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Abstract

Biophysical Lagrangian particle tracking models used to predict larval transport and dispersal are potentially sensitive to input parameters. Here we test the effects of four common input parameters (release interval, number of particles, diffusion, and release depth) for a 2D particle tracking model in the North Central Pacific Ocean. We evaluated the effects on modeled larval transport (particle movement) and dispersal (import) into the Hawaiian Archipelago from eight different regions for a shallow reef organism. Model results were sensitive to all input parameters to varying degrees across the planktonic larval duration/settlement windows and output metrics (transport vs. dispersal) tested. Variation in larval transport pathways 180 days after release was only evident when evaluating depth of release. In contrast, larval transport at 30 days post release did not vary when testing depth of release. Larval dispersal was not different for shorter settlement windows (30 days) regardless of the parameter tested. Occasional connections between distant archipelagos (e.g., Kiritimati, Okinawa, Wake) only occurred when larval duration was at its maximum (180 days), but these long-distance connections were also variable with depth of release. Out of the four parameters tested, changes in release depth resulted in the most significant differences for larval transport and had inconsistent connections for larval dispersal. These outcomes emphasize the importance of choosing a depth layer in future modeling studies. Because factors that affect larval depth distribution, such as spawning depth, buoyancy changes, and swimming behavior, are typically unknown for many taxa, future research should focus on field sampling to determine these *in situ* behaviors for better parameterization of models.

Introduction

Dispersal capabilities of marine organisms are a key factor determining connectivity among populations [1,2]. For many demersal or sessile marine organisms, the majority of dispersal occurs during a pelagic embryonic and larval phase that can last from hours to days to months, followed by a comparatively sedentary adult phase [3–6]. The degree to which local populations are connected by dispersal has important implications for management including stock assessment, biodiversity conservation, and the design of networks of protected areas [7–11]. For these species, larval supply plays an important role in determining the structure and dynamics of idealized marine metapopulations in which local recruitment is supplemented by significant larval supply from other places [12–15]. However, measuring larval dispersal in the field directly (e.g., observations, mark-and-recapture) [16,17] or indirectly (e.g., chemical or genetic tags, parentage analyses) [18–20] presents many challenges and is often constrained by time and resources [21].

Biophysical models are a common method that avoids the constraints inherent to direct observation of larval dispersal. Biophysical approaches such as Lagrangian particle tracking models use hydrodynamic model output and biological parameters to predict larval transport and dispersal and have become an important tool for interdisciplinary efforts to estimate larval transport and connectivity [6,14,22,23]. One of the benefits of particle tracking models is that their parameters can be modified to best fit any species of interest.

However, as with all modeling efforts, the applicability of model results to real-world observations and processes depends on the accuracy of model inputs [24]. First, there is considerable uncertainty in biological and physical parameterization. Some uncertainty stems from stochasticity of natural processes [25] but much comes from a lack of information about life history traits for species and their interactions with environmental conditions (e.g., laboratory determined planktonic larval duration, PLD, versus realized PLD in the field; [24–27]. Additionally, there is often a mismatch in the scale of biological (small to large scale; μm to km) and physical oceanographic (large scale; m to km) data, especially for large domains [24,28–30].

Sensitivity analyses are frequently used to manage the challenges of parameterizing particle tracking models by testing the influence of input parameters on model output. These analyses allow assessment of the stability of output to adjustments in input parameters, with the goal of increasing confidence in the model or highlighting model weaknesses. Sensitivity tests also determine the saturated state (i.e., minimum computational power needed so that the results no longer change) of each unique model. For example, sensitivity analyses revealed that physical variables (e.g., model resolution, temporal variability in circulation) strongly affected model output for large

regions of the Atlantic Ocean [29,31]. In other studies, biological parameters (e.g., spawning seasonality, larval mortality) largely determined predicted dispersal patterns [32–34]. These outcomes from previous sensitivity studies highlight the complexity of assessing models parameterized with different physical and biological data, and the importance of parameterization through sensitivity analyses.

