



Consequences of the life history traits of pelagic larvae on interisland connectivity during a changing climate

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ABSTRACT: Many coral reef organisms possess a pelagic larval phase during which some larvae are retained near spawning sites and others are dispersed to more distant locations via ocean currents. Planktonic duration, distances traveled, and recruitment success can vary due to natural development rate, mortality rate, and sensory and swimming capabilities of particular taxa. Elevated water temperatures and acidification due to climate change can also influence recruitment by generally accelerating metabolism and growth, raising mortality rate, impairing development of calcified structures, and reducing sensory capabilities. We used hydrodynamic models and drifter data to investigate these various life history and climate-related influences on larval connectivity in and around the Samoan Archipelago. In general, virtual larvae spawned in the Samoan Archipelago seeded their natal reefs with relatively short-lived larvae, and their island neighbors to the west with longer-lived larvae. Larval duration, mortality rate, and sensory zone variables all had a significant effect on connectivity. Effect size was largest for mortality rate followed by larval duration. Shortened larval longevity due to climate change reduced interisland connectivity and changed the life history traits (and therefore taxa) that result in successful connections. Islands will generally become increasingly more reliant on self-seeding as the ocean warms, although the role of most islands primarily as a source or destination was robust to climate change.

KEY WORDS: Biogeography · Climate change · Connectivity · Dispersal · Pelagic larval duration · Samoan Archipelago

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INTRODUCTION

A variety of physical and biotic factors can affect the transport of marine fish and invertebrate larvae among locations. Most obviously it is necessary to understand the speed, direction, and seasonality of the ocean currents by which larvae are transported. It is also necessary to understand how aspects of the

larvae themselves can affect their transport. Size of source populations, timing of spawning, duration of the larval period, mortality rates, and sensory and swimming capabilities can all affect the probability that larvae will be transported from a source location to a particular destination (Leis 2007, Siegel et al. 2008, Trembl et al. 2008, Cowen & Sponaugle 2009). These factors are incompletely understood for most

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species, and values can range widely even among related taxa such that connectivity patterns of one species will not necessarily predict those of another (Byrne 2012).

Further complications arise in that several of these factors are likely in flux due to climate change (Munday et al. 2009b, Luo & Rothstein 2011, Byrne 2012). Ocean temperatures have been increasing and pH levels have been decreasing, although the magnitude and spatial variability of these trends are being refined (Folland et al. 2003, IPCC 2007). Climate change not only alters ocean temperature, chemistry, currents, and stratification, but it can also affect larvae themselves. Warmer water generally increases larval development rate and shortens the time required for larvae to become competent to settle (O'Connor et al. 2007). Empirical studies on reef fish larvae suggest a 4 to 8% reduction in larval duration for every 1°C increase in ocean temperature (McCormick & Molony 1995, Green & Fisher 2004, Sponaugle et al. 2006, Munday et al. 2009b, Rankin & Sponaugle 2011, but see Booth & Parkinson 2011). Temperatures above growth optima have been shown to negatively affect respiration, fitness, and mortality of coral planulae larvae in a diversity of genera (Edmunds et al. 2001, 2011, Bassim & Sammarco 2003, Randall & Szmant 2009, Heyward & Negri 2010, Rankin & Sponaugle 2011). Acidification levels predicted to occur by the end of this century have been shown to impair larval homing, hinder calcification, reduce larval size, depress coral and fish recruitment, and increase mortality of larval fish and invertebrates (McCormick & Molony 1995, Przeslawski et al. 2008, Munday et al. 2009a, 2010, Byrne 2012, Doropoulos et al. 2012). Interactions between warming and acidification are poorly understood and may partly offset or act synergistically depending on taxa (Byrne 2012).

These various life history and climate-related influences make it necessary to explore connectivity through a range of scenarios to achieve a more complete understanding of their potential effects on larval transport. By simulating connectivity through a range of life history parameters, the connectivity expected in today's ocean environment can be compared among life history traits or tailored to specific taxa when life history parameters are known. Having calculated connectivity through a range of values, it becomes possible to then shift predictions to shorter larval durations, higher mortalities, or reduced sensory capabilities that are expected in a warmer and more acidic ocean environment due to climate change.

Island systems provide an effective model to evaluate the complex tradeoffs in the factors affecting connectivity because they often involve different sizes of source populations, represent discrete spawning sites and destinations, and possess a range of inter-island distances. In this study, we focus on islands and shallow seamounts of the Samoan Archipelago due to several recent management initiatives that will be improved with an understanding of larval connectivity. These include selection of marine protected areas (MPAs; Johannes 2002, ONMS 2012), the goal of protecting 20% of reefs in American Samoa as no-take zones (Oram 2008), and an international environmental collaboration with the adjacent nation of Samoa ('2 Samoas Initiative'). Selecting fisheries targets and appropriate placement of MPAs are often improved by knowledge of larval source/destination patterns and distances of larval import and export (Gaines et al. 2003, Almany et al. 2007, McCook et al. 2009).

Many marine organisms important to coral ecosystems of the south Pacific possess a pelagic larval phase. Bony fish, broadcast spawning corals, giant clams, crown-of-thorns starfish, and a diversity of other fauna are subject to transport by ocean currents for at least some portion of their larval life. To place the Samoan Archipelago into regional context and understand key import and export pathways for larval connectivity more broadly, as must be done in regional management or MPA network planning, we also included the surrounding island nations (Fig. 1).

There are 3 main ocean currents in this region (Fig. 1). The South Equatorial Current (SEC) flows west/southwestward along the northern edge of the study area, with year-long flow, strongest from March to July at $\sim 25 \text{ cm s}^{-1}$ (Kessler & Taft 1987, Kendall & Poti 2011). Overlying the SEC between $\sim 8^\circ$ and 12° S is the eastward flowing South Equatorial Counter Current (SECC; Kessler & Taft 1987, Chen & Qiu 2004, Domokos et al. 2007, Kendall & Poti 2011). The eastern end of this current typically weakens and narrows to the east and then generally curls south between $\sim 160^\circ$ and 170° W and ultimately joins the southern component of the SEC headed west across the Samoan Archipelago (Chen & Qiu 2004, Kendall & Poti 2011). The seasonal SECC is typically well developed by October, achieves peak speed (22 to 30 cm s^{-1}) and width during January, and dissipates by May (Chen & Qiu 2004, Qiu & Chen 2004, Kendall & Poti 2011). South of the SECC, the SEC continues its generally westward flow between $\sim 13^\circ$ and 19° S ; however, in contrast to the northern component of the SEC described above, this region is

