

Climate change and larval transport in the ocean: fractional effects from physical and physiological factors

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Abstract

Changes in larval import, export, and self-seeding will affect the resilience of coral reef ecosystems. Climate change will alter the ocean currents that transport larvae and also increase sea surface temperatures (SST), hastening development, and shortening larval durations. Here, we use transport simulations to estimate future larval connectivity due to: (1) physical transport of larvae from altered circulation alone, and (2) the combined effects of altered currents plus physiological response to warming. Virtual larvae from islands throughout Micronesia were moved according to present-day and future ocean circulation models. The Hybrid Coordinate Ocean Model (HYCOM) spanning 2004–2012 represented present-day currents. For future currents, we altered HYCOM using analysis from the National Center for Atmospheric Research Community Earth System Model, version 1-Biogeochemistry, Representative Concentration Pathway 8.5 experiment. Based on the NCAR model, regional SST is estimated to rise 2.74 °C which corresponds to a ~17% decline in larval duration for some taxa. This reduction was the basis for a separate set of simulations. Results predict an increase in self-seeding in 100 years such that 62–76% of islands experienced increased self-seeding, there was an average domainwide increase of ~1–3% points in self-seeding, and increases of up to 25% points for several individual islands. When changed currents alone were considered, approximately half (i.e., random) of all island pairs experienced decreased connectivity but when reduced PLD was added as an effect, ~65% of connections were weakened. Orientation of archipelagos relative to currents determined the directional bias in connectivity changes. There was no universal relationship between climate change and connectivity applicable to all taxa and settings. Islands that presently export large numbers of larvae but that also maintain or enhance this role into the future should be the focus of conservation measures that promote long-term resilience of larval supply.

Keywords: Caroline Archipelago, connectivity, coral reef, larvae, Marianas, Micronesia, pelagic larval duration

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Introduction

Populations of many coral reef organisms are sustained through the transport of eggs and larvae in ocean currents. Perturbations in the magnitude of larval import, export, and self-seeding will likely affect the resilience and community structure of reef ecosystems (Almany *et al.*, 2009; Kendall *et al.*, 2013). These early life stages may be particularly vulnerable to negative impacts from climate change through several mechanisms including ocean warming, acidification, decreased CaCO₃ saturation, increased water column stratification, and modification of the ocean currents by which larvae are transported (Munday *et al.*, 2009a,b; Ottersen *et al.*, 2010; Byrne, 2011; Llopiz *et al.*, 2014).

Within this century, annual mean sea surface temperatures (SST) in the western tropical Pacific are expected to rise by ~3 °C relative to the late 20th century (IPCC, 2013). Based on laboratory experiments and field collec-

tions among various latitudes and environmental conditions, warmer waters have been demonstrated to increase growth and metabolic rates of many fish and invertebrate larvae. This amount of warming is generally expected to shorten larval durations of reef fish and other organisms by ~10–25% (Green & Fisher, 2004; Munday *et al.*, 2009b; Heyward & Negri, 2010; Byrne, 2012). Pelagic larval duration (PLD) is defined as the total period of time larvae spend in the water column and is a composite of early development, onset of larval behaviors for some taxa (e.g., feeding, vertical migration, swimming), and maximum larval lifespan (Leis, 2006 for a summary of fish larvae and Harrison & Wallace, 1990 for coral larvae behaviors). Larvae simply die in the open ocean at the end of their maximum PLD if they lack a suitable settlement habitat.

The inverse relationship between temperature and PLD is not universal; its interspecies variability and response to diet and other factors are areas of active research (Byrne, 2012; McLeod *et al.*, 2015). Some taxa show no effect or nonlinear responses such as levelling

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off or even increasing PLD at high temperatures and low food availability (Heyward & Negri, 2010; Booth & Parkinson, 2011; Takahashi *et al.*, 2012; McLeod *et al.*, 2013). Shorter PLD could lead to lower fitness and survival of earlier settling larvae and may ultimately be selected against (Rankin & Sponaugle, 2011). Shorter PLD due to moderate warming may be counterbalanced by longer PLD due to acidification and reduced skeletal growth for some species (Byrne, 2012). Because the effects of temperature on larval physiology can vary among species, it is important to understand the potential magnitude of its impact on larval transport for a range of life-history scenarios.

Spawned gametes, eggs, and developing larvae spend at least some time as plankton being moved by ocean currents even for those taxa with late-stage larvae known to be competent swimmers. Climate change is predicted to alter ocean currents that transport eggs and young larvae through changes in atmospheric circulation and ocean stratification (Munday *et al.*, 2009b; Aiken *et al.*, 2011). As the climate warms, most global climate models predict a weakening of the Walker circulation and lead to spatially nonuniform changes in ocean currents (Vecchi & Soden, 2007; Zhang & Li, 2014). The strength, and in some cases position, of important currents comprising the ocean general circulation including western boundary currents, zonal surface currents such as the North Equatorial Current (NEC) and North Equatorial Counter Current (NECC) (Luo *et al.*, 2009), and equatorial subsurface currents (Karnauskas & Cohen, 2012) will be affected. Slower surface currents, for example, may increase larval connectivity for islands in close proximity to each other and decrease connectivity between more distant island pairs depending on their orientation relative to prevailing flow. These and other climate factors are likely to affect the probability that larvae from any particular source will reach a suitable settlement habitat downstream. However, the relative strength of these mechanisms has proved difficult to untangle with the approaches applied to date (Lo-Yat *et al.*, 2011; Andrello *et al.*, 2014).

Computer-based simulation of larval transport has emerged as an effective approach for examining larval connectivity and its relationship to ocean circulation. In this approach, Lagrangian particle-tracking software is coupled with an ocean general circulation model (OGCM) to follow the movements of virtual larvae. Biological attributes are applied to the virtual larvae to simulate important aspects of life-history such as PLD and mortality rate (Trembl *et al.*, 2008; Kendall *et al.*, 2013; Wood *et al.*, 2013). By simulating the transport of larvae among the sources and destinations within a region, a comprehensive understanding of potential

regional connectivity can be obtained. With selection of proper parameters, results compare favorably to other approaches including drifter, biogeographic, and genetic datasets (Christie *et al.*, 2010; Kool *et al.*, 2011; Kendall *et al.*, 2013).

This type of physical–biological modeling is uniquely useful for examining future scenarios and comparing outcomes where different environmental or biological parameters are used (Munday *et al.*, 2009b; Lett *et al.*, 2010; Llopiz *et al.*, 2014). Transport simulations based on present-day ocean conditions can be compared to simulations incorporating expected climate and physical conditions in the future and the associated biological response to those conditions. Recent simulation studies have examined the effect of climate change on connectivity due to altered circulation patterns (Aiken *et al.*, 2011) or expected biological changes (Kendall *et al.*, 2013). Less well-developed are studies examining the effects of both climate-driven changes in ocean circulation and biological parameters (Lett *et al.*, 2010; Lo-Yat *et al.*, 2011; Andrello *et al.*, 2014).

The objective of the present study was to investigate the relative effects of climate change on larval connectivity due to changes in physical transport and altered physiology. Specifically, we seek to provide quantitative estimates of the expected future changes in connectivity due to: (1) physical transport of larvae from circulation changes alone, and (2) the combined effects of both altered ocean currents and warming temperatures with the expected physiological responses of larvae. Our basic approach was to simulate larval transport among islands using a present-day OGCM, modify the velocities of the surface current fields using a global climate forcing scenario, rerun the transport simulation using a version of the regional OGCM adapted to future changes in large-scale currents due to global climate change and potential biological response, and compare connectivity outcomes in the present-vs.-future scenarios.

The connectivity analysis applied to both the present and future simulations quantifies multiple parameters that are important for understanding and maintaining the long-term resilience of coral reef ecosystems, including overall effects on regional connectivity, sign and range of effect sizes among individual islands, change in self-seeding, influence of archipelago orientation with respect to ocean currents, and which islands may experience enhanced or reduced larval arrivals or exports in the future. Each of these parameters is an important part of planning for long-term conservation in the context of climate change such as through MPA network placement and sustainable use through ecosystem-based fisheries management plans (Hughes *et al.*, 2003; Almany *et al.*, 2009; Heenan *et al.*, 2015).

Spatial planners need to know which islands effectively self-seed, which sustain neighboring reef populations in today's climate, and how those patterns may be altered in the future due to climate change (Hastings & Botsford, 2006; O'Connor *et al.*, 2007; Munday *et al.*, 2009b).

Materials and methods

Study environment

The study area was centered on Micronesia including the Mariana and Caroline Archipelagos in the northwestern tropical Pacific Ocean (Fig. 1). The Marianas are spread over ~900 km along a north–south axis at ~145 °E. The Mariana Archipelago is oriented perpendicular to the westward flowing NEC which passes through the southern part of the archipelago with typical speeds of 0.2–0.3 m s⁻¹ (Kendall & Poti, 2015). The Caroline Archipelago is scattered over ~3000 km along an east–west axis at ~8 °N. The Carolines lie parallel to the NEC and the eastward flowing NECC south of it which has typical speeds of 0.2–0.4 m s⁻¹ (Kendall & Poti, 2015).

A 1/12° (~9 km) grid derived from an uncoupled OGCM (*i.e.*, with prescribed atmospheric boundary conditions) was used as a spatial framework (Fig. 1). In separate transport simulations, virtual larvae began at random locations within each coastal grid cell and moved in the direction and speed specified by the corresponding current vectors for each date and position from present-day and future simulated ocean circulation. Custom Python scripts were used to implement the larval transport simulations and track positions of the virtual larvae in the General NOAA Operational Modeling Environment (GNOME, version 2) (Zelenke *et al.*, 2012). GNOME is an environmental simulation system designed for modeling trajectories in the marine environment that has been extensively tested and verified. The lagrangian model interpolates time-dependent currents linearly, uses an Euler scheme to advect particles, and incorporates user-defined uncertainty in vector magnitude and direction as a percentage of velocity (Zelenke *et al.*, 2012 for mathematical details). Custom scripts in R were applied to GNOME outputs to record sources and destinations of larval transport and to simulate the various life-history and climate change scenarios described in subsequent sections.