Lagrangian particle tracking models have required input parameters that can be assessed with sensitivity analysis. Four of these required parameters include: 1) particle release interval (the time between simulated reproductive events); 2) number of particles, equivalent to number of larvae included in the simulation; 3) scale of horizontal diffusivity, added random 2D motion of particles, and 4) particle release depth. By varying the release interval and number of particles released, sensitivity analyses can identify a functional balance between computational power and a saturated model. Too few particles (and too few release intervals) may not capture all potential pathways, while an excess of particles (and release intervals) is unnecessary and leads to memory storage and RAM issues. Ideally, *in situ* reproductive output can be used to parameterize release interval and numbers of particles. However, reproductive effort is difficult to approximate because knowledge of the number of adults, fecundity, and spawning periodicity in the study region are all needed to calculate reproductive output. The third parameter, diffusivity, is a sub-grid scale stochastic process that adds general randomness to particle movement which can represent unaccounted movement that is missed due to low resolution oceanographic data. Despite diffusion's likely important role in particle movement, diffusion is not well characterized, and published inputs for diffusion encompass a wide range of values (0.01-1000 m^2/s) [33, e.g., 35,36] that are either uniform or vary with time and space [37–39]. Lastly, release/dispersal depth are often similarly unknown and are typically chosen based on limited or no information, or inferred from related species. Although previous studies have investigated the sensitivity of Langrangian models to variation in these four parameters [33,38–45] [but see 46] [33,38–45]), most sensitivity analyses have been performed in small geographic regions. These smaller regions have oceanographic data at finer spatial and temporal resolutions, which captures finer-scale processes such as in Torres Strait (650 m and 30 minutes) [44], Southern California Bight (1 km and 6 hours) [41], and the Gulf of Maine (500 m and 1 hour) [40]. A large domain and coarse-grained circulation models would likely lead to differences in model sensitivities [29,47,48].

The Hawaiian Archipelago is one of the most isolated island chains in the world. There are two main hypotheses for the pathways marine species take to disperse to Hawai‘i [49,50]. First, species distributions, transport models, and population genetic analyses suggest a likely pathway between Johnston Atoll and the Hawaiian Archipelago [51–59] and that Johnston Atoll might in turn be a gateway for the central Pacific (e.g., Kiritimati

in the Line Islands) into Hawai‘i through the North Equatorial current and the Hawaiian Lee Countercurrent [49,60]. Another proposed pathway to Hawai‘i is Okinawa via the Kuroshio Current and North Pacific Current [50,61–63]. Particle tracking models can be used to investigate these more widely recognized larval dispersal pathways for marine species (Johnston Atoll, Kiritimati, and Okinawa) and other understudied potential stepping stones (Wake, Guam, Saipan, Majuro, Rongelap Atoll, and Pohnpei) into the Hawaiian Archipelago.

In this study, we investigated the impacts of variation (i.e., sensitivity) in four important and necessary input variables (release interval, number of particles, horizontal diffusivity and release depth) on the output of a 2D particle tracking simulation within the North Central Pacific Ocean. Our study encompasses a spatial domain that is many magnitudes greater than most previous sensitivity tests [but see 46] and has a coarser spatial and temporal circulation model. Our analysis focused on assessing the influence of these variables on simulated larval transport (Table 1) patterns (particle trajectory) and the extent of dispersal (import, Table 1) to the Hawaiian Archipelago, in the context of a shallow reef-dwelling organism with weak swimming planktotrophic larvae.

Table 1. Glossary of often used terms.

Term	**Definitions used in this study**
Settlement window	The window of time that modeled particles can begin to settle. For our study all settlement begins 15 days after release and can continue until either 30, 60, 90, or 180 days after release.
Larval Transport	The 2D oceanographic path of particles.
Particle Density Distribution, PDD	The distribution of particles at PLD (30, 60, 90, or 180 days) across our study domain divided into 40 x 40 km grid cells.
Fraction of Unexplained Variance, FUV	A measurement of dissimilarity. FUV = 1 - r2, where r is the correlation coefficient.
Larval Dispersal	The movement of particles from their origin to their settlement site.
Larval Import	Particles that were transported within 10 km of the NWHI, MHI, or Johnston Atoll after a pre-competency period of 15 days but by the maximum PLD (30, 60, 90, or 180 days).
Simulation	A run of our model testing each parameter.