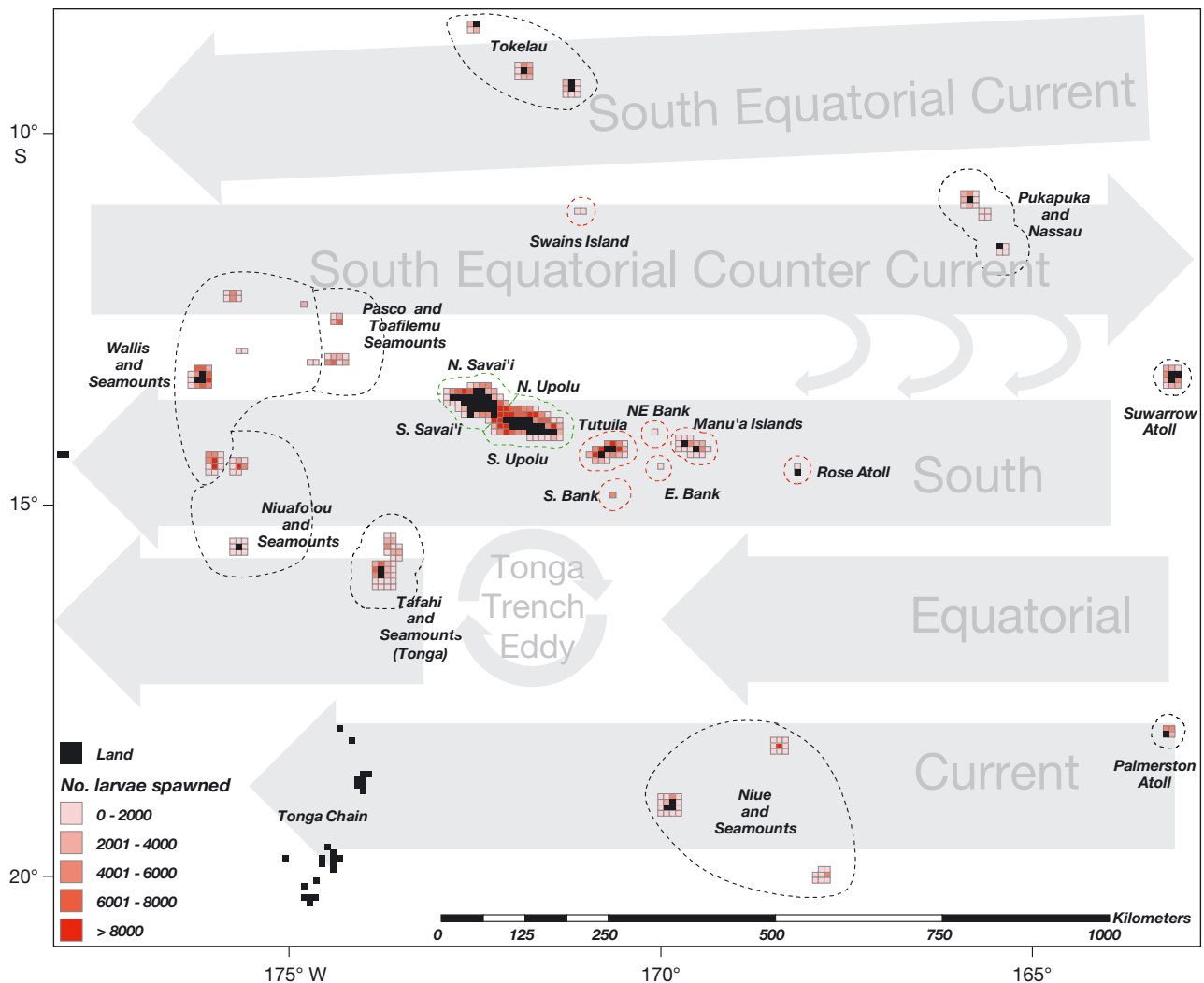


Fig. 1. Major currents in the Samoan Archipelago study region. HYCOM grid cells are shown with islands represented as black cells and coastal grid cells colored according to potential reef ecosystem area and modeled larval production. Dashed lines denote the 20 islands/island groups used in the study. Red lines denote American Samoa, green denotes Samoa

characterized by many irregular meanders and eddies (Domokos et al. 2007, Kendall & Poti 2011).

Our general approach was to evaluate a range of model parameters that have the potential to affect dispersal (Leis 2007) rather than narrowly specifying values for the life history and behaviors of a particular species according to present climate conditions. We examined how a wide range of combinations of larval durations, sensory and swimming capabilities, and mortality rates reported in the scientific literature may impact the connectivity of Samoan reef ecosystems. This allows results to be contrasted among taxa with known larval parameters, compared for current or projected climate conditions, and re-evaluated once larval parameters are defined for less studied species.

The objectives of this study were to:

- (1) Describe the transport pathways of virtual larvae among island sources in and around the Samoan Archipelago;
- (2) Quantify and compare the influence of various combinations of larval life history characteristics (i.e. longevity, daily mortality rate, sensory/swimming capabilities) on successful settlement and connectivity patterns;
- (3) Quantify each island's role as a source or destination of successfully settling larvae;
- (4) Quantify each island's dependence on local larval production relative to external larval sources;
- (5) Evaluate how climate change, specifically reduced larval longevity, may alter connectivity among islands.

METHODS

Two datasets were used to quantify larval connections: actual ocean current data from passive drifters and transport simulations of virtual larvae based on a hydrodynamic model. The NOAA Global Drifter Program (www.aoml.noaa.gov/phod/dac/gdp.html) uses satellites to track drogues deployed at 15 m depth. Drifter position, speed, and heading are calculated every 6 h. These data were used to validate the current vectors of the hydrodynamic model and select realistic diffusion parameters. The Hybrid Coordinate Oceanographic Model (HYCOM) is a 3-dimensional hydrodynamic model (Bleck & Boudra 1981, Bleck & Benjamin 1993, Halliwell et al. 1998, Christie et al. 2010) with a horizontal resolution of $1/12^\circ$ (approximately 9 by 9 km grid cells) and a 1 d time step. We used the Global Hindcast modeled dataset downloaded in NetCDF format from the HYCOM consortium via the NASA/REASON Ocean Data Portal using Matlab OPeNDAP Toolbox version 2.0 (www.oceanographicdata.org/Toolbox/toolbox.html). Current vectors for the 0–10 m depth layer from 2004 to 2009 were used. These years represent a typical 6 yr period of various El Niño and La Niña conditions. The 9 km model resolution is not sufficient to capture local currents close to shore (Swearer et al. 1999, Harlan et al. 2002), and we therefore used it only to evaluate broader scales of larval transport among islands.

HYCOM validation

Modeled currents from HYCOM were compared to drifter data on daily and monthly timescales. To evaluate daily current vectors, average daily latitudinal and longitudinal drifter velocities were compared to the corresponding average daily model velocities at 100 randomly chosen drifter dates/positions using linear regression. To evaluate the modeled current vectors on longer timescales, average monthly current vectors were plotted over the tracks of drifters present (216 total) during the corresponding month/year. Drifter positions were color-coded by heading, and vectors were plotted on a $1/3^\circ$ grid to visualize comparisons.

Larval sources

Virtual larvae were started at each of 20 island groups and shallow seamounts in the study area (Fig. 1). Islands and seamounts close together were

grouped for analysis especially at the edges of the study region to simplify and focus presentation of the results on the Samoan Archipelago. Only the northern extent of the Tonga chain and eastern Wallis chain were included as larval sources since preliminary analysis indicated that most larvae from more outlying locations quickly left the study area to the west.

Larval production was scaled to the area of each island's potential coral reef habitat. This was the only surrogate available for the entire region and was defined as the area shallower than the 150 m isobath. This captures the approximate depth limits of both photic and mesophotic coral communities (Bare et al. 2010, Mesophotic Coral Ecosystems: www.mesophotic.org). Initially, a set of 10 000 larvae were randomly distributed within each coastal grid cell in HYCOM. This number of larvae was then adjusted based on the proportion of the grid cell with water depths between 0 and 150 m. This provided a very large but computationally reasonable number of virtual larvae that could be 'spawned' or started moving in transport simulations on any date specified.

