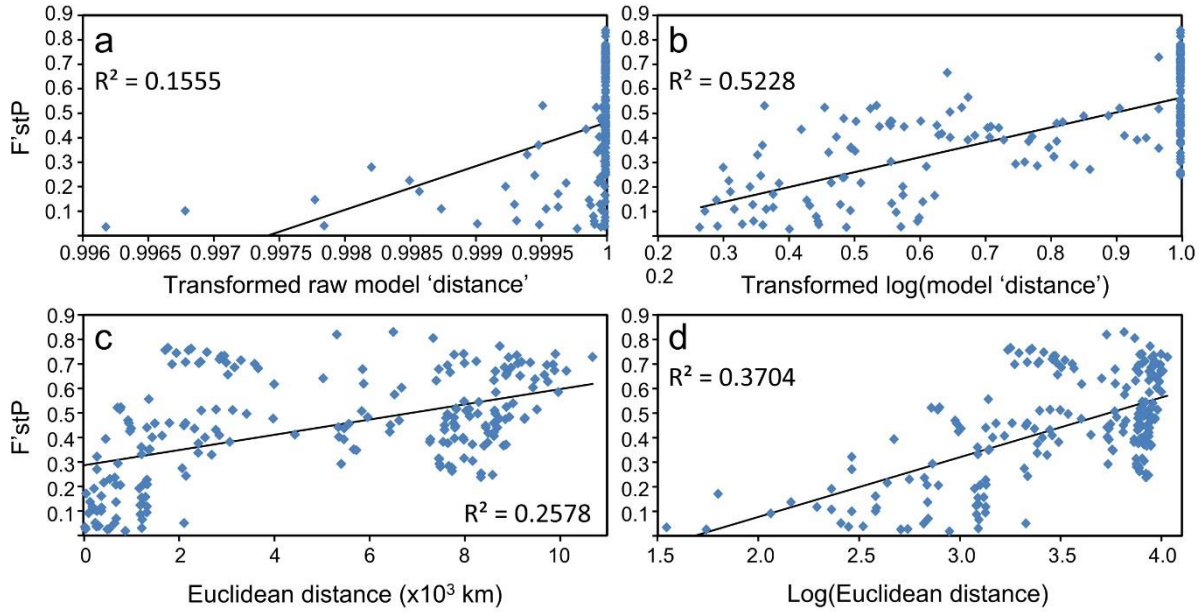

a
5139
5354
97-98 El Niño
Neutral
08-09 La Nina
10-11 La Nina
09-10 El Niño
EP
CP
CP
EP
CP
BEST ENSO index
No. of cross-EPB connections
3
2
1
0
-1
-2
-3
1800
1600
1400
1200
1000
800
600
400
200
0
Jan-97
Jan-98
Jan-99
Jan-00
Jan-01
Jan-02
Jan-03
Jan-04
Jan-05
Jan-06
Jan-07
Jan-08
Jan-09
Jan-10
Jan-11
Jan-12
b
1997
1998
1999
2000
2001
2002
2003
2007
2008
2010
2011
No. of cross-EPB connections
6000
5000
4000
3000
2000
1000
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec


Central Pacific
ETP
a
b
c
d
e
f
All
1997-2011
2005-06
Neutral
1997-98
El Niño
2009-10
El Niño
2008-09
La Niña
2010-11
La Niña
Source Location
Receiving Location
ETP
Central Pacific
Log no. particles
20
18
16
14
12
10
8
6
4
2
GAL
MAL
COC
COL
CRP
CAM
MEX
GOC
REV
CLI
MAR
NLI
SLI
EAS
PIT
TUA
SOC
JOH
EHW
NHW