Virtual larvae were started at each of 105 island groups and shallow seamounts in the study area (Fig. 1). Larval production in each coastal grid cell was scaled to the area of potential coral reef habitat (10 000 * percentage of the grid cell with 0–150 m depth). Habitat area was the best surrogate variable for spawning potential that was available for the entire region. Islands and seamounts close together were grouped for analysis especially at the edges of the study region to simplify and focus the results on the Mariana and Caroline Archipelagos. The large islands at the western edge of the study area including Taiwan and Japan were only considered as larval destinations as preliminary analysis indicated that larvae spawned from them were very unlikely to reach Micronesia.

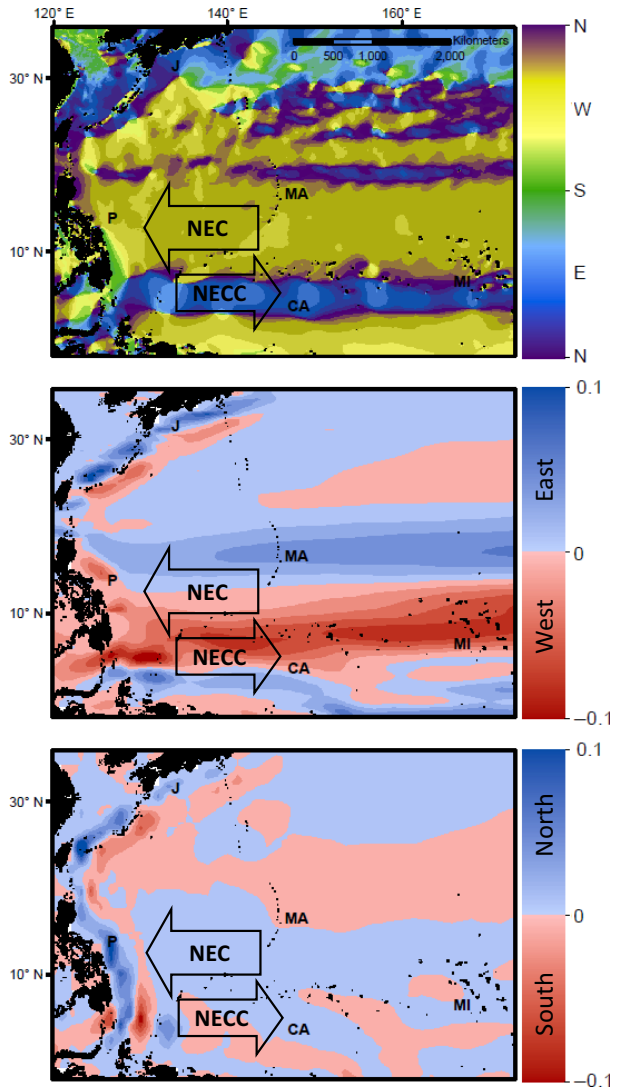


Fig. 1 a–c (a-top) Average heading of present-day ocean currents based on 2004–2012 HYCOM Global Hindcast vectors. (b-middle) Predicted change in zonal velocity (eastward/westward) added to present-day current vectors in m s⁻¹ per century. (c-bottom) Predicted change in meridional velocity (northward/southward) added to present-day vectors in m s⁻¹ per century. MA, Mariana Archipelago; CA, Caroline Archipelago; MI, Marshall Islands; J, Japan; P, Philippines; NEC, North Equatorial Current; NECC, North Equatorial Counter Current.

Some taxa in the study area spawn throughout the year whereas others spawn during particular seasonal peaks (Harrison & Wallace, 1990; Richmond & Hunter, 1990; Lester *et al.*, 2007). To investigate the long-term, cumulative patterns of connectivity, we began simulations seasonally (*i.e.*, on the first day of January, April, July, and October).

Spawned gametes, fertilized eggs, and young larvae must spend some time developing in the plankton prior to settlement (Harrison & Wallace, 1990; Fisher, 2005). To simulate this precompetent period, virtual larvae were prevented

from settlement until a minimum of 60% of their maximum PLD was completed. This generic value was determined based on a review of the range in dates for settlement marks on otoliths within reef fish species and settlement windows for coral larvae in laboratory experiments (Kendall & Poti, 2015). To compare connectivity among diverse taxa, we simulated larval transport for maximum PLDs of 10, 50, and 100 days. These categories, based on otolith analysis of settling fish and laboratory experiments, encompass the range of values expected for a variety of the fish, corals, and other reef organisms in the region (e.g., compiled in Lester *et al.*, 2007; Graham *et al.*, 2008; and Jones *et al.*, 2009). Note that these are maximum PLD values and that larvae in our simulations are competent to settle any time after 60% of this duration. Therefore, the settlement windows for these maximum PLDs were 6–10, 30–50, and 60–100 days. For brevity, these maximum PLD values will hereafter be referred to simply as PLD unless otherwise specified.

Although the precise distance at which larvae can orient toward reefs and actively overcome ambient currents is debated, it is clear that some need simply to come sufficiently close to settlement habitat such that they can sense, orient toward, swim to, or otherwise indirectly improve their chances of arrival (Gerlach *et al.*, 2007; Leis, 2007). In our simulations, if a larva passed into any of the 9-km grid cells containing potential coral reef habitat after its precompetency period, it was considered to have successfully settled at that destination.

Larval mortality rates have a significant effect on recruitment strength and vary with larval age, environmental conditions (Edmunds *et al.*, 2001; Graham *et al.*, 2008; Connolly & Baird, 2010), and no doubt in response to direct and indirect aspects of climate change (Hays *et al.*, 2005). Larval mortality in each simulation began at the end of precompetency and was applied to randomly selected larvae at a linear rate such that no larvae survived by the end of each PLD.

Present-day conditions

We used the Hybrid Coordinate Ocean Model (HYCOM) for our present-day ocean currents (hereafter referring to today's conditions as scenario *T* for brevity). HYCOM is a three-dimensional ocean circulation model (Bleck & Boudra, 1981) with a 6-h time step and a horizontal resolution of 1/12 degree (~9-km grid cells). It has been used recently in a number of larval transport studies and has shown good correspondence to actual ocean currents based on satellite-tracked drifters (Christie *et al.*, 2010; Fossette *et al.*, 2012; Kendall *et al.*, 2013). The current vectors from the HYCOM Global Hindcast model for the 0- to 10-m-depth layer from 2004 to 2012 were downloaded via the NASA/REASON Ocean Data Portal. This constrains our scope of inference to larvae inhabiting these depths. These years represent a typical 9-year period encompassing a range of El Niño and La Niña conditions. The average heading of ocean currents from today are shown in composite (Fig. 1a).

Realistic values for horizontal diffusivity and uncertainty in current vectors were determined by examining the influence

of a range of values for these parameters on the paths of virtual particles and comparing these paths to actual trajectories of satellite-tracked surface drogues (Kendall & Poti, 2014, 2015). It was determined that 10% vector uncertainty and a 100 cm²/s diffusion coefficient encompassed actual drifter tracks and would simulate the stochasticity in larval paths arising from sub-grid scale turbulent processes and random variation. Larval positions were output daily for analysis.

Projected changes in broad-scale ocean circulation

To impose projected future changes in broad-scale ocean circulation upon the study region (including major currents such as the NEC and NECC), while retaining not only the higher spatial and temporal resolution of HYCOM but also its inter-annual variation to realistically portray transport of virtual larvae within and among years, we used output from the National Center for Atmospheric Research Community Earth System Model, version 1-Biogeochemistry (NCAR CESM1-BGC). The NCAR CESM1-BGC is a fully coupled, global Earth system model (ESM) based on the NCAR Community Climate System Model, version 4 (Gent *et al.*, 2011), which simulates the physical processes within and interactions between the atmosphere, ocean, sea ice, land surface, plus ocean carbon biogeochemistry (Hurrell *et al.*, 2013; Long *et al.*, 2013). We used the NCAR CESM1-BGC simulation, in part, because it directly incorporates influential environmental variables on larval physiology including SST. This enabled our ESM-based estimates for the future ocean circulation and values of future SST change to be internally consistent rather than drawn from different sources and allows future work to incorporate changes in other parameters such as pH or nutrients provided by the same global model. The ocean component of the NCAR CESM1-BGC model (Danabasoglu *et al.*, 2012) has a horizontal resolution of 1.1° zonal × 0.6° meridional in our study region.

The ESM simulation was run at NCAR as part of the Coupled Model Intercomparison Project, phase 5 (CMIP5) and Intergovernmental Panel on Climate Change, Fifth Assessment Report (IPCC AR5). We used the Representative Concentration Pathway 8.5 experiment (RCP8.5) as our future scenario, which is equivalent to 8.5 W m⁻² global anthropogenic radiative forcing by the end of the present century (Riahi *et al.*, 2011; Van Vuuren *et al.*, 2011; Taylor *et al.*, 2012). The RCP8.5 is distinct from the other three standard RCPs (2.6, 4.5, and 6.0) in that it does *not* assume that global emissions of greenhouse gases will begin to decline sharply by mid-century or sooner. Present rates of global emissions as well as observed CO₂ concentrations indicate that RCP8.5 cannot be ruled out as a likely outcome (9.2 GtC actual in 2010 [Boden *et al.*, 2010/http://cdiac.ornl.gov/trends/emis/glo_2010.html] vs. 10 GtC assumed in RCP8.5 [Fig. 6 of Van Vuuren *et al.*, 2011/http://cdiac.ornl.gov/trends/emis/glo_2010.html]). Practically, the use of RCP8.5 also enables a maximization of signal-to-noise of the forced response amid the presence of natural variability and other uncertainties. The velocity fields in the northwestern Pacific Ocean as simulated by the NCAR CESM1-BGC (averaged over 2006–2015 of the RCP8.5 experiment) agree well with observed present-day

estimates as well as the HYCOM simulation but obviously with less mesoscale and high-frequency energy due to the coarser spatial resolution of all global coupled models relative to HYCOM as well as temporal (monthly) averaging of the ESM output (Fig. S1).