Mass spawning events and start dates of larval transport

Many coral species, reef fish, and other organisms in the study region have a well-documented annual mass spawning (Mildner 1987, 1991, Itano & Buckley 1988, Mundy & Green 1996) which was the focus of our simulations. Spawning dates for each model year were identified as 6 d after the first full moon to occur later than 12 October (Mundy & Green 1996, Craig 2009). It is recognized that some spawning can occur across several days or even following successive full moons in October and November. Preliminary tests indicated that transport patterns did not differ substantially when start dates were separated by even as much as a month among various phases of the moon, a finding similar to other studies (James et al. 2002) and consistent with time scales of variation in ocean current patterns within the region.

Larval transport and current model uncertainty

In simulations, virtual larvae began at random locations within each coastal grid cell and moved in the direction and speed specified by the corresponding HYCOM vectors for that date and position. The General NOAA Operational Modeling Environment

(GNOME v.1.3.0) (Zelenke et al. 2012) was used to track positions of virtual larvae based on procedures modified from Wynne et al. (2011). At this stage, all virtual larvae were treated as immortal, non-settling particles. Custom scripts in ArcGIS 9.3 were applied to GNOME outputs to simulate the various life history scenarios described in subsequent sections.

Random variability in larval paths originating from the same location is an important aspect of connectivity studies (Polovina et al. 1999, Cowen et al. 2000, Siegel et al. 2003, Kobayashi 2006, Chiswell & Booth 2008, Treml et al. 2008, Rudorff et al. 2009). GNOME enables a controlled amount of random variability to be applied to vectors at each time step (see Zelenke et al. 2012 for technical details). This was used to simulate the stochasticity in larval paths arising from both sub-grid-scale turbulent processes as well as diffusion. To identify an appropriate level of variability in HYCOM vectors, actual current paths tracked by drifters were compared to paths predicted by HYCOM for virtual larvae originating at the same date and location as the drifters. We ran test models using random perturbations in current vectors ranging from 10 to 50% of down-current and cross-current velocity. Model and drifter paths were compared while recognizing that a given drifter represents only one possible track out of a potential distribution that reflects variation in drift. Using 50% uncertainty nearly always encompassed drifter tracks and provided reasonable clouds of larval pathways which highlighted more likely tracks while also depicting less likely, but still possible, pathways. All subsequent model runs were conducted using 50% uncertainty in down-current and across-current vectors to reflect this realistic level of variability.

Precompetency

Spawned gametes, fertilized eggs, and young larvae must spend some time developing and cannot immediately swim or settle even if they encounter suitable habitat. This planktonic phase prior to achieving a body form capable of settlement is termed precompetency. For a wide variety of reef fish species it is evident that individuals begin to settle once 60 to 90% of their maximum larval lifespan, termed pelagic larval duration, has elapsed (calculated from values reported by Victor 1986, Thresher et al. 1989, Wellington & Victor 1989, and Juncker et al. 2006). Precompetency periods for coral larvae are less known and appear somewhat more variable

(Harrison et al. 1984, Wilson & Harrison 1998, Miller & Mundy 2003, Graham et al. 2008, Jones et al. 2009). To simulate this developmental period here, virtual larvae were prevented from settlement until a minimum of 60% of their maximum pelagic larval duration (see next section) was completed.

Pelagic larval duration

Pelagic larval duration (PLD) is defined as the period of development spent in the water column as plankton. Total PLD is a composite of early development, onset of larval behaviors for some taxa (feeding, vertical migration, swimming), precompetency, and maximum larval lifespan (see Leis 2006 for a summary of fish larvae and Harrison & Wallace 1990 for coral larvae behaviors). Larvae simply die in the plankton at the end of their PLD if they lack a suitable settlement habitat or energy source. PLD is quite varied among coral reef organisms and can last for days, weeks, or months (e.g. Bonhomme & Planes 2000, Blanco-Martin 2006, Juncker et al. 2006, Graham et al. 2008). There can be variability within genera or even among individuals of the same species (Wilson & Harrison 1998, McCormick 1999, Juncker et al. 2006), with influences such as water temperature and availability of suitable settlement habitat (McCormick & Molony 1995, Munday et al. 2009b, Heyward & Negri 2010). In addition, some larvae can lengthen their time as plankton by delaying or partly reversing metamorphosis until a suitable habitat is encountered (Richmond 1985, McCormick 1999).

Although some PLDs >200 d are documented (e.g. some corals, Graham et al. 2008), these are relatively rare, and preliminary tests revealed that many tracked particles left our study area after >100 d. We therefore evaluated PLDs of 10, 20, 30, 50, and 100 d, which encompasses the range of PLDs expected for a wide variety of the fishes and corals of the region (e.g. summary tables in Bonhomme & Planes 2000, Blanco-Martin 2006, Graham et al. 2008, Jones et al. 2009). Note that PLD for fish taxa can be reported as the number of days until a settlement mark is observed on an otolith, but some taxa may develop sufficiently to be considered nekton rather than plankton at an earlier time. In such cases, it may be more appropriate to consider the shorter duration of only the planktonic portion of their PLD in our results, rather than their total PLD. Equally important, this range of intervals also allows predictions to be shifted toward shorter PLDs expected under increased ocean temperatures due to climate change.

'Settlement zone' buffers

Some larvae can sense reefs from some distance away through odor plumes or even sound and may perform behaviors that help them reach desirable settlement habitats including vertical migrations into current fields moving toward reefs, intentional entrainment into coastal eddies to avoid extensive offshore transport (Swearer et al. 1999, Harlan et al. 2002, Paris et al. 2007), or simply out-swimming the currents in which they are embedded (Atema et al. 2002, Leis 2002, 2006, 2007, Gerlach et al. 2007). For as much as the last 50% of their PLD, some fish larvae are capable of sustained directional swimming that is sufficient to overcome their treatment as merely passive particles (Leis & Carson-Ewart 2003, Fisher 2005, Leis 2006). Although the precise distance at which fish larvae can begin to orient towards reefs and the effectiveness of such mechanisms against ambient currents are topics of active debate, it is clear that some larvae need simply to come within a 'settlement zone' sufficiently close such that they can sense and swim to the settlement habitat. Buffers of appropriate size around suitable habitats are used to represent this 'settlement zone' depending on the species under investigation (Lugo-Fernández et al. 2001, James et al. 2002, Cowen et al. 2006, Chiswell & Booth 2008). In our simulations, if a larva passed into an island's settlement zone after its pre-competency period, it was considered to have successfully settled at that island. We investigated a range of potential settlement zone distances around islands and seamounts including 9 km (resolution of HYCOM grid cells, most representative of coral planulae or poorly-swimming fish larvae), 18 km (representative of swimming larvae with moderate range), and 36 km (representative of strong-swimming fish larvae with good sensory capabilities) to accommodate a wide spectrum of organisms and potential sensory and swimming capabilities. Equally important, these intervals allow predictions to shift toward smaller buffer categories as sensory abilities are hampered due to climate change (e.g. Munday et al. 2009a).

Mortality

Mortality in larval populations has a significant effect on successful recruitment. Mortality estimates for fish larvae of a diversity of taxa show a wide range from 3 to 46% d^{-1} with a mode of 18% (Cowen et al. 2000). Coral planulae had a similar range of daily mortality rates at reduced, ambient, and ele-

vated rearing temperatures that could simulate ocean warming (e.g. Edmunds et al. 2001, Bassim & Sammarco 2003). We investigated the influence of this range of daily mortality rates (3, 18, and 46%) in separate simulations. For each rate, these percentages of the larval population were randomly selected and removed from the larvae remaining at each daily time step.