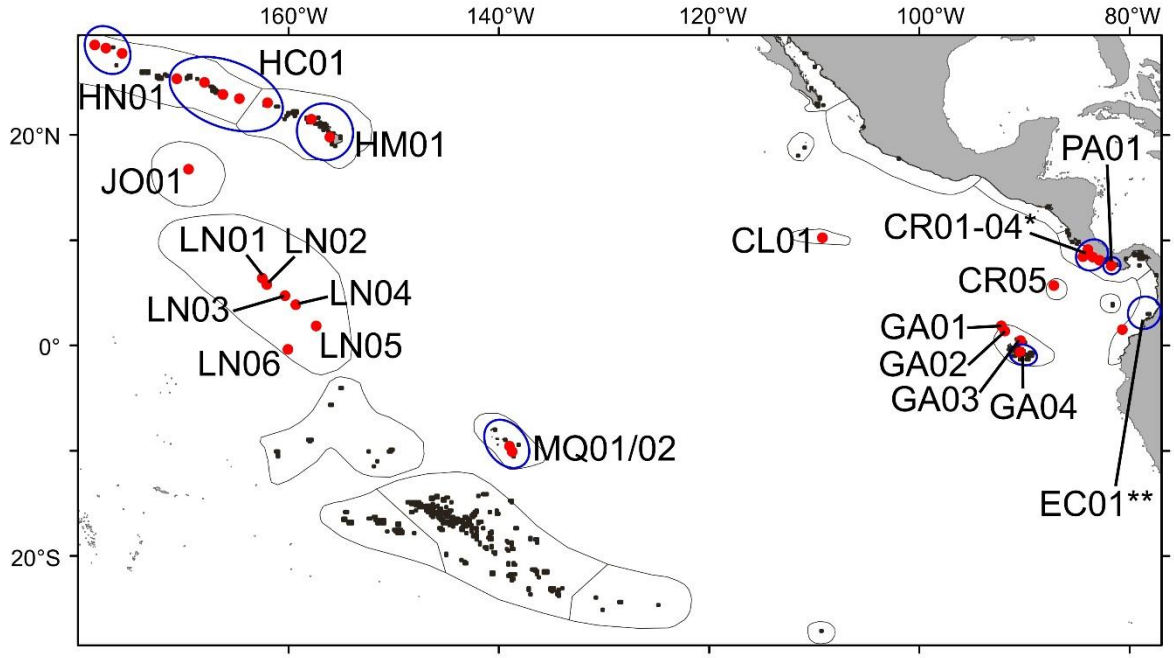

a)
Galapagos
b)
Clipperton
c)
Line Islands
i)
2005-06 Neutral
ii)
1997-98 El Niño
iii)
2009-10 El Niño
iv)
2008-09 La Niña
v)
2010-11 La Niña
25°N
0°
25°S
120°W
120°W
120°W
2
4
6
8
10
Log no. particles