Methods

Study domain

The spatial domain of this study encompassed the North Central Pacific (0º - 50ºN, 120ºE - 120ºW). Within this region, our model included the Hawaiian Archipelago, Johnston Atoll, Wake Island, Guam, Saipan, Majuro Atoll, Rongelap Atoll, Pohnpei, Kiritimati, and Okinawa (Figure 1). We focused on these islands because previous research identified these locations as potential sources of dispersal into the Hawaiian Archipelago and Johnston Atoll [49–51,53,55,57,59–63]. In our model, the aforementioned sites were release sites, while coral reef habitat in the Hawaiian Archipelago and Johnston Atoll were our settlement sites [habitat data from 56].

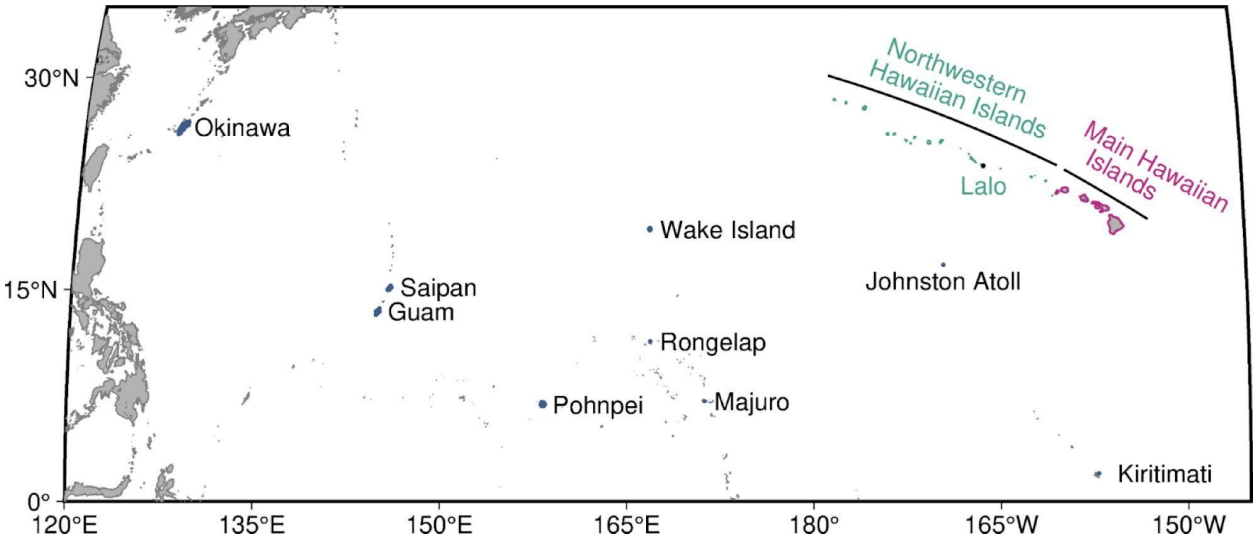

Figure 1. Map of release and settlement sites. We released particles from evenly spaced nearshore locations from each island with variable numbers of release sites per island depending on its size. We released particles from Johnston Atoll, Lalo (i.e., French Frigate Shoals), Wake Island, Guam, Saipan, Majuro Atoll, Rongelap Atoll, Pohnpei, Kiritimati, and Okinawa. Settlement sites included islands and banks in the Northwestern Hawaiian Islands and the main Hawaiian Islands, as well as Johnston Atoll.