Data analysis

Results are first summarized as connectivity matrices that display the sources and destinations of all the virtual larvae tracked in the study. Southern Tonga and western Wallis Islands were modeled only as destinations. For each PLD, buffer size, and mortality rate, we counted the number of simulated larvae released at each source location that traveled to each of the possible destination locations. Values are cumulated over all 5 model years. Matrix cells denote the proportion of larvae from each source (rows) that arrived at a given destination (columns). Rows thus sum to a number $\leq 100\%$. Columns can sum to $> 100\%$, because it is possible for a high proportion of the larvae produced at several sources to travel to the same destination. Note that connectivity calculated in this way depicts the pattern of larval transport pathways, without considering the variation in number of larvae produced at each source due to differences in island size.

Multi-factor ANOVA was used to evaluate the significance and magnitude of effects due to PLD, mortality, and buffer size. Data were pooled across years, and all 2-way interactions were included. Results of these initial tests guided additional aspects of the analyses. The ANOVA and connectivity matrices revealed that, compared to mortality and PLD, the magnitude of settlement rates was only somewhat affected by buffer distance, and the spatial patterns of connectivity were relatively unaffected. In contrast, the mortality levels that we investigated did have a large effect, causing mostly or even all 0s in some connectivity matrices calculated at high mortality. For these 2 reasons and because the effect of climate change is best understood for PLD, we therefore focus on PLD alone in the next components of the analysis.

Focusing only on the islands of the Samoan Archipelago, the proportion of each island's settlers from local versus external sources at various PLDs was evaluated using pie charts and a simple linear regression. All larvae produced from island X and

successfully returning there were summed separately for each PLD. All larvae produced elsewhere but settling at island X were similarly summed. These values were converted to proportions of total settlers at island X from internal and external sources for each PLD. Pie charts display how proportions change with PLD for each island. To test for trends and significance in reliance on self-seeding by PLD, simple linear regression was used on percent of settlers produced locally (logit transformed) versus PLD.

Each island's role as primarily a source or a destination by PLD was evaluated using bar charts. The number of larvae produced at island X that successfully settled anywhere else was summed by PLD. This represents the island's role as a 'source' of larvae. The number of larvae produced anywhere else that successfully settled at island X was similarly summed. This represents the island's role as a 'destination' of larvae. These values were plotted for each island by PLD on the x-axis. Bars above the axis denote source values and those below denote destination values so these relative roles can be compared. Note that this is different than the previous analysis in that self-seeding is not included in the calculations and actual numbers of larvae are shown to understand the magnitude of each island's role as a source or destination.

RESULTS

HYCOM validation

Linear regression of average daily drifter and model velocities at 100 randomly chosen dates/positions showed a significant positive relationship in both the latitudinal ($p < 0.0001$, slope = 0.7, $R^2 = 0.32$) and longitudinal velocities ($p < 0.0001$, slope = 0.5, $R^2 = 0.16$) and more importantly, drifter and model velocities were scattered around the 1:1 line of overall agreement (Fig. 2). Model vectors tended to be biased toward slightly weaker velocity at high and low values of U (east/west component of vector) with no directional bias in V (north/south component of vector). Note that these comparisons were not expected to provide a perfect 1:1 match of velocities given the inherent differences in drifter data (15 m drogue depth with interpolated position from satellite tracking) and model data (0–10 m surface layer with interpolated position and velocity from 9 km grid) and were used only to demonstrate that modeled circulation is broadly representative of regional currents, while also highlighting the uncertainty

associated with the models' lack of resolution of sub-grid turbulence. Current vectors from HYCOM also corresponded well to drifter paths in qualitative overlay comparisons on a monthly timescale (Fig. 2). The validation procedures conducted by the HYCOM consortium (<http://hycom.org>) coupled with our independent, regional assessments indicate that HYCOM provides a realistic representation of actual transport processes on both short (<daily) and long (monthly) timescales.

Larval sources

Based on potential reef area alone, the major sources of larvae in the study region are likely to be Upolu (~25% of the total larvae), Savai'i (~15%), and the Wallis Island group (~15%; Table 1). Moving east along the Samoan Archipelago, the islands of Tutuila and Manu'a are smaller, have much less potential reef area, and therefore have smaller potential spawning populations. Swains Island and the seamounts of American Samoa probably contribute relatively little to the larval pool due to their very small size.

Overall patterns of larval connectivity

All 3 life history variables had a significant individual effect on connectivity (ANOVA, $F_{28,16} = 112.12$, $p < 0.0001$) including PLD ($F_4 = 157.2$, $p < 0.0001$), mortality rate ($F_2 = 935.4$, $p < 0.0001$), and buffer size ($F_2 = 26.2$, $p < 0.0001$) as did 2-way interactions (PLD \times mortality $p < 0.0001$, PLD \times buffer $p < 0.0439$, mortality \times buffer $p < 0.0001$). The magnitude of the effects on connectivity due to these variables differed considerably. The effect was smallest for buffer size. Between the smallest and largest buffer sizes that we considered, there was a mean \pm SD decline of $37 \pm 2\%$ (range 34–43%) in total larvae settled for a given combination of PLD and mortality (Fig. 3). This effect was slightly greater at higher mortality levels. The effect size was huge for mortality. From the lowest to highest mortality rates that we considered, there was an average decline of $99 \pm 1\%$ (range 97–100%) in total larvae settled with no virtual larvae surviving the medium to high mortality rates for the longer PLDs. Effect size was most severe for longer PLDs. The effect size for PLD was also very large. From the shortest to longest PLD that we examined, there was an average decline of $88 \pm 0.1\%$ (range 87–88%) in total larvae settled. Note that only the low mortality