This global climate model characterizes changes in the broad-scale velocity fields associated with major currents but lacks both the spatial and temporal resolution needed to realistically move virtual larvae among islands with the level of high-frequency and finer-scale variability present in the real ocean. This is why we impose the projected changes upon the higher resolution model, rather than simply using the global model for the future simulation. Changes in ocean surface currents for our transport simulations were therefore determined by first computing spatial fields of the linear trends for the zonal and meridional ocean surface velocity components over the course of the RCP8.5 experiment (2006–2100) (Fig. 1b, c). The 95% confidence intervals on these trends are presented in Fig. S2. These spatially dependent trends (m s^{-1} per century) were then resampled to the higher resolution (9 km) grid of HYCOM and added linearly to the daily mean velocity component fields from the original HYCOM model spanning 2004–2012. This approach retained the fine-scale temporal resolution and eddy features around islands along with the inter-annual variation from HYCOM that is needed to realistically simulate and compare larval transport to the present-day conditions but changed the overall velocity of the major currents due to climate change. Transport simulations were then re-run using these future ocean currents in the scenario hereafter referred to as F_C .

Future larval physiology

Projected changes in SST for the study area were evaluated for spatial homogeneity to determine if an average value of temperature change for the region would suffice or if there were spatial patterns in SST change that would need to be accounted for when considering biological effects. The same global model, experiment, and methodology as described above were used for these calculations. This preliminary evaluation revealed that the future SST in the study region was relatively uniform, showed similar spatial patterns to today's ocean, and that the overall change in temperature over 100 years was of a much greater magnitude than any spatial patterns within the Marianas. Average SST starting value was 28.7 °C (the average over the first 10 years of the experiments 2006–2015) and average SST increase was 2.74 °C per 100 years (range of increase throughout the study area was 2.3–2.9 °C). This future average SST value of 31.44 °C was used to adjust the PLD of virtual larvae in a new set of transport simulations.

The three simulated PLDs were shortened based on a value calculated from the universal model for the temperature dependency of larval development of marine animals (6 phyla, 6 fish, and 66 invertebrates) developed by O'Connor *et al.* (2007). Inserting the expected temperature increase of 2.74 °C for the study area into their model equation indicated a decline of ~17% for each PLD. This value was also supported

by a second review study reporting the expected decline in PLD for reef fish of 12–25% (Munday *et al.*, 2009b) with a 3 °C rise in temperature. Using the midpoint of this range and correcting for the 2.74 °C rise in temperature expected in the study region, a decline in PLDs of ~17% is also calculated. Our maximum PLDs were therefore shortened in the future ocean scenario as follows: 10 days reduced to 8.3, 20 days reduced to 16.6, 50 days reduced to 41.5, and 100 days reduced to 83. Precompetency period was recalculated as 60% of the new maximum PLDs. Transport simulations were again repeated using future ocean currents as well as the expected physiological response of larvae in the scenario hereafter referred to as F_{C+P} .

Analyses

Cumulative connectivity over the nine years of transport simulations from each climate scenario (T , F_C , and F_{C+P}) was summarized in separate connectivity matrices. Island locations are listed as sources (rows) and destinations (columns) of larvae with cells in the matrix representing the fraction of larvae released at each source settling at each destination, hereafter simply referred to as the settlement fraction. The diagonal in these matrices therefore represents self-seeding or those larvae from a given source that returned.

Changes in connectivity were determined by subtracting matrices for present conditions from matrices of future conditions for each PLD. Matrix cells then equal the change in settlement fraction of larvae released at each source settling at each destination (Figs S3–S8). Positive values indicate increased connectivity in the future. These change matrices represent all of the changes in connectivity among island pairs in the study area. Histograms were used to summarize the magnitude and frequency of the values from the change matrices. Self-seeding vs. all other values were differentiated in stacked bar format. In addition, summary statistics were calculated including proportion of cells with higher connectivity in future conditions, mean change in overall connectivity, proportion of self-seeding cells with higher connectivity in future conditions, mean change in self-seeding, and the number of the most extreme values that were from self-seeding.

Two statistical tests were performed to determine the significance of the observed differences between the future and present matrices. First, to determine whether the proportion of locations with increased future connectivity was significantly different than random (50 : 50), a G test with Williams' adjustment for sample size was used (Sokal & Rohlf, 1981). In addition, a permutation test was performed to estimate the probability of getting the observed increase in average self-seeding by random chance from this group of islands. In this test, 100 randomly chosen location pairs (same as the actual number of possible self-seeding pairs) from the difference matrix for each PLD were used to calculate a mean change in connectivity. This was performed 1000 times with replacement, to create a population of mean changes from 100 randomly selected locations. The proportion of times the actual mean difference from self-seeding was met or exceeded was

recorded as a P -value. This P -value denotes the probability of the observed mean difference in self-seeding occurring due to random chance.

Because the Mariana and Caroline archipelagos differ in their orientation relative to major ocean currents, it was also desirable to test for spatial bias in connectivity patterns due to distance and direction between source and destination islands. To evaluate these spatial effects, polar plots were used where position in the plot is determined by the direction and distance between each pair of islands that transferred larvae (excludes self-seeding). Point markers denote whether each island pair experienced a positive or negative change in future connectivity. The polar plot format reveals any spatial or distance bias in future connectivity that is not discernable in the matrix, histogram, or other analysis formats. Separate plots were created for comparison of each archipelago (Mariana and Caroline), PLD (10, 50, and 100), and future ocean scenario (F_C and F_{C+P}). A chi-square test for a 2-by-2 contingency table was used to test the patterns in these plots for significance. Cell values in this table indicate whether the change in future connectivity between island pairs was positive or negative and whether the direction of transport was northward or southward in the Marianas, or eastward or westward in the Carolines. A significant result in this test indicates that sign changes (+/-) in connectivity are not independent of transport direction.

The sum of pairwise effects between each source and destination may result in particular islands receiving or being the source of more or fewer larvae in the future. To evaluate the spatial patterns in these cumulative effects, the change in total larvae arriving at each island and also the number of successfully exported larvae expressed as percentages were plotted for each PLD (10, 50, and 100) and future ocean scenario (F_C and F_{C+P}).

Results

Future ocean currents depicted as expected changes to the zonal and meridional components of velocity indicate that the northern half of the NEC in the vicinity of the Marianas will slow by 0.02 – 0.04 m s^{-1} (~10% less westward velocity) whereas the southern half of the NEC will slightly accelerate by 0.0 – 0.02 m s^{-1} . The eastward flow of the NECC in the vicinity of the Caroline Archipelago will slow down by 0.06 – 0.1 m s^{-1} (~25% less eastward velocity) (Fig. 1b). Models suggested that changes in the north/south velocity of currents would be quite small and in the range of only 0.0 ± 0.02 m s^{-1} (Fig. 1c), which is not surprising because the mean strength of meridional currents is also relatively small compared to that of the swift zonal currents in this region.

Histograms depicting the change in connection strength between matrix cells in present and future climate scenarios revealed several consistent patterns (Fig. 2a–f). For all PLDs, the vast majority of changes in connection strength were very small as docu-

mented by the large number of values only slightly above or below zero ($\pm 2\%$ change in connection strength). Mean connectivity increased in the future ocean scenarios compared to connectivity today; however, these changes were small when expressed as averages among all islands (Table 1). Overall, the proportions of matrix cells were evenly split between higher or lower connectivity when comparing T and F_C (~50% : 50% and nonsignificant G -test results). Negative (lower) connectivity dominated when comparing T and F_{C+P} ; however, these were small reductions. On average, there was still a small overall increase in connectivity of less than 1% point. In contrast, self-seeding more consistently experienced positive changes in connectivity with 62–77% of self-seeding values getting higher in future ocean scenarios. All such values were significantly different from random (i.e., 50%) based on the G -test (Table 1). Magnitude of the increase was greater for longer PLDs and when both currents and PLD were altered.

Of particular importance at all PLDs was a rightward skew in the histogram tails toward higher positive values. These increases in connectivity were the largest values observed in the change matrices and were dominated by higher self-seeding. For example, in scenarios involving 50- to 100-day PLDs, a large majority of the highest 20 values were from increased self-seeding and consisted of increases in connectivity of up to 25% points (Fig. 2a–f, Table 1). These effects were less dramatic but still apparent for the 10-day PLD. Average self-seeding increased ~1–3% points with higher values for longer PLDs (Table 1). The probability of randomly obtaining an average change in self-seeding of these magnitudes based on the permutation test was always significantly unlikely ($P < 0.001$ for all PLDs and comparisons).