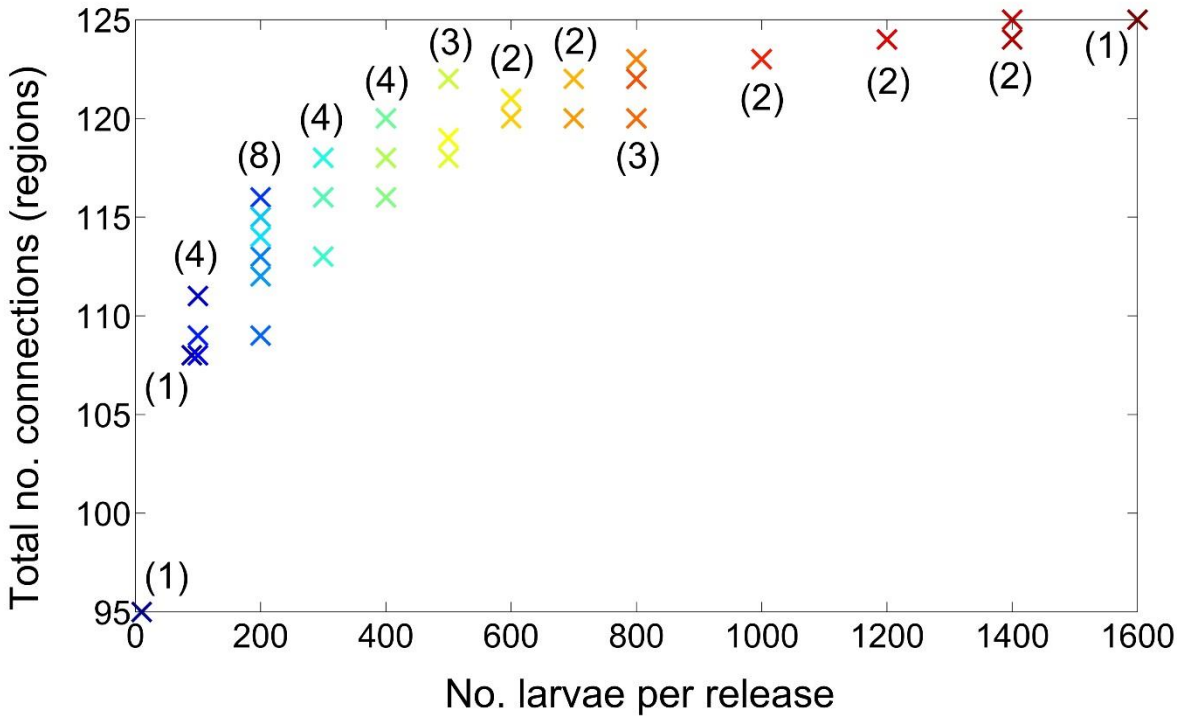
Supplementary Figure 1 | Model sensitivity to mortality and larval duration. Connectivity matrices for the 1997-98 representative El Niño year (releases from 1st June 1997 to 31st May) for **(a)** the original model: 120 day maximum pelagic larval duration (PLD) and 35 day half-life, corresponding to a mortality rate of 0.2 d^{-1} (as Fig. 3c), compared to **(b)** maximum PLD extended to 130 days (mortality rate as in **a**) and **(c)** half-life extended to 70d (mortality rate 0.01 d^{-1}, maximum PLD as in **a**). Plots **(d)** and **(e)** show regional (Fig. 1b) connections