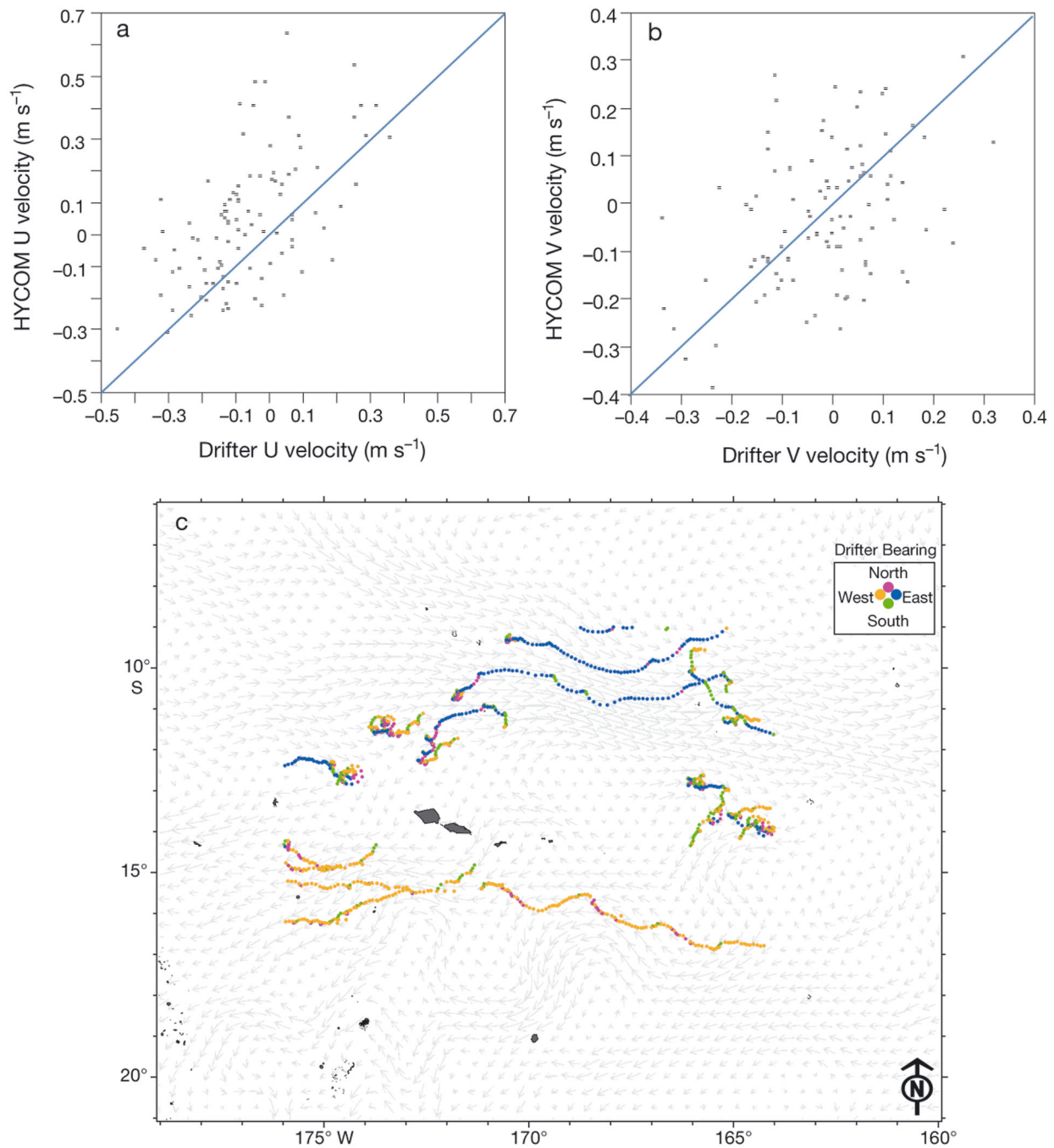


Fig. 2. Daily and monthly HYCOM validation. Comparison of current vectors for HYCOM versus drifters at 100 randomly chosen positions and dates. Comparisons for the (a) latitudinal (U) and (b) longitudinal (V) vectors are plotted against the ideal 1:1 line of perfect agreement. (c) Example from January 2007 of monthly plots of average HYCOM vectors at 1/3° resolution overlaid on drifter position/heading

rate could be included in this comparison since no virtual larvae survived to the 100 d PLD at medium or high mortality.

The connectivity matrices reveal broad patterns of overall larval transport and several island groups

with strong internal connectivity (Fig. 4). Beginning at the origin of the connectivity matrices (western end of the study area) it is clear that Wallis, Tonga, and the many small islands and seamounts associated with them are strongly interconnected but con-

Table 1. Islands, seamounts, or island groups used as source locations in connectivity simulations, their corresponding reef area (0–150 m shelf), number of virtual larvae used in modeling, and the percentage of the simulated larval pool contributed by each source

Site	Potential reef area (km ²)	No. larvae spawned each year	% of larvae spawned
Wallis and seamounts	993	132 722	16.2
Niuafou'ou and seamounts	34	4606	0.6
Pasco and Toafilemu seamounts	279	37 067	4.5
Tafahi and seamounts	400	54 704	6.7
Niue	285	40 304	4.9
Samoa			
Savai'i South	300	39 793	4.9
Savai'i North	600	80 919	9.9
Upolu South	571	76 831	9.4
Upolu North	949	127 661	15.6
American Samoa			
Tutuila	576	77 873	9.5
South Bank/Papatua Guyot	33	4481	0.6
East Bank/Tulaga seamount	3	448	0.1
Northeast Bank/Muli Guyot	10	1335	0.2
Manu'a Islands	186	25 182	3.1
Rose Atoll	12	1564	0.2
Swains Island	16	2133	0.3
Tokelau	350	45 644	5.6
Pukapuka and Nassau	187	24 507	3.0
Suvarrow Atoll	203	26 796	3.3
Palmerston Atoll	90	12 440	1.5
Totals	6077	817 010	100.0

tribute few larvae elsewhere in the study region except when low mortality is combined with long PLDs. The island nation south of American Samoa, Niue and its associated seamounts, is largely self-seeding and isolated from the other islands in the study region. Upolu and Savai'i in Samoa are highly interconnected at a range of PLD and mortality rates and also have a large export of larvae to the islands and seamounts to the west such as Wallis, Niuafou'ou, and Tafahi in all but the longest PLD and mortality rate scenarios. Samoa exports a smaller proportion of its larvae eastward toward American Samoa and only for PLDs longer than 20 d. The islands and seamounts of American Samoa (except Swains) are also internally connected for all PLDs at low mortality and for PLDs up to 30 d for moderate mortality. The overall pattern of transport is such that most of the larvae spawned along the archipelago either settle at the source or are transported to successive destinations to the west at increasing PLDs until mortality rates prevent the connections. Swains Island and Tokelau were relatively minor sources of larvae to the Samoan Archipelago only at moderate PLDs and low mor-