Biophysical model

We modeled larval transport and dispersal using a Lagrangian particle tracking framework, Parcels (Probably A Really Computationally Efficient Lagrangian Simulator) [64,65] coupled with HYCOM (HYbrid Coordinate Ocean Model; hycom.org), an open-access circulation model. We used model output from January 1, 2013, until June 30, 2014, at the highest available resolution (0.08°) using daily HYCOM reanalysis GOFS 3.1[66]. HYCOM vertical resolution allowed us to test multiple individual depth profiles and create averaged current velocities from HYCOM using pyFerret (version 7.64) (https://github.com/NOAA-PMEL/PyFerret/). HYCOM has 40 z-coordinate layers with

thinner upper layers. In this study, we only used the top 50 m comprising 15 layers and we limited particle release to a neutral ENSO year, 2013. By focusing on only one year, we were able to run 18 simulations testing 72 combinations of varying parameters and include a complete range of intra-annual variability (seasonal, lunar, etc.). Since this study is a sensitivity analysis and not an ecological study, running the model for ≤ 1 `year` is common [e.g., 32,40,42,44,48]. Interannual variability is not a concern when testing the sensitivity of the Lagrangian model, but will be one of several important sources of variability evaluated in larger studies that could follow this analysis. HYCOM model output was not available for a total of 72 days dispersed throughout the year (max 3 consecutive days), but Parcels linearly interpolates currents over missing days [65]. Here we varied values of our test parameters (i.e., number of particles, release interval, diffusivity, and release depth) in our simulation runs to test the sensitivity of the particle tracking model and how this changed with PLD/settlement windows.

Simulations

For all sensitivity analysis runs, particles were released from nearshore locations at Lalo (Northwestern Hawaiian Islands, NWHI), Johnston Atoll, Wake Island, Guam, Saipan, Majuro, Rongelap Atoll, Pohnpei, Kiritimati, and Okinawa (Figure 1, S1). All particles were released daily (except when testing release intervals) at 5 m depth (except when testing depth) from each site over the span of a year (2013) and tracked for 180 days after release. All particles were treated as passive meaning horizontal and vertical swimming behaviors were not incorporated into the model. To prevent particles from getting stuck on land (signified by 0 m/s velocity fields in Parcels), we implemented the free-slip boundary condition available in Parcels for all simulations [64,65]. Parameters tested in sensitivity runs include: release intervals (daily, every 4 days, every 7 days), number of particles released from each site at each interval (100, 250, 500, 1000), horizontal eddy diffusivity (0 m^2/s, 10 m^2/s, 50 m^2/s), and depth strata of currents fields used in the particle tracking model (hereafter release depth) (surface, 5 m, 10 m, 20 m, 30 m, 50 m, 0-25 m averaged, and 0-50 m averaged) (Table 2). These depths were chosen based on the depth ranges of shallow reef dwelling organisms [67,68]. Diffusivity values were chosen based on a previous study done in the region [69]. The model timestep was set to 1 hour and particle locations were saved daily.

Table 2. Parameters used in simulations. Each row represents a different sensitivity test and describes the parameters used in each set of simulations. The parameters being tested are italicized. The fourth column is the number of particles released at one time point per release location. The sixth column is the range of total number of particles released across the entire simulation run.

Parameter Tested	**Release Depth (m)**	**Horizontal Diffusivity (m^2/s)**	**Number of Particles**	**Release Interval**	**Total Number of Particles**
Release Interval	5	0	1	*Daily, 4-days, 7-days*	2,173 - 15,006
Number of Particles	5	10	*100, 250, 500, 1000*	Daily	1,500,600 - 15,006,000
Horizontal Diffusivity	5	*0, 10, 50*	1*, 100, 100	Daily	15,006 - 1,500,600
Release Depth	*0, 5, 10, 20, 30, 50, 0-25, 0-50*	0	1	Daily	15,006

*Only 1 particle is released since diffusivity is set to 0 m^2/s.