In the Marianas, most connections were along the north/south axis of the archipelago, extending ~200 km in either direction for PLDs ≤ 10 days and up to the full 900 km along the archipelago for PLDs of 41–100 days (Fig. 3a–f). Connections to the West Mariana Ridge were almost always lower in future scenarios for PLDs ≤ 10 days. Contingency table analysis suggested that there was no relationship between higher future connectivity and transport direction (north or south in the Marianas) until PLDs reached 83–100 days (Table 2). In those cases, direction of transport was not independent of change in connectivity such that northward connections were more likely to be higher in future scenarios. When direction is coupled with distance, a more complex picture emerges. Longer distance connections (i.e., >50% of maximum transport in each scenario) most often had reduced future connectivity when PLD was ≤ 50 days. This pattern

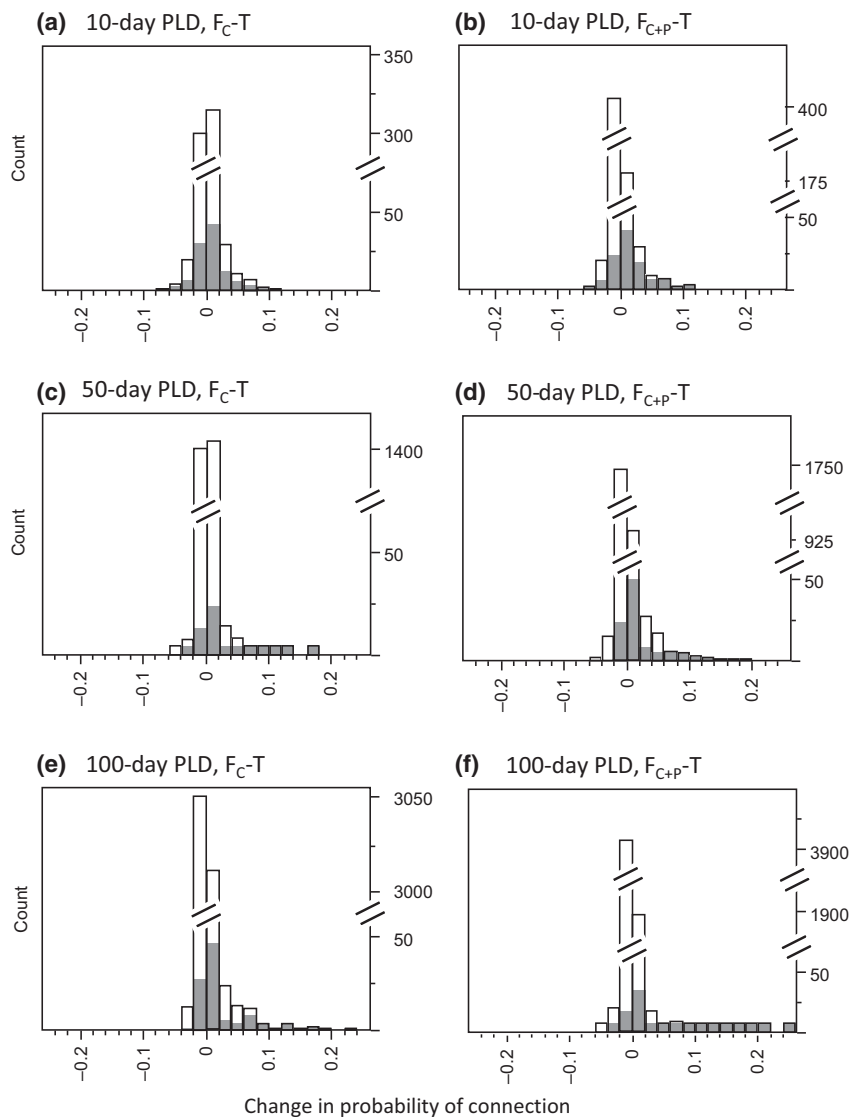


Fig. 2 a–f—Histograms of differences between location pairs in the connectivity matrices from climate change scenarios. Stacked bar format shows self-seeding values in gray and all others in white. Headers a–f above each plot denote which matrices/scenarios are subtracted. X axis depicts the magnitude (change in probability of connection), and Y axis depicts frequency of each change (count axis).

was reversed for PLDs of 83–100 days where longer connections most often had positive change in connectivity, but only for transport to the north.

In the Carolines, connections were along the east/west axis of the archipelago, extending ~700 km in either direction when PLDs were ≤ 10 days and up to the full 3000 km along the island chain in either direction when PLDs were ~100 days (Fig. 4a–f). Contingency table analysis suggested that change in connectivity was not independent of transport distance in the Carolines (Table 2). In all cases, except for the 100-day F_C scenario, future connectivity was lower for eastward transport, and higher for westward transport. This effect was most apparent for longer distance trans-

port (i.e., >50% of maximum transport in each scenario) where far westward connections were dominated by positive change and far eastward connections were dominated by negative change. These patterns were most obvious in the F_C scenarios compared to the F_{C+P} scenarios.

Maps of percentage change in larval arrivals reveal which islands will receive more or less larvae in the future due to climate change (Fig. 5a–f). Spatial patterns in arrivals differed considerably among PLDs and climate scenarios. Within the Marianas, most locations experienced a future increase in arrivals for the 50-day PLD and F_C scenario (Fig. 5c) and most experienced a decrease in arrivals for the 100-day PLD and F_{C+P} sce-

Table 1 Summary of changes in connectivity by PLD from ocean conditions today (T) to future conditions with (F_{C+P}) and without physiological effects (F_C)

PLD	Variable	T to F_C	T to F_{C+P}
10 day	Island pairs with connectivity	687	660
	% of all cells with increased connectivity*	53% ^{NS}	35% ^{$P < 0.001$}
	Mean change in settlement fraction	0.0021	0.0018
	% self-seeding cells with increased connectivity*	62% ^{$P < 0.025$}	72% ^{$P < 0.001$}
	Mean change in settlement fraction for self-seeding†	0.0073 ^{$P < 0.001$}	0.0156 ^{$P < 0.001$}
	Extreme values (number of highest increases that were from self-seeding)	10 of 20	15 of 20
50 day	Island pairs with connectivity	2886	2753
	% of all cells with increased connectivity*	51% ^{NS}	36% ^{$P < 0.001$}
	Mean change in settlement fraction	0.0011	0.0009
	% self-seeding cells with increased connectivity*	73% ^{$P < 0.001$}	77% ^{$P < 0.001$}
	Mean change in settlement fraction for self-seeding†	0.02 ^{$P < 0.001$}	0.0234 ^{$P < 0.001$}
	Extreme values (number of highest increases that were from self-seeding)	18 of 20	17 of 20
100 day	Island pairs with connectivity	6170	5919
	% of all cells with increased connectivity*	50% ^{NS}	33% ^{$P < 0.001$}
	Mean change in settlement fraction	0.0006	0.0003
	% self-seeding cells with increased connectivity*	72% ^{$P < 0.001$}	76% ^{$P < 0.001$}
	Mean change in settlement fraction for self-seeding†	0.0243 ^{$P < 0.001$}	0.0267 ^{$P < 0.001$}
	Extreme values (number of highest increases that were from self-seeding)	17 of 20	18 of 20

*Row values were tested using a G -test, wherein significance (superscript) indicates that the observed percentage differs from random (i.e., 50%).

†Row values were tested using a permutation test where the P -value (superscript) represents the probability of getting the observed value by chance.

nario (Fig. 5f). Results in all other scenarios were more mixed with declines in arrival occurring variously for islands in the northern (Fig. 5b), central, (Fig. 5e, f), and southern islands (Fig. 5d, f) depending on PLD and climate scenario. Within the Caroline Archipelago, most locations experienced a decline in arrivals for the 10-day PLD, F_{C+P} scenario (Fig. 5b). Results in other scenarios were more mixed with individual islands experiencing a large increase or decrease in arrivals depending on the PLD and climate scenario. The western chain of the Marshall Islands was most consistent and always experienced an increase in arrivals in all scenarios.

Maps of percentage change in successful larval exports reveal which islands are the source of more or less successful larvae in the future due to climate change (Fig. 6a–f). Spatial patterns of export differed considerably among PLDs and climate scenarios. Within the Marianas, islands in the southern half of the archipelago generally experienced an increase in future exports in both scenarios for the 50-day PLD (Fig. 6c, d). Results in all other scenarios were more mixed. In the Carolines for the 10-day PLD, islands in the eastern half of the archipelago greatly increased future exports in the F_C scenario (Fig. 6a), but decreased exports in the F_{C+P} scenario (Fig. 6b). For the 100-day PLD, islands in the central Carolines experienced a moderate increase

in exports in the F_C scenario (Fig. 6e), but a moderate decrease in the F_{C+P} scenario (Fig. 6f). Climate scenarios had similar effects on export change in the Carolines for the 50-day PLD (Fig. 6c, d).

Discussion

Strength of self-seeding is predicted to increase in 100 years and experience the largest and most consistent change in our simulations by several measures. Depending on the PLD and climate scenario, 62–76% of islands had increased self-seeding, there was an average domainwide increase of ~1–3% points in self-seeding, and much higher increases of up to 25% points for several individual islands relative to today's conditions. The sign of this increase had been hypothesized (O'Connor *et al.*, 2007; Munday *et al.*, 2009b; Pankhurst & Munday, 2011; Kendall *et al.*, 2013), but the strength and relative contribution from physical transport vs. physiological mechanisms are only beginning to be quantified (Lett *et al.*, 2010; Lo-Yat *et al.*, 2011; Andrello *et al.*, 2014).