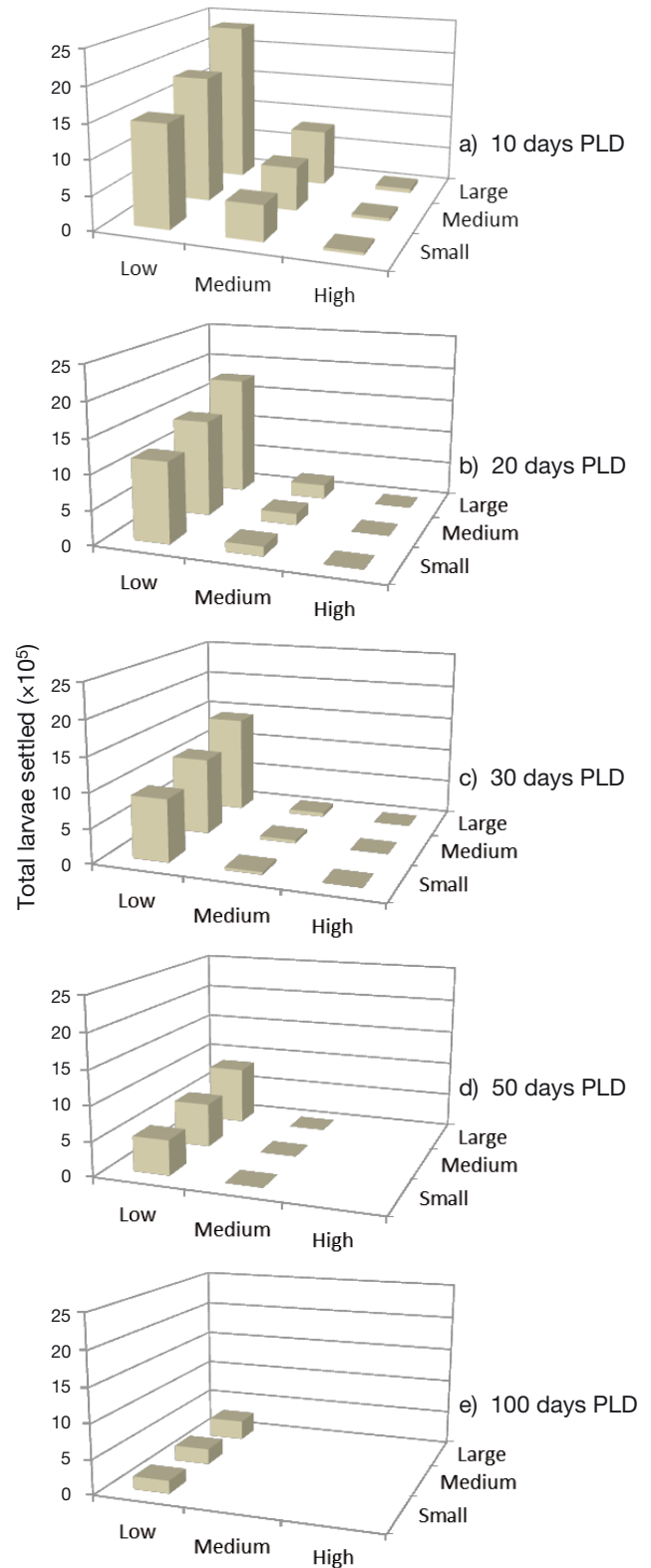


Fig. 3. Total larvae settled by each combination of pelagic larval duration (PLD), buffer size (small = 9 km, medium = 18 km, large = 36 km), and mortality rate (low = 3% d⁻¹, medium = 18% d⁻¹, high = 46% d⁻¹)

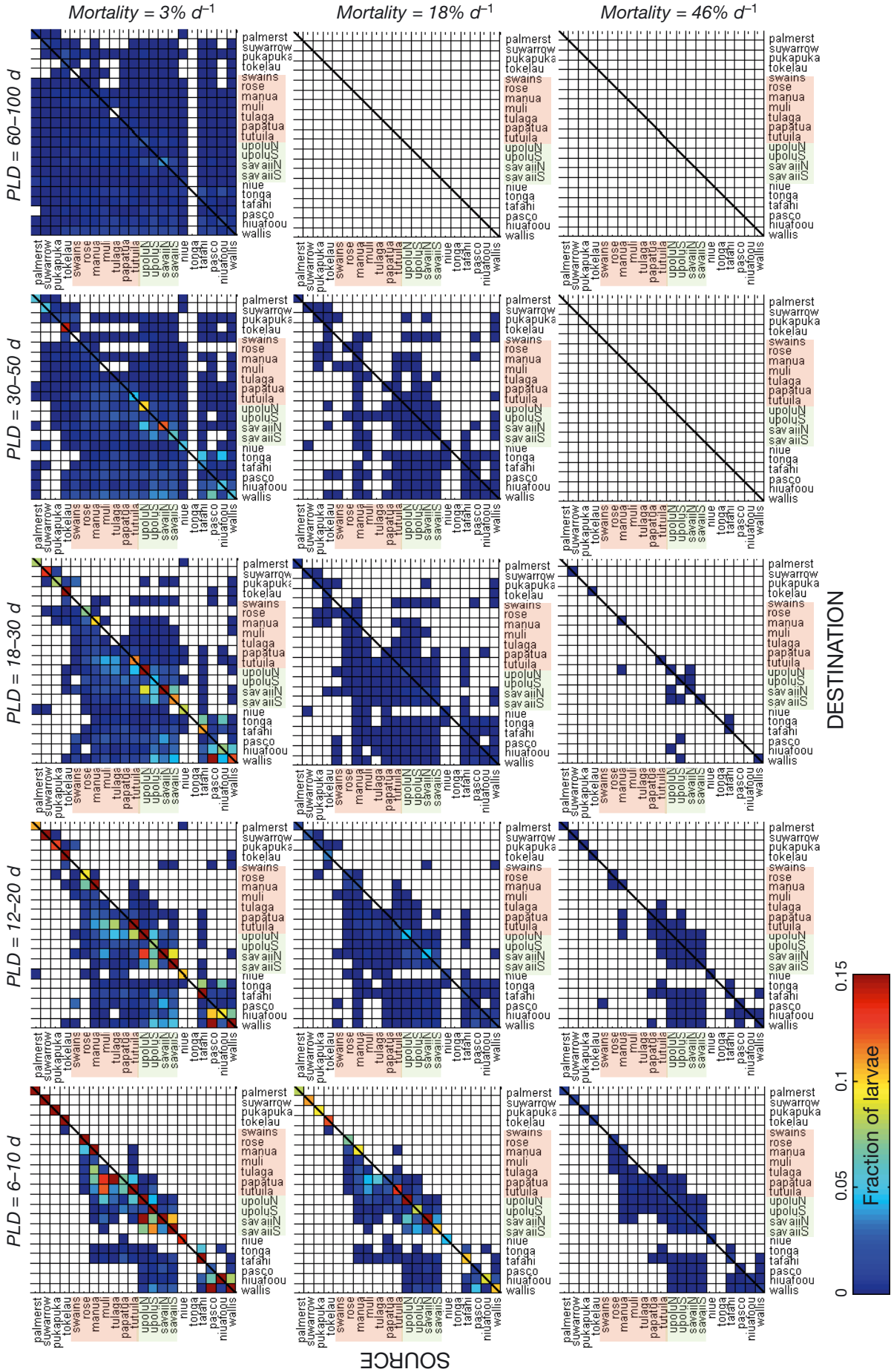


Fig. 4. Matrices of cumulative connectivity by pelagic larval duration (PLD) and mortality rate from the 18 km settlement zone. Color scale indicates fraction of simulated larvae released at source (vertical island labels) settling at destination (horizontal labels). Red labels denote American Samoa, green denotes Samoa

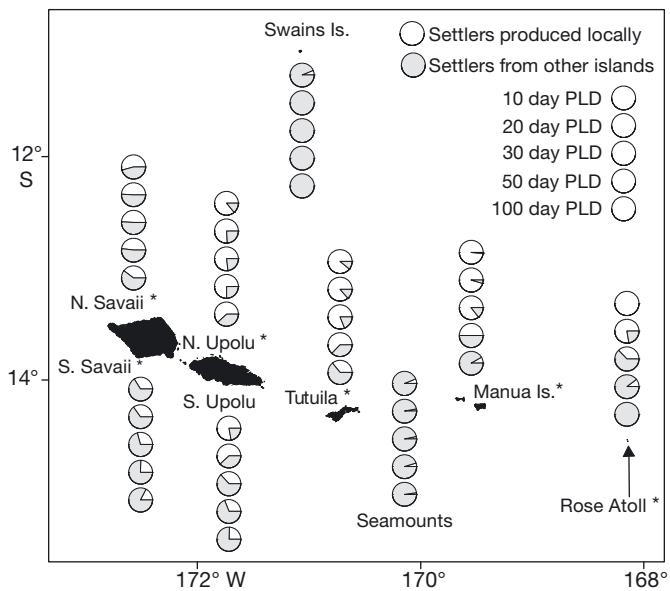


Fig. 5. Reliance of each island on larvae produced locally versus those produced elsewhere. Proportion of all larvae arriving at each island or group that originated from that island or were from elsewhere. Results by island are separated into individual pies from top to bottom for pelagic larval durations (PLDs) of 10, 20, 30, 50, and 100 d. All years, mortality rates, and buffer sizes are combined. * denotes island groups for which linear regression on logit-transformed % of settlers produced locally versus PLD was significant ($p < 0.05$)

tality rates. Cook Islands considered here (Suvarrow, Palmerston, and Pukapuka and Nassau) were largely isolated even from each other, and show few connections with other sites in any scenarios except those with the longest PLD and lowest mortality rate.