Sensitivity analyses can be evaluated at three different perspectives: larval transport (oceanographic pathways), larval dispersal (movement of settled particles), and population connectivity (recruitment and reproduction) [5]. Since connectivity requires knowledge of post-larval survival and reproduction, this metric is difficult to calculate accurately and we did not consider connectivity in this study. Instead, we focused on larval transport [41,47] and larval dispersal (Table 1).

Statistical analyses

Larval transport

To estimate larval transport, a 2D particle density distribution (PDD) (Table 1) was calculated for each simulation run for each PLD (i.e., 30, 60, 90, 180 days). PLDs were chosen to allow for the potential of long-distance dispersal. PDDs were calculated across the entire study domain divided into grid cells ~40 km x 40 km. This size is based on the shortest inter-island distance in the main Hawaiian Islands (MHI). It provides enough resolution for island-level differences. In order to quantify the differences between PDDs, we calculated the fraction of unexplained variance (FUV) from the correlation coefficient (r) using the equation:

$$FUV = 1 - r^2 \quad (1)$$

PDDs allow for direct grid cell comparisons between two simulations in order to calculate *r.* Higher values of FUV indicated PDDs were less correlated and had different spatial distributions. We used a cutoff of 0.05, representing the amount of dissimilarity (5%) that was acceptable [see 41,44].

We performed all calculations and created all tables in R (version 4.1.0) [70] using the packages *ncdf4* (version 1.17) [71], *dplyr* (version 1.0.8) [72], and *MASS* (version 7.3-54) [73].

Larval dispersal to the Hawaiian Archipelago and Johnston Atoll

Since PDDs do not capture larval connections, we also examined larval dispersal as estimated by larval import to three regions: NWHI, the main Hawaiian Islands (MHI), and Johnston Atoll (Table 1). Differences in larval sources to the Hawaiian Archipelago (NWHI and MHI) and Johnston Atoll were calculated among simulation runs and varying settlement windows. Settlement can begin after a pre-competency period (the period of time before settlement can occur) of 15 days [74,75], and particles can settle if they pass near land before a PLD of 30, 60, 90, and 180 days. The Hawaiian Archipelago and Johnston Atoll were chosen as part of a larger project investigating dispersal from other islands and archipelagos in the North Central Pacific Ocean into Hawai‘i and Johnston Atoll. We defined an import or connection as any successful larval transport from an island in the study domain to NWHI, MHI, or Johnston Atoll. Successful larval import occurred if a particle’s closest distance to coral reef habitat on islands in the Hawaiian Archipelago and Johnston Atoll [habitat data from 56] was ≤ 10 km during the settlement window. A large radius was chosen because of the coarse resolution of the circulation model (~9 km). Proportional larval import estimates to each region were calculated from successful larval import to a region from one source island divided by

the total larval import to that region from any source island. There were a total of 30 potential connections between source islands and regions settled.

We determined larval connections in Python (version 3.9.5) [76] using *pandas* (version 1.3.3) [77], *numpy* (version 1.21.2) [78], *netCDF4* (version 1.5.7) [79], and *scikit-learn* (version 1.1.1) [80]. We then determined the differences and created tables and heatmap in R (version 4.1.0) [70] using the packages *dplyr* (version 1.0.8) [72], *ggplot2* (version 3.3.6) [81], *viridis* (version 0.6.2) [82], and *tidyr* (version 1.1.3) [83].

Results

Release interval

Increasing release intervals from daily to every 4 days did not significantly alter PDDs for any PLD (FUV < 0.05; Table 3A). However, increasing from every 4 days to every 7 days did significantly alter PDDs for the PLDs up to 90 days (Table 3A).

Table 3. Fraction of unexplained variance (FUV) results from comparing particle density distributions (PDDs) for sensitivity tests of (A) release intervals, (B) number of particles released per release event, (C) horizontal diffusivity, and (D) release depth. See Table 2 for parameterization of remaining variables. Columns 1 and 2 indicate the PDDs for the manipulated parameter and the remaining columns are the FUV values at each PLD. For A and B, PDD 1 is the more saturated but time-intensive simulation. For D, all release depths are compared to 5 m as all other simulations testing other parameters used the 5 m release depth layer. PDDs were calculated at ~40 km resolution. The FUV is italicized if over the threshold of 0.05 (> 5% difference).