lost (red) or gained (black) in the extended PLD **(d)** and reduced mortality **(e)** runs compared to the original run **(a)**.



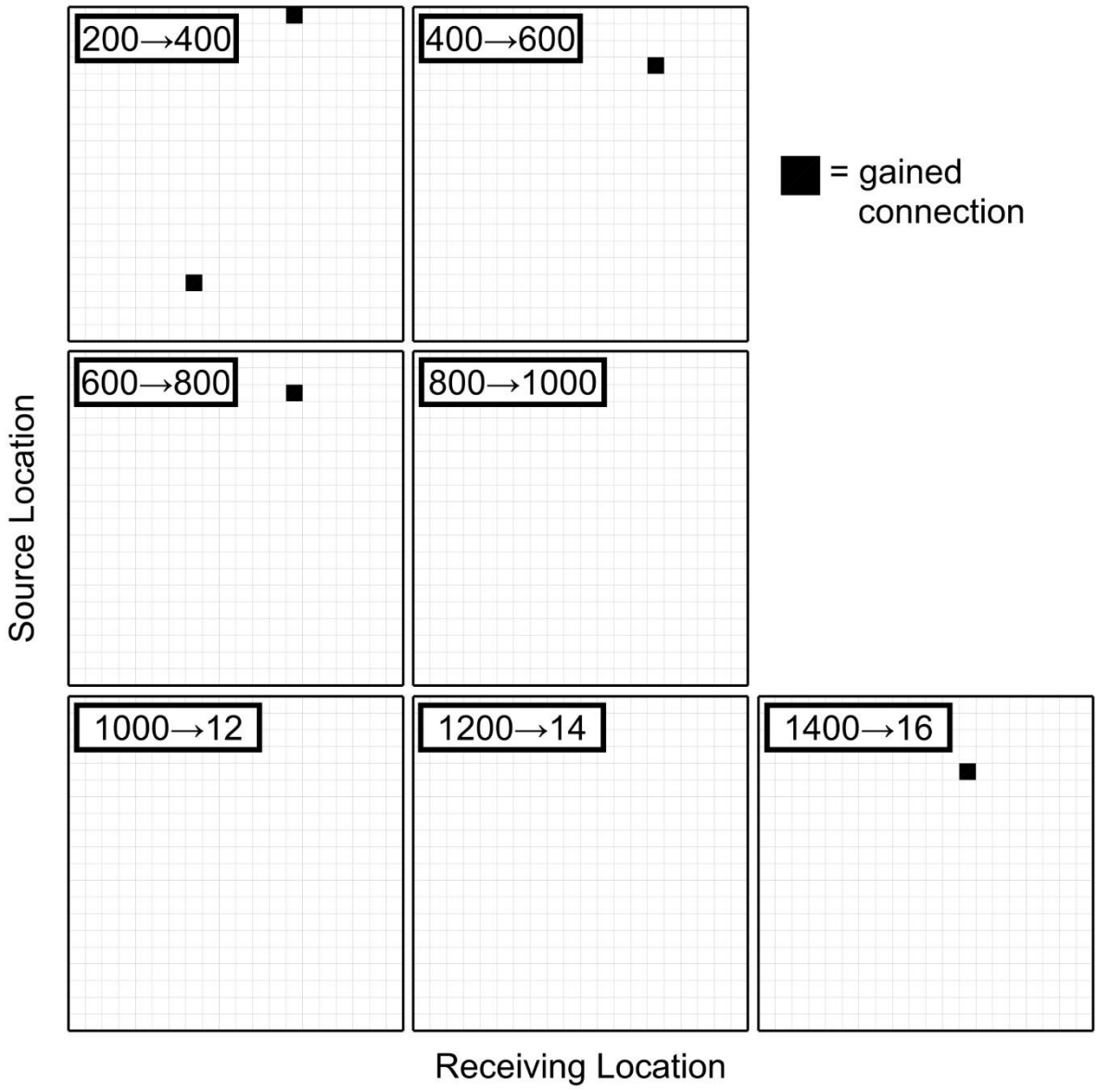
Supplementary Figure 2 | Model-genetic comparison. Mantel test results for the **(a)** raw and **(b)** log model output (i.e. 'biophysical distance') for the full 1997-2011 model run (see Methods for details of transformation), and **(c)** raw and **(d)** log Euclidean distance versus the measure of genetic differentiation (F'stP) for samples of *P. lobata* for the locations shown in Supplementary Figure 3 and Supplementary Table 1. P = 0.01.