Self-reliant or externally dependent?

For most islands, there was a significant ($p < 0.05$) negative relationship between PLD and reliance on self-recruitment (Fig. 5). Longer PLD generally resulted in greater reliance on outside sources of larvae. The effect was noticeable nearly everywhere, but the magnitude of the effect varied widely among islands. Manua'a and Rose showed the most striking increase in reliance on external sources of larvae going from almost 100% self-seeding for species with a 10 d PLD to almost 100% reliance on external sources of larvae with a 100 d PLD. Tutuila and S. Upolu went from reliance on <25% of settlers from external sources at short PLDs of 10 d to ~75% from external sources at 100 d. N. Upolu and N. and S. Savai'i experienced a more modest (but still signif-

icant) increase in reliance on externally produced larvae. Exceptions to these patterns included the small island of Swains and the seamounts which had near total reliance on external larval sources at all PLDs (non-significant regressions of % self-seeding versus PLD). Overall, N. Upolu was the least reliant on external sources of larvae. N. Savai'i was nearly evenly split between local and external larval sources at all PLDs.

Shortened PLD due to climate change meant greater reliance on local production for most islands. Of those islands with a significant linear regression ($p < 0.05$) of PLD and percent self-seeding, the slope was always negative (greater proportion of self-seeding at shorter PLD) and surprisingly linear in most cases ($R^2 > 0.9$; Fig. 5). Average slope among these significant regressions indicated a 1% increase in the proportion of self-seeded larvae for every ~2.3 d that a PLD was shortened. Exceptions for this pattern were Swains and seamounts, which showed no significant relationship between these variables, and N. Upolu and N. Savai'i, which had rather steady proportions of self-seeding for intermediate PLDs of 20, 30, and 50 d.

Source or destination?

In general, the big islands farther to the west played large roles as both sources and destination at all PLDs (Fig. 6). Upolu was the largest source of larvae. Savai'i was the largest destination. Counter to expectations, source/destination roles were insensitive to PLD almost without exception (but see S. Savai'i at 100 d PLD). If an island was primarily a destination at one PLD, it was at all other PLDs as well. Swains Is., as well as the seamounts, were primarily destinations. Tutuila and the Manua'a islands were primarily sources of larvae. Tutuila delivered 3 to 5 times more larvae to other islands than it received depending on PLD. The range for Manua'a was larger, delivering 1 to 59 times more larvae to other islands than it received depending on PLD. Upolu was a larger source of larvae relative to being a destination, delivering 2 to 7 times more larvae than it received depending on PLD. Savai'i was a larger destination of larvae compared to being a source (but was still a source of many larvae), delivering only $\frac{1}{4}$ to $\frac{3}{4}$ as many larvae to other islands as it received from those sources depending on PLD. Shifting predictions toward shorter PLDs due to climate change did not alter an island's role as a larval source or destination.

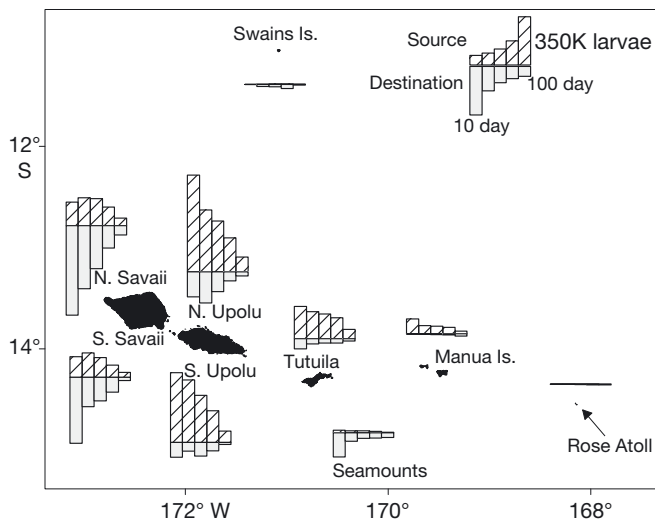


Fig. 6. Role of each island as a source or destination of regional larvae. Source denotes the number of larvae produced at a given island that settle elsewhere (slashed bars). Destination denotes the number of larvae produced elsewhere that settle at a given island and are shown as negative values (grey bars). Results by island are separated into individual columns from left to right for pelagic larval durations (PLDs) of 10, 20, 30, 50, and 100 d. Magnitude of an island's role as a source or destination can be evaluated by comparing the size of the source and destination columns for a given PLD

DISCUSSION

Connectivity among islands of the Samoan Archipelago and surrounding region is heavily influenced by the specific life history traits of pelagic larvae. Longer PLDs had 3 general effects. First, the proportion of self-seeding (fraction of larvae produced at a source location that settled at the same location) was reduced overall because larvae were not competent to settle until they had been transported farther from sources. Second, connectivity with islands farther downstream increased noticeably after PLDs of 10 d. This was especially noticeable in seeding of Wallis, Niuafu'ou, Tafahi, and the nearby seamounts with larvae from American Samoa. Third, larvae with PLDs of 50 or 100 d could be transported nearly any place in the study area, although in very low abundance, provided that the mortality rate was low. This widespread potential for transport at long PLDs suggests that the low amount of connectivity needed to prevent species divergence by genetic drift is easily possible throughout the study area.

The fate of long-lived larvae is highly dependent on mortality rates. For low to moderate mortality rates at PLDs up to 30 d, the islands involved in pre-

dicted larval exchange changed little, but mortality and PLD did affect the strength of the connection (cell color changed but pattern of empty cells in the connectivity matrix did not). In contrast, the higher mortality rates investigated here affected both the strength of the connections (cell color) as well as the spatial pattern of island connections (many more blank cells denoting severed connections), especially at longer PLDs. At high levels of mortality, only those islands that were large larval sources or that were close together had any measureable connectivity. This highlights the importance of better information on larval mortality and possible shifts in mortality due to climate change, particularly for taxa with long PLDs.

Our results indicate a high but variable degree of interisland connectivity in the Samoan Archipelago and surrounding region under present climate conditions. There is substantial larval retention at most locations, but also considerable larval export and some degree of dependency of any individual reef on outside sources even at the shortest PLDs considered. The overall picture is of an inter-connected system in which no single location operates in complete isolation. Although some locations are isolated in the sense that they are not important sources for other reefs, these same locations are in general dependent on larval arrival from external sources (e.g. Swains Is.). Conversely, some sites that are not particularly common destinations can be significant sources to other reefs (e.g. Rose Atoll).