(A)

PDD 1	PDD 2	Day 30	Day 60	Day 90	Day 180
Daily	4-day	0.039	0.034	0.03	0.022
Daily	7-day	*0.079*	*0.064*	*0.054*	0.044

(B)

PDD 1	PDD 2	Day 30	Day 60	Day 90	Day 180
1000	500	0.0072	0.0073	0.0069	0.0022
1000	250	0.028	0.028	0.026	0.0085
1000	100	*0.075*	*0.073*	*0.067*	0.021

(C)

PDD 1	PDD 2	Day 30	Day 60	Day 90	Day 180
10 m^2/s	50 m^2/s	0.005	0.036	*0.072*	0.038
0 m^2/s	10 m^2/s	*0.273*	*0.207*	*0.162*	*0.077*
0 m^2/s	50 m^2/s	*0.236*	*0.136*	*0.094*	*0.125*

(D)

PDD 1	PDD 2	Day 30	Day 60	Day 90	Day 180
5 m	0 m	0.024	0.048	*0.064*	*0.076*
5 m	10 m	0.007	0.015	0.027	*0.07*
5 m	20 m	0.038	*0.089*	*0.125*	*0.194*
5 m	30 m	*0.062*	*0.17*	*0.202*	*0.313*
5 m	50 m	*0.091*	*0.221*	*0.259*	*0.384*
5 m	0-25 m	0.011	0.03	0.047	*0.089*
5 m	0-50 m	0.038	*0.104*	*0.152*	*0.266*

There were no larval import estimate differences among any release intervals for settlement windows of 15-30, 15-60, and 15-90 days (Figure 2A, Table S1). At a settlement window of 15-180 days, daily release interval had 1 more predicted larval connection to the NWHI than the 4-day and 7-day release intervals (Figure 2A, Table S1).