When changed currents alone were considered, approximately half (i.e., random) of all pairwise connections experienced a decrease in connectivity but when reduced PLD was added as an effect, ~65% of connections were lower. The relative influence of

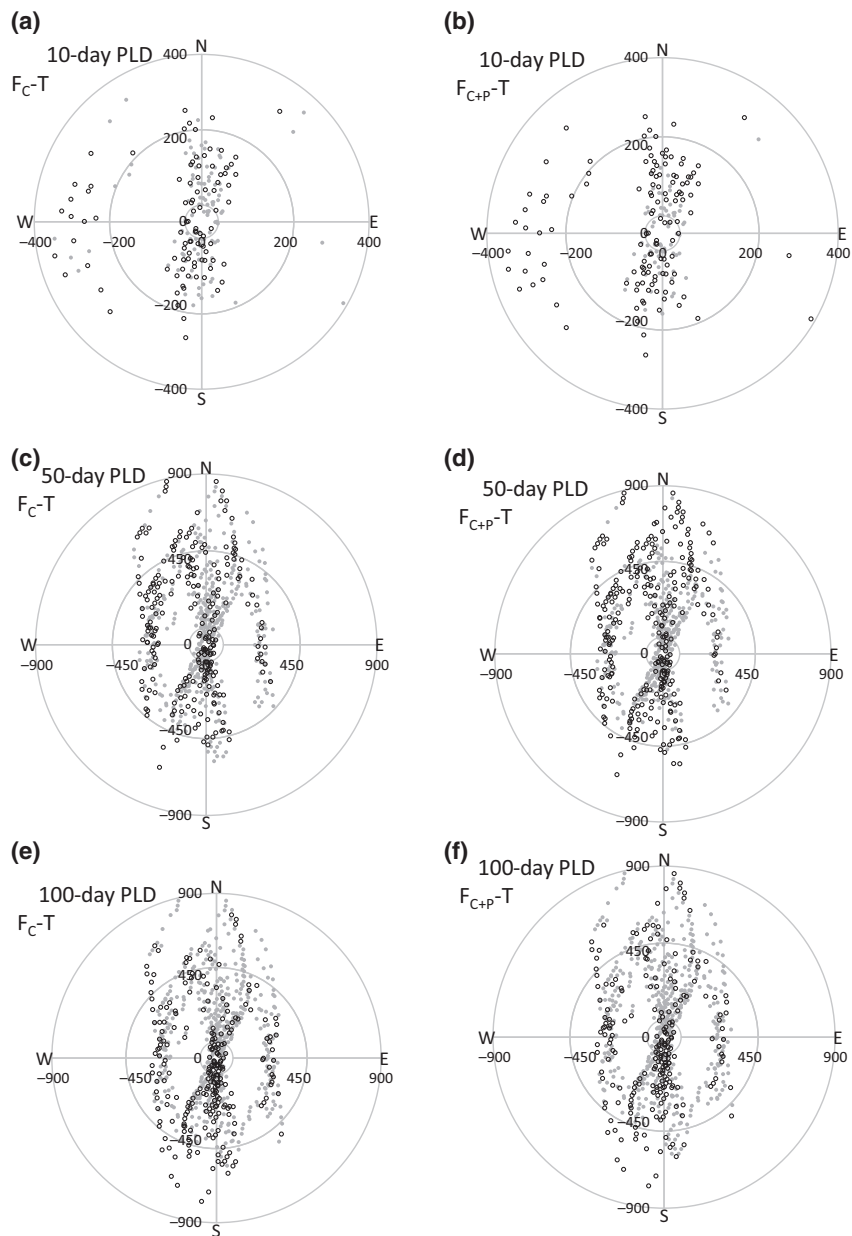


Fig. 3 (a–f) Polar plot of direction, distance, and sign of changes in connectivity among island pairs in the Mariana Islands. Gray dots denote higher connectivity in the future ocean, and black circles denote lower. Headers a–f above each plot denote which climate scenarios are compared. Distances are in kilometers. Note that distance scale increases with PLD.

altered currents alone vs. altered currents and shorter PLD could also differ among the PLDs that were evaluated. For the 10-day PLD, increases in self-seeding due to the combined effects of currents plus shorter PLD were approximately twice the magnitude of the effects due to altered currents alone. For the 50- and 100-day PLDs, there was a relatively greater effect due to currents alone and a smaller increase in self-seeding when both currents and PLD were altered. Other recent studies have found that

hydrodynamics had a small effect relative to biological mechanisms (Lo-Yat *et al.*, 2011; Andrello *et al.*, 2014). This demonstrates that the relative physical and physiological effects of climate change on connectivity will differ among taxa depending on their PLD and physiological sensitivity or adaptive capacity to handle warmer water (Lett *et al.*, 2010). There is no universal relationship between climate change and connectivity applicable to all taxa and settings (Lo-Yat *et al.*, 2011).

Table 2 Contingency table analysis results. A significant result denotes that change in future connectivity (positive or negative) is not independent of transport direction (north/south in the Marianas and east/west in the Carolines)

PLD, climate scenario	Marianas		Carolines	
	Chi-square	P value	Chi-square	P value
10-day PLD, F_C to T	0.91	ns	28.75	<0.001
10-day PLD, F_{C+P} to T	0.53	ns	8.21	<0.005
50-day PLD, F_C to T	0.60	ns	57.35	<0.001
50-day PLD, F_{C+P} to T	0.31	ns	39.88	<0.001
100-day PLD, F_C to T	38.96	<0.001	0.03	ns
100-day PLD, F_{C+P} to T	18.60	<0.001	9.18	<0.005

Climate change will also affect connectivity in different ways depending on the spatial arrangement of island chains. Using polar plots, we show that orientation of island chains relative to ocean currents will determine the directional bias in connectivity changes. A slower eastward flow of the NECC resulted in weaker eastward connectivity and stronger westward connectivity among island pairs in the Caroline Archipelago. The northward connectivity bias in the Marianas at long PLDs could be due to a slower northern half of the NEC and faster southern half as predicted here. This increase in horizontal shear within the NEC may enhance formation of the eddies that are routinely shed off the northern edge of the NEC and spin northward through the Marianas carrying larvae with them (Kendall & Poti, 2015). Munday *et al.* (2009b) note that reduced PLD can have opposite effects on connectivity in regions with fragmented distribution of reefs compared to those with contiguous arrangements. Findings such as these confound the desire to identify universal impacts of climate on connectivity or to provide generic advice to policy-makers that is independent of local settings.

Domainwide average connectivity increased in all scenarios; however, most pairwise values seem very small to the point that they lack demographic significance capable of affecting the fate of local populations. A study in the Samoan Archipelago found a similarly low 1% increase in self-seeding for every 2.3 days that PLD was shortened (Kendall *et al.*, 2013). Researchers in the Mediterranean Sea found a 5% increase in larval retention in 100 years (Andrello *et al.*, 2014). An increase in self-seeding of only 1–3% points as calculated here also appears unimportant when considered only on an annual or even decadal basis. However, small percentages over long timescales can add up like compounding interest in a bank account. For example, \$100 earning 1% interest annually yields >\$207 in 100 years. Similar population increases fueled by self-

seeding could occur until density-dependent feedback or carrying-capacity limits are reached. Similarly, receiving a slightly smaller number of larvae on an annual basis may at first seem unimportant, but the effect compounded over many years may take a toll on long-term population resilience once insufficient recruits arrive to fill available niche space. For example, consider the many locations in the Marianas and Carolines already in a degraded state which could receive just 10% fewer larvae during our future climate scenarios. Such an effect on an annual basis could eventually alter the resilience and sustainability of those reef communities. Some islands experienced >50% decline in arrivals. For them, the effects could be much more rapid.

Transport simulations here held constant many potential effects of climate change on pelagic larvae. This simple approach focused the comparison of results on PLD and ocean current without the confounding influences of other variables, but also was kept simple due to a lack of data on many key variables associated with climate change (Llopiz *et al.*, 2014). Mortality rates may increase for larvae of some reef fish, corals, and other invertebrates with 3 °C warming (Lucas, 1973; Edmunds *et al.*, 2001; Lo-Yat *et al.*, 2011; Schnitzler *et al.*, 2012; Fitzgibbon & Battaglene, 2012;). Warming may increase swimming efficiency, thereby increasing retention of fish larvae at natal reefs or their ability to reach other settlement habitats from greater distances (Von Herbing, 2001; Green & Fisher, 2004; Lett *et al.*, 2010). Several studies have documented climate-induced shifts in abundance, community structure, seasonal peaks, and geographical range of phyto- and zooplankton food sources (Hays *et al.*, 2005), which are likely to affect larval fitness and survival (Meekan *et al.*, 2003; Lett *et al.*, 2010; Lo-Yat *et al.*, 2011; McLeod *et al.*, 2013). Aspects of larval behavior not considered here, such as vertical migration, can affect dispersal patterns and will likely be affected by altered currents and increased stratification due to climate change as well (Aiken *et al.*, 2011). These and other variables will affect transport success and should be added to the next generation of models as larval parameters once sufficient data become available (Llopiz *et al.*, 2014).