Current flow, and consequently larval transport, is primarily westward along the Samoan Archipelago via the SEC. In general, larvae produced at any given location in the Samoan Archipelago tend to seed their natal reefs at relatively shorter PLDs and their island neighbors to the west at longer PLDs. An overall effect of this directional tendency is that the islands of American Samoa export considerable larval production to Samoa especially for organisms with shorter to moderate PLDs of 10 to 30 d. That would be the extent of the connectivity pattern, and probably is for much of the year, were it not for the seasonally strong SECC. The north coasts of Samoa are far enough west and north that many larvae produced there are entrained in the east-flowing SECC and can ultimately settle along the islands of American Samoa via the feedback loops connecting the SECC with the SEC at ~165 to 170° W longitude. These currents are often well developed throughout the PLDs of organisms spawned in late October or November as simulated here. These feedback currents make Samoa an important source of larvae

for American Samoa, especially for organisms with intermediate to longer PLDs of 30 to 100 d. The connections established by this larval conveyor belt, although based on organisms with different PLDs (short PLD for transport from American Samoa to Samoa, longer PLDs for transport from Samoa to American Samoa), demonstrate the potential benefits of coordinated management of marine resources and conservation planning between Samoa and American Samoa (Johannes 2002, Oram 2008, McCook et al. 2009, ONMS 2012). The need for archipelago-scale management is heightened in that the orientation of the dominant currents and the long distances downstream from any source (e.g. Cook Islands) of larvae suggest that much of the Samoan Archipelago overall is largely dependent on internal sources of larvae.

The patterns of connectivity documented here have important implications for the resilience of reef ecosystems to disturbance events, design of MPA networks, and management of sustainable fisheries. Sufficient larval sources must be protected and spaced appropriately such that interdependent islands can successfully repopulate between local disturbance events and in the face of managed use such as fisheries extraction (Shanks et al. 2003, Jones et al. 2007, Gaines et al. 2010). Sites such as Swains Is. and Rose Atoll are far from any large larval sources and thus may be among the slowest to recover following a disturbance due to a lack of recruits. One reason these 2 locations have a biogeographically distinct community structure relative to the rest of the archipelago (Tribollet et al. 2010, Williams et al. 2010) may be a preponderance of either species with short or no pelagic dispersal, or species with very long PLDs that are capable of making the trip from distant sources. Given their probable slower recovery potential following disturbance and biogeographic uniqueness/isolation, these sites may be worthy of consideration for special protection status (ONMS 2012). In contrast to the isolation of Rose Atoll and Swains Is., Samoan islands are an important source of larvae for themselves and the entire region. Recovery from localized disturbance elsewhere in the archipelago may depend on larvae from Upolu and Savai'i, which make them important to consider when devising a resilient regional MPA network. Existing MPAs on these islands are quite small and have a wide range of regulations and effectiveness (Johannes 2002, Kendall & Poti 2011). Were these 2 islands dramatically disturbed (e.g. crown-of-thorns seastar infestation and overfishing have occurred), recovery may be slow due to their

high reliance on self-seeding and may depend primarily on the relatively more modest larval sources from American Samoa.

In the last 3 decades alone, ocean surface temperature has already increased by 1.0°C in the region of the Samoan Archipelago (Folland et al. 2003, Kendall & Poti 2011). Ongoing increases in temperature and decreases in pH are inevitable for the near future (IPCC 2007). Our results indicate that management actions such as fisheries quotas and optimum MPA network design may change for some islands in the region between now and future ocean conditions due to the influence of warmer water temperature on larval life history. Our model results demonstrate that shifting PLDs to shorter duration due to climate change can reduce interisland connectivity (as suggested by O'Connor et al. 2007 and Munday et al. 2009b). With few exceptions, islands will become increasingly more reliant on self-seeding as the ocean warms. The magnitude of the shift will vary by taxa, occur quite gradually, and fall between the particular PLD intervals examined here. The magnitude of this effect may at first seem small (1% greater reliance on self-seeding for every 2.3 d that PLD is shortened), but could have a substantial impact considering that PLDs are predicted to be shortened by several days with climate change, and that yearly increases in the proportion of self-seeding will have a cumulative, long-term effect on population connectivity. Compounding this, global warming may weaken Pacific currents including the SEC (Luo & Rothstein 2011), although the magnitude and detailed patterns remain speculative. Slower currents will likely mean even less transport for larvae, further reductions in connectivity among islands, and enhanced self-recruitment at levels beyond those predicted here based on shorter PLD alone. The combined effects of these factors will likely force managers to shift their expectations of recruitment strength or connectivity among network locations planned under today's climate conditions. Where possible, MPAs may need to be closer together in the ocean of the future to maintain connections among island populations that are present today. Many islands may still be well connected, just not for the same suite of species that are connected today. Those species with presently longer PLDs may settle in greater numbers at shorter transport distances and constrain scales of population dynamics. Some islands, already somewhat independent as sources or destinations, simply lack island neighbors at which to place MPAs or manage source populations and will become increasingly isolated. Some existing connec-

tions may be broken, such as the present-day long PLD transport from Samoa to American Samoa. There are no islands along this route that could be added to a future network to preserve this link.

A shift toward shorter PLDs had a surprisingly negligible effect on the strength of an island's role as a source or a destination. Due to a shift in climate, we expected that islands playing a source role at one PLD may change to primarily a destination role at another, but this was not the case in our simulations. Source and destination roles in our study region may be robust to managers' expectations despite climate change.

There are several key caveats to interpretation of these results. It is important to recognize that our findings are the direct result of the various levels of mortality rate, buffer size, and PLD examined. Although selected based on current literature, results would obviously change had a different range of life history variables been used. Rather than focusing on individual numbers in our results, the value of our approach is in comparing relative values and trends that emerge among the range of life history parameters that were investigated. Also important to note, some combinations of life history traits may only rarely occur but are useful for understanding extreme events. Unusual conditions may result in recruitment failure (e.g. anomalously high larval mortality rates due to extreme high water temperatures), or at the other end of the spectrum, a recruitment spike (e.g. very lowest mortality rate due to highly favorable conditions such as a plankton bloom that enhanced survivorship). In such cases, there is high uncertainty in precision of the predictions and results are best interpreted in a relative context. For example, we tracked >800 000 virtual larvae each year; however, real larval output of these reefs is orders of magnitude higher. Our results show several cases in which no virtual larvae made a connection, but in a real world spawning event involving many more larvae, some may have actually made it. For this reason, 0 values in our simulations should not be viewed as impossible connections but instead thought of as relatively less probable.

Fish and corals do not spawn at random coastal positions as modeled here. Many fish species perform behaviors conducive to broadcast spawning. Some move to areas where currents sweep eggs and larvae rapidly away from coasts, and many exhibit a vertical 'spawning rush' away from reefs toward the surface. For example, mature surgeon fish in American Samoa are most abundant on points and headlands where strong currents are found (Ochavillo et

al. 2011), and spawning can often be observed in reef channels where water flows in a seaward direction as it drains the reef flat (Craig 1998). These behaviors may promote offshore transport; however, such localized currents are not resolved at HYCOM's 9 km scale, are outside the scope of this study, and require using models with greater spatial resolution.

Also of note, we focused on cumulative connectivity over a recent and representative 5 yr period. However, if current patterns were to shift due to climate change or even if a different time of year is simulated such as when the strongly seasonal SECC is not active (e.g. spawning during June or July), connectivity patterns may differ from those reported here.

Some priorities for future work should include measuring connectivity over smaller increments in mortality to better understand its effects on connectivity, incorporating demographics and meta-population concepts, modeling recruitment-limited species by propagating the effects of connectivity through successive model years, studying how climate change may affect larval mortality and sensory abilities of various taxa, understanding the relative contribution of finer scale larval-retention mechanisms than was possible here, and quantifying connectivity of a variety of taxa in field studies through mark/recapture, tracer analysis, and genetic/parentage studies (Almany et al. 2007, Botsford et al. 2009, Jones et al. 2009, Planes et al. 2009).

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