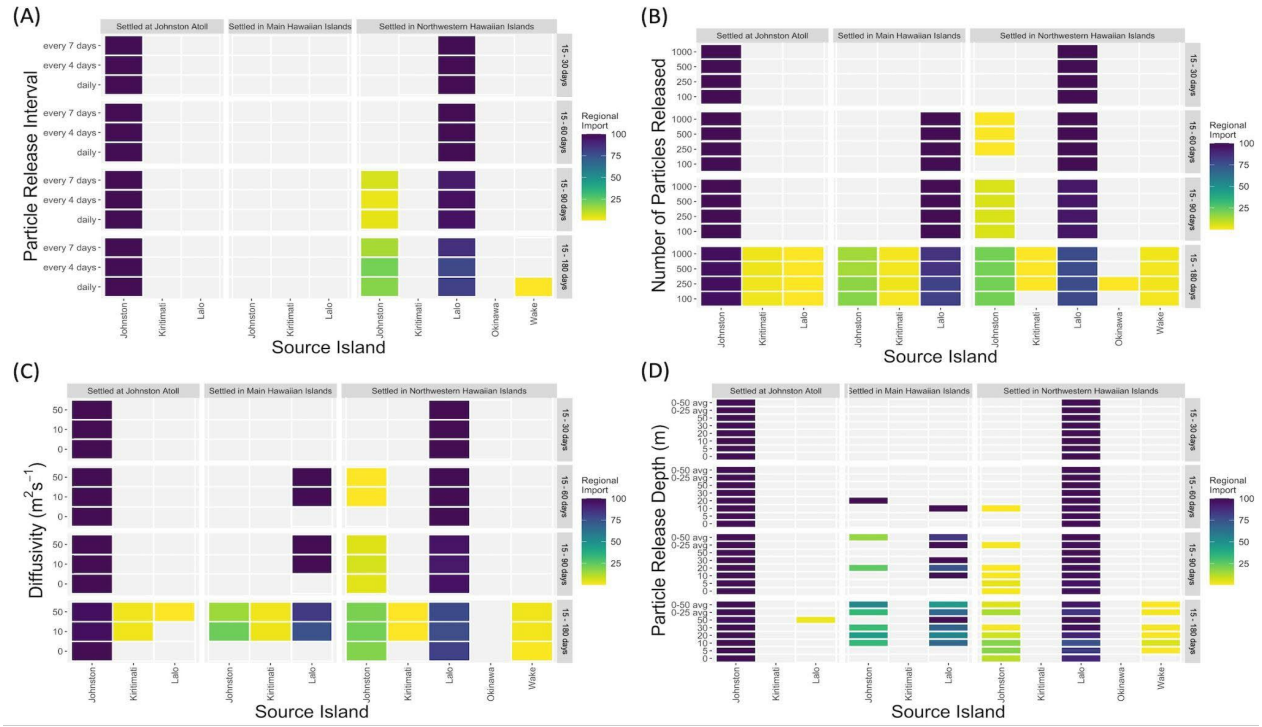

Figure 2. Estimated larval import across sensitivity tests of (A) release intervals, (B) number of particles released per release event, (C) horizontal diffusivity, and (D) release depth. Predicted larval import is grouped by settlement window (15-30 days, 15-60 days, 15-90 days, and 15-180 days) vertically and by region (Johnston Atoll, MHI, NWHI) horizontally. Predicted regional larval import is a percentage defined by the number of particles imported to a region from a source island divided by the total number of particles imported to that region from all source islands. White indicates no connection.

Number of particles

PDDs indicated that the model reached saturation at 250 particles released for PLDs <180 days (Table 3B), with a horizontal diffusivity of 10 m^2/s. For long PLDs (180 days), all of the PDDs were statistically indistinguishable from the most complex model (1000 particles released) (Table 3B).

Larval import estimates also reached saturation at 250 particles released. All possible predicted connections observed across all sensitivity simulations were observed when ≥ 250 particles were released daily per location with a diffusivity of 10 m^2/s at a depth of 5m (Figure 3).