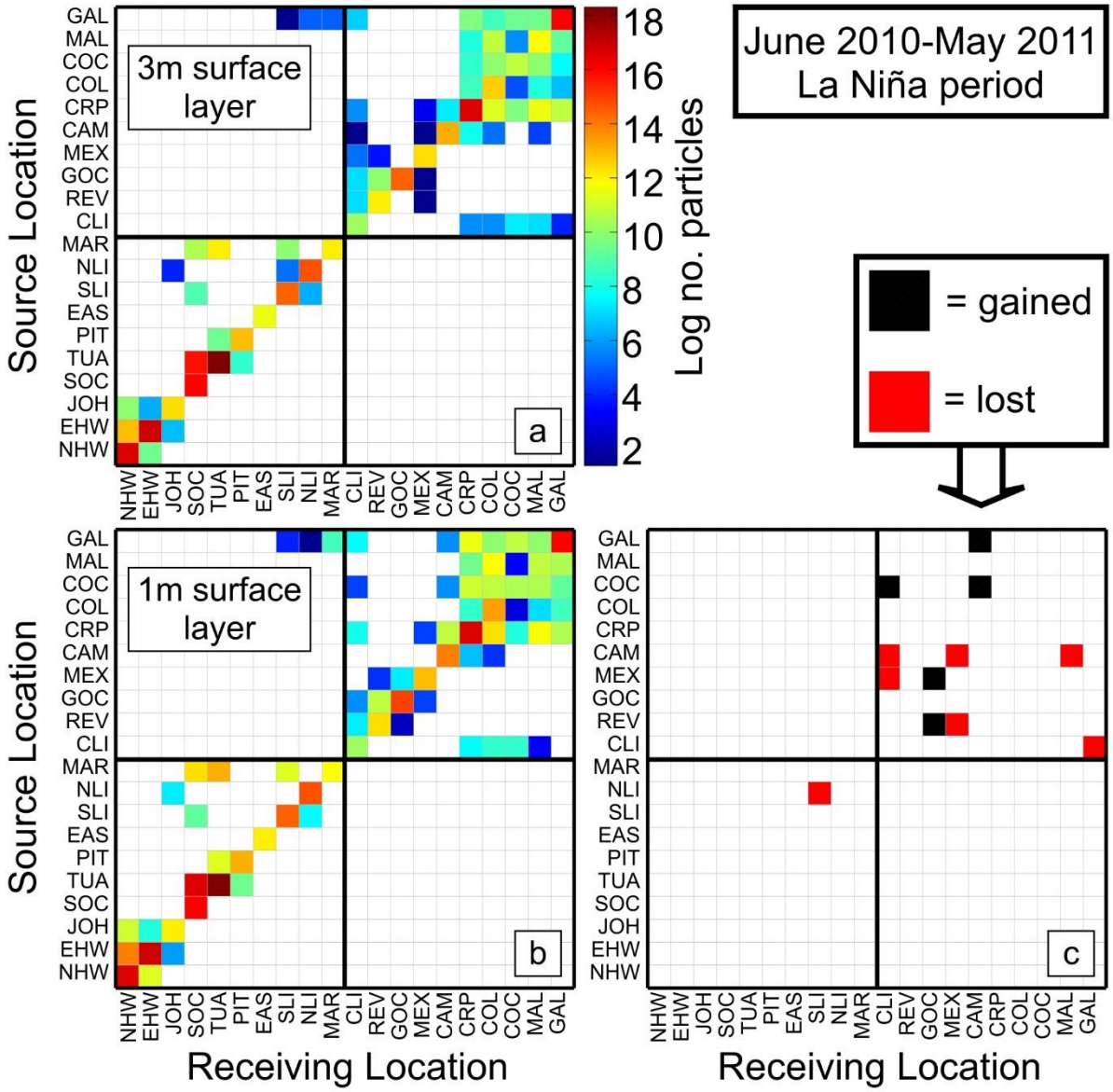
Supplementary Figure 3 | Genetic sampling locations. Locations for which genetic data for *Porites lobata*, used in the model-genetic comparison, were available (red circles). Codes correspond to the locations given in Supplementary Table 1. The blue circles indicate where output from multiple model habitat cells was combined to correspond to the appropriate sampling location, with the exception of the area marked as CR01-04* which has simply been pooled for ease of viewing. For the Hawaiian region, multiple genetic sampling sites were combined to create 3 regions (HM01, HC01 and HN01). The 2 sampling sites in the Marquesas (MQ01/02) were also combined for the analysis. **There was no habitat cell corresponding to the EC01 sampling location, therefore the nearest cell (in fact the only one on the Ecuadorian coast) was used. The thin grey lines show the outlines of the region divisions used in the connectivity matrices (Fig. 1b; i.e. only the NHW, EHW, NLI, MAR, CLI, GAL, COC, CRP and COL regions contain corresponding genetic data used in the comparison).