Acidification was also not explicitly included in our biological effects but was a part of the NCAR CESM 1-BGC model that we used to derive future ocean currents. In the RCP8.5 experiment that we used, ocean pH is predicted to decline by 0.38 per 100 years for our study area. This increase in acidity is expected to have both positive and negative effects on plankton including larval forms (Hays *et al.*, 2005; Munday *et al.*, 2009a; Byrne, 2011, 2012). Photosynthesis is likely to be stimulated whereas calcification of skeletal elements will be

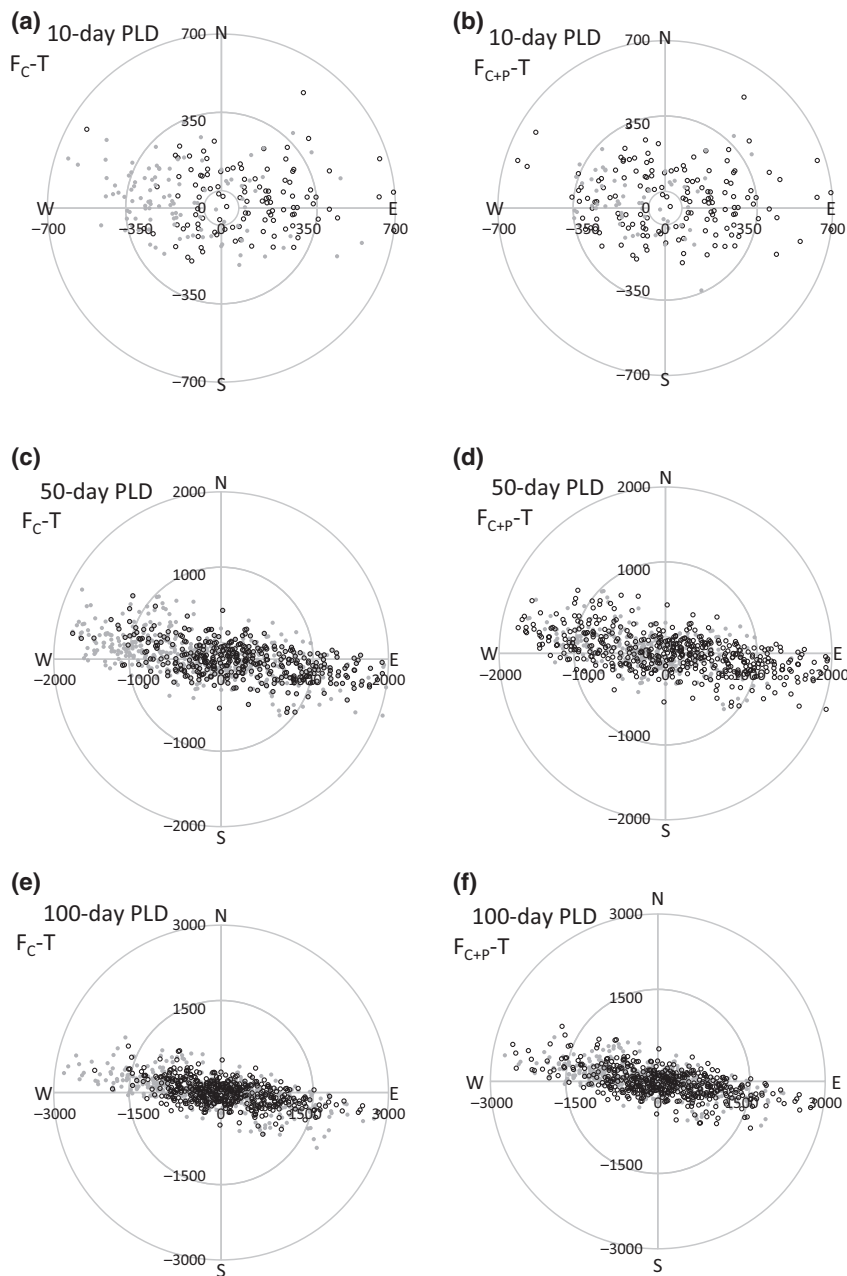


Fig. 4 (a–f) Polar plot of direction, distance, and sign of changes in connectivity among island pairs in the Caroline Islands. Gray dots denote higher connectivity in the future ocean, and black circles denote lower. Headers a–f above each plot denote which climate scenarios are compared. Distances are in kilometers. Note that distance scale increases with PLD.

hindered. This may result in longer development but smaller larvae for those taxa that calcify skeletal elements (Byrne, 2012). Especially relevant for larval organisms seeking settlement habitat, acidification may hinder olfactory senses and reduce their capability to discriminate among settlement habitats and navigate to them (Pankhurst & Munday, 2011). Additional research is needed on these aspects of larval biology to define

appropriate parameters for modeling effects of a changing climate (Llopiz *et al.*, 2014).

Climate change and other anthropogenic impacts will affect other aspects of reef organisms or their habitat independently of the larval stage and will ultimately affect connectivity (Hughes *et al.*, 2003; Munday *et al.*, 2009b). Spawning population size may be lower for both fish and corals assuming that present trends in

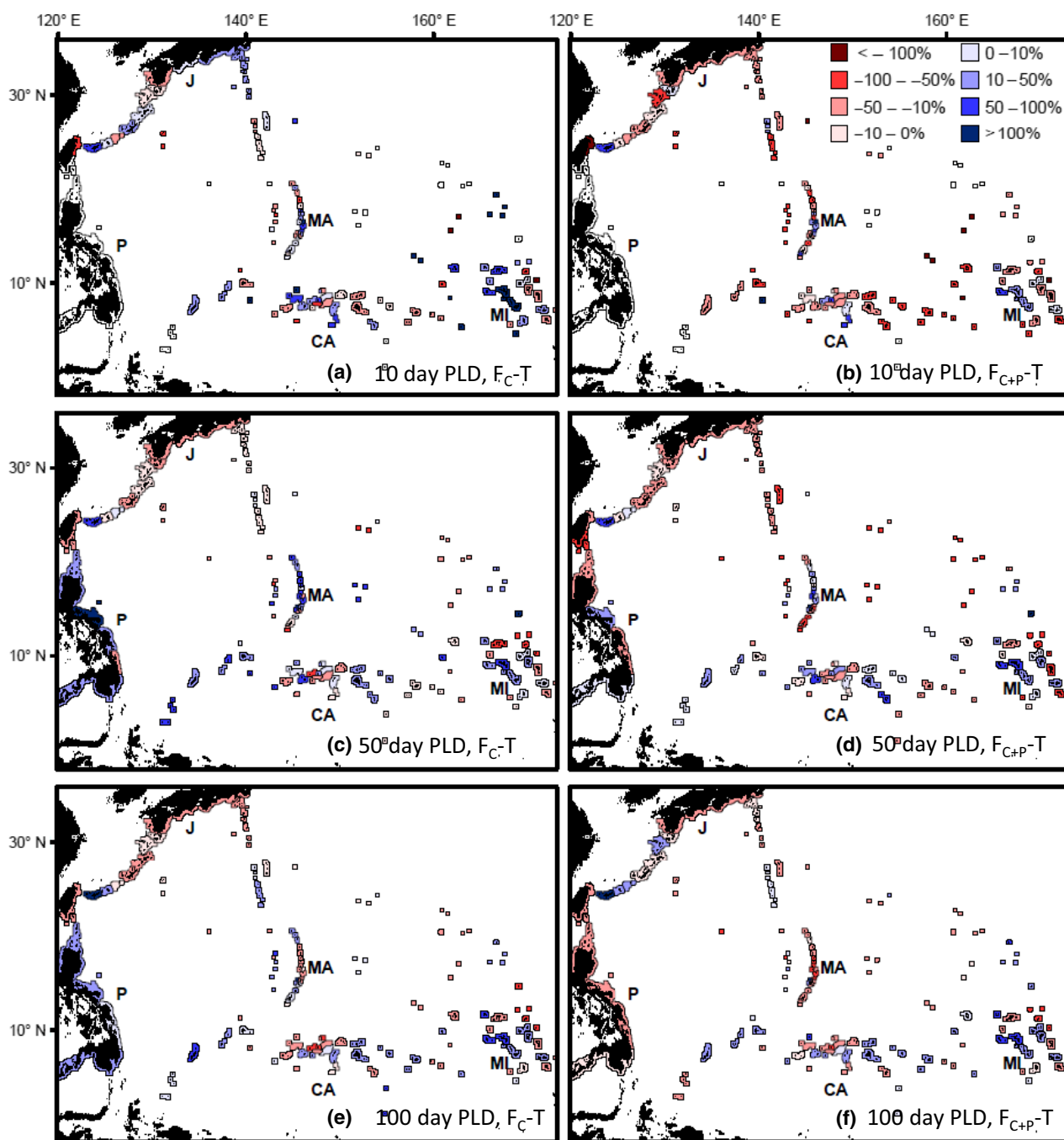


Fig. 5 (a–f) Percentage change in future arrivals for each island by PLD and climate change scenario. Letter definitions are: MA, Mariana Archipelago; CA, Caroline Archipelago; MI, Marshall Islands; J, Japan; P, Philippines.

overfishing, land-based pollution, habitat degradation, coral bleaching, and disease continue. Changes in adult fitness (Johansen & Jones, 2011) and reproductive output (Pankhurst & Munday, 2011) would require different numbers of starting larvae when comparing present-day vs. future connectivity models. Altered seasonal peaks in reproduction (i.e., phenology) where ocean currents differ seasonally (Reverdin *et al.*, 1994;

Kendall & Poti, 2015) will also affect cumulative annual transport patterns (Lett *et al.*, 2010; Pankhurst & Munday, 2011; Andrello *et al.*, 2014). These factors will impact source populations and should also be evaluated in future simulations.