Supplementary Figure 4 | Model sensitivity to larval numbers. Total number of between-region (see Fig. 1b) connections obtained for increasing numbers of larvae per release (N) for 2004-2011 (excluding the earlier model period). Points along the same value of N (x axis) show independent runs (i) of the same number of releases in order to demonstrate within-model variability (values of i given in brackets on plot), although note that from N=800 and upwards not all runs are independent (see Supplementary Table 2 for further details).



Supplementary Figure 5 | Model sensitivity to larval numbers 2. Inter-regional (Fig. 1b) connections gained (black) between runs conducted with incrementally increasing numbers of larval releases per release (200 larvae per increase, numbers given in white boxes), for 2004-2011 (excluding the earlier model period).



Supplementary Figure 6 | Model sensitivity to depth of surface layer. Connectivity matrices for the 2010-11 representative annual period (releases from 1st June 2010 to 31st May 2011) for **(a)** the original HYCOM data with a 3m surface layer, used for the 2004-11 model period, and **(b)** the newer date, in which the surface layer is 1m, used for the earlier 1997-2003 period. **(c)** shows differences in regional connections (Fig. 1b; red = lost connection, black = gained connection) between the two runs.

Region	Code	Group	Reefs
Hawaii	HN01	Hawaii North	Midway, Kure, Pearl & Hermes
	HC01	Hawaii Central	Maro, Necker, French Frigate Shoals, Gardner Pinnacles, Nihoa
	HM01	Hawaii Main	Oahu and Hawaii
Johnston	JO01	Johnston Atoll	
Line Islands	LN01	Kingman Reef	
	LN02	Palmyra	
	LN03	Teraina	
	LN04	Tabuaeran	
	LN05	Christmas	
	LN06	Jarvis	
Marquesas	MQ01/02		Fatu Hiva, Tahuata/**Motane**/**Hiva Oa**, Nuku Hiva/Ua Huka, Motu One *
Clipperton	CL01		
Galapagos	GA01	Darwin	
	GA02	Wolf	
	GA03	NW Islands	Marchena, Genovesa, Pinta
	GA04	Southern Galapagos	Floreana, Espanola, S. Cristabal, S. Cruz, south and east Isabela, Santiago
Costa Rica	CR01	Marino Ballena	
	CR02/03	Caño Is./Drake Bay	
	CR04	Golfo Dulce	
	CR05	Is. Cocos	

Panama	PA01		Uvas, Coiba, Gulfo de Chuiriqui,
Ecuador	EC01	La Llorona**	

Supplementary Table 1 | Locations used in the model/genetic data comparison. See also Supplementary Figure 3. *Whilst there were only 2 genetic sampling locations in the Marquesas (in bold), the entire island chain in the model was included in the analysis. ***Sampling site does not match model habitat, used nearest cells (see Supplementary Figure 3)

	i	Combination	Full combination breakdown
10			
90			
100	**A**		
	B		
	C		
	D	10 + 90	
200	**A**		
	B		
	C		
	D		
	E		
	F		
	G	100A + 100B	
	H	100C + 100D	100C + 10 + 90
300	**A**	200A + 100A	
	B	200B + 100B	

	C	200C + 100C	
	D	200D + 100D	200D + 10 + 90
400	**A**	200A + 200B	
	B	200C + 200D	
	C	200E + 200F	
	D	200G + 200H	100A + 100B + 100C + 10 + 90
500	**A**	400A + 100A	200A + 200B + 100A
	B	400B + 100B	200C + 200D + 100B
	C	400C + 100C	200E + 200F + 100C
600	**A**	400A + 200C	200A + 200B + 200C
	B	400C + 200D	200D + 200E + 200F
700	**A**	600A + 100A	200A + 200B + 200C + 100A
	B	600B + 100B	200D + 200E + 200F + 100B
800	**A**	700A + 100C	200A + 200B + 200C + 100A + 100C
	B	700B + 100D	200D + 200E + 200F + 100B + 10 + 90
	C	400A + 400B	200A + 200B + 200C + 200D
1000	**A**	500A + 500B	200A + 200B + 200C + 200D + 100A + 100B

	B	800C + 200E	200A + 200B + 200C + 200D + 200E
1200	**A**	600A + 600B	200A + 200B + 200C + 200D + 200E + 200F
	B	800C + 400D	200A + 200B + 200C + 200D + 100A + 100B + 100C + 10 + 90
1400	**A**	700A + 700B	200A + 200B + 200C + 200D + 200E + 200F + 100A + 100B
	B	1200B + 200F	200A + 200B + 200C + 200D + 200F + 100A + 100B + 100C + 10 + 90
1600	**A**	800A + 800B	200A + 200B + 200C + 200D + 200E + 200F + 100A + 100B + 100C + 10 + 90

Supplementary Table 2 | Breakdown of runs for release number sensitivity analysis. For each subset of the number of larvae per release (N), a number of different runs were conducted (i). Those in black are original runs, while those in red were built up by summing the output of the smaller runs (columns 2 and 3) into independent larger runs (i.e. with no overlap of output, plotted in Supplementary Figure 4). Runs highlighted in blue from N=800 and upwards are comprised of progressively increasing numbers of larval releases (i.e. non-independent, plotted in Supplementary Figure 5).