Although we based future ocean temperature and circulation changes on a single, widely used and well-documented global climate model experiment, some

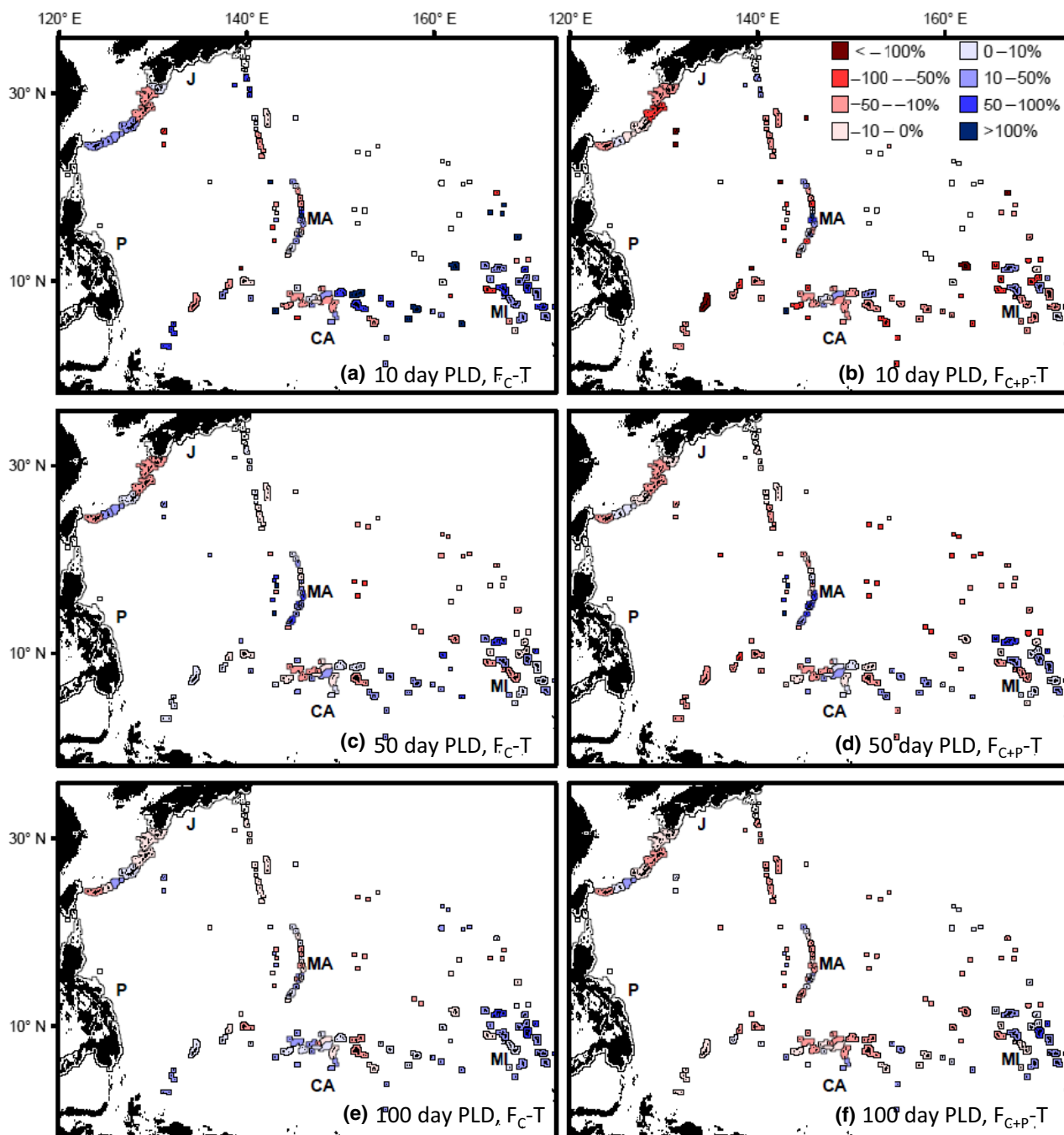


Figure 6 (a–f) Percentage change in future exports for each island by PLD and climate change scenario. Letter definitions are: MA, Mariana Archipelago; CA, Caroline Archipelago; MI, Marshall Islands; J, Japan; P, Philippines.

quantitative sensitivity to particular model and forcing scenarios likely exist. For example, in contrast to the 2.74 °C temperature increase projected in the study area with the RCP8.5 experiment that were used in this study, average SST change based on the RCP4.5 forcing experiment for the same model are not as severe (0.91 °C per 100 years), and would obviously lessen reductions in PLD. Furthermore, based on previous

generation (CMIP3/AR4) models and a different forcing experiment, Luo *et al.* (2009) predicted both the NEC and the NECC to slow by $\sim 4 \text{ cm s}^{-1}$ as measured along 180 W longitude, which differs from our AR5-based prediction of a small increase or no change in speed for at least the southern half of the NEC. As in most global studies of the regional impacts of global climate change, future work expanding on the number of

GCMs may reduce the quantitative uncertainty of these results.

Although a growing diversity of studies investigate the impact of temperature and pH, there are no data on the effects of these variables for the vast majority of marine larvae (Byrne, 2012). We used a single value of 17% to shorten PLDs using information from separate review studies (O'Connor *et al.*, 2007; Munday *et al.*, 2009b) to obtain a generic understanding of this parameters effect on connectivity. It is recognized that individual species will experience more or less decline or nonlinear changes in PLD due to a variety of factors and that some may be able to evolve over multiple generations toward genotypes more adapted to new climate conditions (Munday *et al.*, 2009b; Byrne, 2011). As additional information becomes available, our approach of examining multiple PLDs and scenarios with or without physiological effects can be used to place those studies into context.

Identifying a universal suite of predictions on how climate change will affect connectivity has proven difficult. Conflicting results can emerge due to: (1) the differences in physiological response among biota to future climate conditions, (2) the spatial arrangement of archipelagos relative to dominant ocean currents, and (3) the spatially variable changes in future current vectors that will cause some currents to slow down and others to speed up. For these reasons, advice to policy-makers must be both organism- and locality-specific. In situations where existing long-range connections among populations are diminished or broken, gene flow is hampered. With less exchange of individuals with climate-tolerant traits, the adaptive capacity of reef populations to future environmental conditions may be hindered (Visser, 2008; Munday *et al.*, 2009b). MPAs in less connected areas may need to be more abundant and closer together in the future to achieve the same network effects expected today (Munday *et al.*, 2009b; Kendall *et al.*, 2013; Andrello *et al.*, 2014). An international conservation initiative, the Micronesia Challenge (www.micronesiachallenge.org), seeks to protect 20% of coral reefs in the study region as no-take reserves. Some islands in the region presently export large numbers of larvae (Kendall & Poti, 2014, 2015) and may be prioritized for protection. Those locations identified in the present study that maintain or enhance this role as a source of larvae into the future could be the focus of conservation measures that promote long-term resilience of larval supply.

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References

- Aiken CM, Navarrete SA, Pelegri JL (2011) Potential changes in larval dispersal and alongshore connectivity on the central Chilean coast due to an altered wind climate. *Journal of Geophysical Research*, **116**, 1–14.
- Almany GR, Connolly SR, Heath DD *et al.* (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs*, **28**, 339–351.
- Andrello M, Mouillot D, Somot S, Thuiller W, Manel S (2014) Additive effects of climate change on connectivity between marine protected areas and larval supply to fished areas. *Diversity and Distributions*, **2014**, 1–12.
- Bleck R, Boudra D (1981) Initial testing of a numerical ocean circulation model using a hybrid (quasigeostrophic) vertical coordinate. *Journal of Physical Oceanography*, **11**, 755–770.
- Boden TA, Marland G, Andres RJ (2010) *Global, Regional, and National Fossil-Fuel CO₂ Emissions*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, TN, USA.
- Booth DJ, Parkinson K (2011) Pelagic larval duration is similar across 23° of latitude for two species of butterflyfish (Chaetodontidae) in eastern Australia. *Coral Reefs*, **30**, 1071–1075.
- Byrne M (2011) Impact of ocean warming and ocean acidification on marine invertebrate life history stages: vulnerabilities and potential for persistence in a changing ocean. *Oceanography and Marine Biology: An annual review*, **49**, 1–42.
- Byrne M (2012) Global change ecotoxicology: identification of early life history bottlenecks in marine invertebrates, variable species responses and variable experimental approaches. *Marine Environmental Research*, **76**, 3–15.
- Christie MR, Tissot BN, Albins MA *et al.* (2010) Larval connectivity in an effective network of marine protected areas. *PLoS ONE*, **5**, e15715.
- Connolly SR, Baird AH (2010) Estimating dispersal potential for marine larvae: dynamic models applied to scleractinian corals. *Ecology*, **91**, 3572–3583.
- Danabasoglu G, Bates S, Briegleb BP *et al.* (2012) The CCSM4 ocean component. *Journal of Climate*, **25**, 1361–1389.
- Edmunds PJ, Gates RD, Gleason DF (2001) The biology of larvae from the reef coral *Porites astreoides*, and their response to temperature disturbances. *Marine Biology*, **139**, 981–989.
- Fisher R (2005) Swimming speeds of larval coral reef fishes: impacts on self-recruitment and dispersal. *Marine Ecology Progress Series*, **285**, 223–232.
- Fitzgibbon QP, Battaglene SC (2012) Effect of water temperature on the development and energetics of early, mid and late-stage phyllosoma larvae of spiny lobster *Sagamariusus verreauxi*. *Aquaculture*, **344–349**, 153–160.
- Fossette S, Putman NF, Lohmann KJ, Marsh R, Hays GC (2012) A biologist's guide to assessing ocean currents: a review. *Marine Ecology Progress Series*, **457**, 285–301.
- Gent PR, Danabasoglu G, Donner LJ *et al.* (2011) The community climate system model version 4. *Journal of Climate*, **24**, 4973–4991.
- Gerlach G, Atema J, Kingsford MJ, Black KP, Miller-Sims V (2007) Smelling home can prevent dispersal of reef fish larvae. *Proceedings of the National Academy of Sciences*, **104**, 858–863.
- Graham EM, Baird AH, Connolly SR (2008) Survival dynamics of scleractinian coral larvae and implications for dispersal. *Coral Reefs*, **27**, 529–539.
- Green BS, Fisher R (2004) Temperature influences swimming speed, growth and larval duration in coral reef fish larvae. *Journal of Experimental Marine Biology and Ecology*, **299**, 115–132.
- Harrison PL, Wallace CC (1990) Chapter 7: reproduction, dispersal and recruitment of scleractinian corals. In: *Ecosystems of the World 25 Coral Reefs* (ed. Dubinsky Z), pp. 133–207, Elsevier Science Publishing Company, Inc., Amsterdam, the Netherlands.
- Hastings A, Botsford LW (2006) Persistence of spatial populations depends on returning home. *Proceedings of the National Academy of Sciences*, **103**, 6067–6072.

- Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. *Trends in Ecology and Evolution*, **20**, 337–344.
- Heenan A, Pomeroy R, Bell J *et al.* (2015) A climate-informed, ecosystem approach to fisheries management. *Marine Policy*, **57**, 182–192.
- Heyward AJ, Negri AP (2010) Plasticity of larval pre-competency in response to temperature: observations on multiple broadcast spawning coral species. *Coral Reefs*, **29**, 631–636.
- Hughes TP, Baird AH, Bellwood DR *et al.* (2003) Climate change, human impacts, and the resilience of coral reefs. *Science*, **301**, 929–933.
- Hurrell JW, Holland MM, Gent PR *et al.* (2013) The community earth system model a framework for collaborative research. *Bulletin of the American Meteorological Society*, **94**, 1339–1360.
- IPCC (2013) Annex I: atlas of global and regional climate projections supplementary material RCP8.5 (eds van Olden-borgh GJ, Collins M, Arblaster J, Christensen JH, Marotzke J, Power SB, Rummukainen M, Zhou T). In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Stocker TF, Qin D, Plattner GK *et al.*), pp. 1311–1393. Cambridge University Press, Cambridge, UK.
- Johansen JL, Jones GP (2011) Increasing ocean temperature reduces the metabolic performance and swimming ability of coral reef damselfishes. *Global Change Biology*, **17**, 2971–2979.
- Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs*, **28**, 307–325.
- Karnauskas KB, Cohen AL (2012) Equatorial refuge amid tropical warming. *Nature Climate Change*, **2**, 530–534.
- Kendall MS, Poti M (2014) Potential larval sources, destinations, and self-seeding in the Mariana Archipelago documented using ocean drifters. *Journal of Oceanography*, **70**, 549–557.
- Kendall MS, Poti M (eds) (2015) *Transport Pathways of Marine Larvae Around the Mariana Archipelago*. NOAA Technical Memorandum NOS NCCOS 193, Silver Spring, MD, USA.
- Kendall MS, Poti M, Wynne TT, Kinlan BP, Bauer LB (2013) Consequences of the life history traits of pelagic larvae on interisland connectivity during a changing climate. *Marine Ecology Progress Series*, **489**, 43–59.
- Kool JT, Paris CB, Barber PH, Cowen RK (2011) Connectivity and the development of population genetic structure in Indo-West Pacific coral reef communities. *Global Ecology and Biogeography*, **20**, 695–706.
- Leis JM (2006) Are larvae of demersal fishes plankton or nekton? *Advances in Marine Biology*, **51**, 59–141.
- Leis JM (2007) Behavior as input for modeling dispersal of fish larvae: behavior, biogeography, hydrodynamics, ontogeny, physiology and phylogeny meet hydrography. *Marine Ecology Progress Series*, **347**, 185–193.
- Lester SE, Ruttenberg BI, Gaines SD, Kinlan BP (2007) The relationship between dispersal ability and geographic range size. *Ecology Letters*, **10**, 745–758.
- Lett C, Ayata SD, Huret M, Irissou JO (2010) Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. *Progress in Oceanography*, **87**, 106–113.
- Llopiz JK, Cowen RK, Hauff MJ *et al.* (2014) Early life history and fisheries oceanography: new questions in a changing world. *Oceanography*, **27**, 26–41.
- Long MC, Lindsay K, Peacock S, Moore JK, Doney SC (2013) Twentieth-century oceanic carbon uptake and storage in CESM1(BGC)*. *Journal of Climate*, **26**, 6775–6800.
- Lo-Yat A, Simpson SD, Meekan M, Lecchini D, Martinez E, Galzin R (2011) Extreme climatic events reduce ocean productivity and larval supply in a tropical reef ecosystem. *Global Change Biology*, **17**, 1695–1702.
- Lucas JS (1973) Reproductive and larval biology of *Acanthaster planci* (L.) in Great Barrier Reef Waters. *Micronesica*, **9**, 197–203.
- Luo Y, Rothstein LM, Zhang RH (2009) Response of pacific subtropical–tropical thermocline water pathways and transports to global warming. *Geophysical Research Letters*, **36**, L04601.
- McLeod IM, Rummer JL, Clark TD, Jones GP, McCormick MI, Wenger AS, Munday PL (2013) Climate change and the performance of larval coral reef fishes: the interaction between temperature and food availability. *Conservation Physiology*, **1**, 1–12.
- McLeod IM, McCormick MI, Munday PL *et al.* (2015) Latitudinal variation in larval development of coral reef fishes: implications of a warming ocean. *Marine Ecology Progress Series*, **521**, 129–141.
- Meekan MG, Carleton JH, McKinnon AD, Flynn K, Furnas M (2003) What determines the growth of tropical reef fish larvae in the plankton: food or temperature? *Marine Ecology Progress Series*, **256**, 193–204.
- Munday PL, Donelson JM, Dixson DL, Endo GGK (2009a) Effects of ocean acidification on the early life history of a tropical marine fish. *Proceedings of the Royal Society of London B: Biological Sciences*, **276**, 3275–3283.
- Munday PL, Leis JM, Lough LM, Paris CB, Kingsford MJ, Berumen ML, Lambrechts J (2009b) Climate change and coral reef connectivity. *Coral Reefs*, **28**, 379–395.
- O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences*, **104**, 1266–1271.
- Ottersen G, Kim S, Huse G, Polovina JJ, Stenseth NC (2010) Major pathways by which climate may force marine fish populations. *Journal of Marine Systems*, **79**, 343–360.
- Pankhurst NW, Munday PL (2011) Effects of climate change on fish reproduction and early life history stages. *Marine and Freshwater Research*, **62**, 1015–1026.
- Rankin TL, Sponaugle S (2011) Temperature influences selective mortality during the early life stages of a coral reef fish. *PLoS ONE*, **6**, e16814.
- Reverdin G, Frankignoul C, Kestenare E (1994) Seasonal variability in the surface currents of the equatorial Pacific. *Journal of Geophysical Research*, **99**, 20323–20344.
- Riahi K, Krey V, Rao S *et al.* (2011) RCP-8.5: exploring the consequence of high emission trajectories. *Climatic Change*, **109**, 33–57.
- Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. *Marine Ecology Progress Series*, **60**, 185–203.
- Schnitzler CE, Hollingsworth LL, Krupp DA, Weis VM (2012) Elevated temperature impairs onset of symbiosis and reduces survivorship in larvae of the Hawaiian coral, *Fungia scutaria*. *Marine Biology*, **159**, 633–642.
- Sokal RR, Rohlf FJ (eds.) (1981) *Biometry*, 2nd edn, pp. 691–778. W.H. Freeman, New York, NY.
- Takahashi M, McCormick MI, Munday PL, Jones GP (2012) Influence of seasonal and latitudinal temperature variation on early life-history traits of a coral reef fish. *Marine and Freshwater Research*, **63**, 856–864.
- Taylor KE, Stouffer RJ, Meehl GA (2012) An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society*, **93**, 485–498.
- Trembl EA, Halpin PA, Urban DL, Pratson LF (2008) Modeling population connectivity by ocean currents, a graph theoretic approach for marine conservation. *Land-scape Ecology*, **23**, 19–36.
- Van Vuuren DP, Edmonds J, Kainuma M *et al.* (2011) The representative concentration pathways: an overview. *Climatic Change*, **109**, 5–31.
- Vecchi GA, Soden BJ (2007) Global warming and the weakening of the tropical circulation. *Journal of Climate*, **20**, 4316–4340.
- Visser ME (2008) Keeping up with a warming world: assessing the rate of adaptation to climate change. *Proceedings of the Royal Society of London B: Biological Sciences*, **275**, 649–659.
- Von Herbing H (2001) Effects of temperature on larval fish swimming performance: the importance of physics to physiology. *Journal of Fish Biology*, **61**, 865–876.
- Wood S, Paris CB, Ridgwell A, Hendy EJ (2013) Modelling dispersal and connectivity of broadcast spawning corals at the global scale. *Global Ecology and Biogeography*, **23**, 1–11.
- Zelenke B, O'Connor C, Barker C, Beegle-Krause J, Eclipse L (eds) (2012) *General NOAA Operational Modeling Environment (GNOME) Technical Documentation*. U.S. Department of Commerce, NOAA Technical Memorandum NOS ORR 40, Emergency Response Division, NOAA, Seattle, WA, pp. 105.
- Zhang L, Li T (2014) A simple analytical model for understanding the formation of sea surface temperature patterns under global warming. *Journal of Climate*, **27**, 8413–8421.

Supporting Information

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

Figure S1. Comparison of zonal (left) and meridional (right) ocean surface velocity components from the CESM global model (top), the Simple Ocean Data Assimilation (SODA) reanalysis dataset (middle), and the HYCOM ocean model (bottom) for the study area demonstrating consistent broad-scale circulation patterns. Black line denotes the position of the Mariana Archipelago.

Figure S2. Spatial fields of the linear trends for the zonal (left) and meridional (right) ocean surface velocity components over the course of the RCP8.5 experiment (2006–2100) (top) and the 95% confidence intervals on those trends (bottom) based on internal variability. Black line denotes the position of the Mariana Archipelago.

Figure S3–S8. Change Matrices: cumulative connectivity over the 9 years of transport simulations from each climate scenario (T , F_C , and F_{C+P}) were first summarized in separate connectivity matrices (not shown). Island locations are listed as sources (rows) and destinations (columns) of larvae with cells in these initial matrices representing the fraction of larvae released at each source settling at each destination. Note that individual islands are not labeled due to font size and some were modeled only as destinations. Changes in connectivity shown here were determined by subtracting matrices for present conditions from matrices of future conditions for each PLD. Matrix cells shown here equal the change in settlement fraction of larvae released at each source settling at each destination. Blue denotes increased future settlement whereas red denotes decreased future settlement.