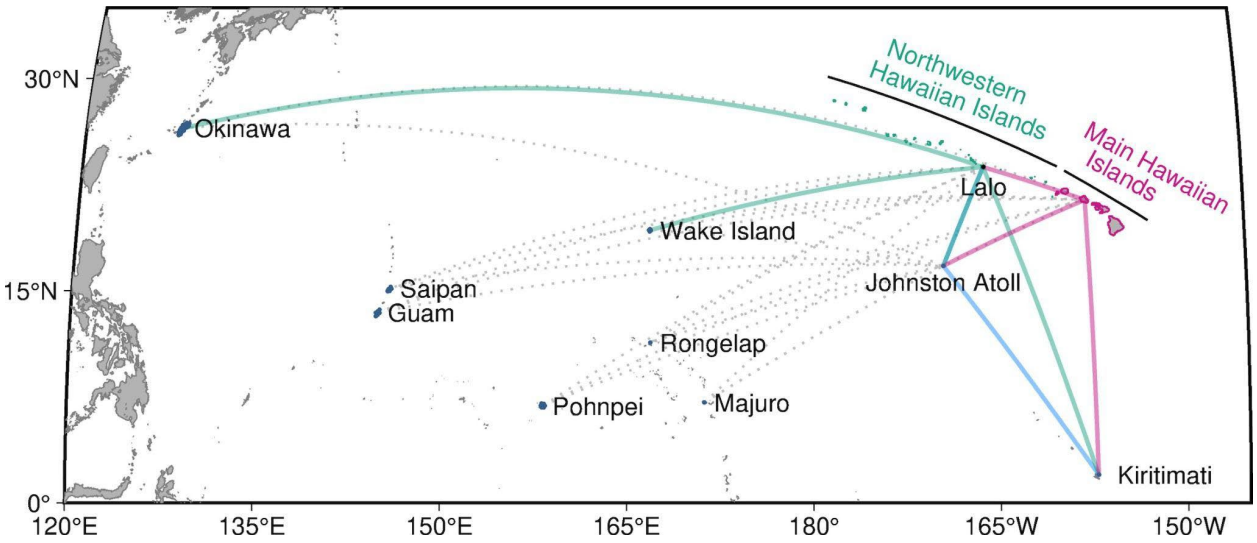

Figure 3. Estimated larval dispersal map. Map of all dispersal pathways into the MHI (pink), NWHI (green), and Johnston Atoll (blue) across all simulations and settlement windows. Solid lines are pathways that were predicted in our model. Dashed gray lines are pathways that did not occur in the model but were tested for. All predicted dispersal routes into the Hawaiian Archipelago and Johnston Atoll across simulations were observed in a simulation with 250 particles released daily with a diffusivity of 10 m^2/s and a settlement window of 15-180 days. Lines entering NWHI and MHI at Lalo and O‘ahu, respectively, represent input into their particular regions.

Larval import estimates did not change among differing numbers of particles released, except for long settlement windows (15-180 days) which had 1 more consistent predicted source (Kiritimati) into the NWHI with ≥ 250 particles (Figure 2B, Table S2). Additionally, there was a single source (Okinawa) to the NWHI that was only seen in the 250 particles released (Figure 2B). As this connection was so rare and unexpected, we repeated the 250 particles released simulation one more time to see if this connection persisted. However, there was no successful predicted settlement from Okinawa in this repeated run.

Horizontal diffusivity

Increasing horizontal diffusion from 0 m^2/s to 10 m^2/s and 50 m^2/s significantly increased the FUV for all PLDs (FUV > 0.05; Table 3C). There were no significant differences (FUV < 0.05) between 10 m^2/s and 50 m^2/s except at a PLD of 90 days (Table 3C).

At a settlement window of 15-30 days, larval import estimates to the MHI, the NWHI, and Johnston Atoll did not differ between diffusivity coefficients (Figure 2C, Table S3). As the settlement window increased to 180 days, 10 m^2/s and 50 m^2/s had 2 more predicted larval sources to Johnston Atoll than 0 m^2/s. They also had 3 more predicted larval connections to the MHI compared to the simulation without diffusivity. The 50 m^2/s run had 1 more predicted larval source to the NWHI than the simulation with 10 m^2/s diffusivity (Figure 2C, Table S3). In repeated runs of 10 and 50 m^2/s, there was variation in the presence of rare connections (Table S3).

Release depth

At a PLD of 30 days, PDDs of simulations testing the release depth layers of 0 m to 20 m, 0-20 m averaged, and 0-50 m averaged were similar to the 5 m layer (Table 3D). All combinations of PDDs were significantly different by day 180, except 20 m and 0-50 m averaged (Table S5).

Estimated larval import was the same across release depths during short settlement windows (15-30 days) but became variable at longer settlement windows (Figure 2D, Table S4). While predicted connections increased with increasing the settlement window, estimated larval import varied without a clear pattern across release depth (Figure 2D, Table S4). Increasing the number of particles released to 250 with a diffusivity of 10 m^2/s removed some variability in larval import connections across depth but not all (Figure S2).

Discussion

Our analysis shows that large-scale Lagrangian particle tracking models can be sensitive to all four parameters we considered. The extent of model sensitivity, however, changed with both the output metric tested (larval transport or dispersal) and PLD/settlement window. Short settlement windows (15-30 days) had consistent larval import estimates for all simulations but no predicted successful imports into the Hawaiian Archipelago or Johnston Atoll. The longest PLD in our model (180 days) had relatively similar predicted larval transport compared to shorter PLDs, except in simulations testing release depth (Table 3D). Larval transport sensitivity in the model may have decreased with longer PLDs because at longer PLDs, oceanographic features like mesoscale eddies and fronts can be the dominant forces affecting transport estimates [see 41,84]. The strength and direction of these oceanographic features likely differ with release depth resulting in a greater sensitivity of larval transport estimates across release depths.

Larval import estimates across release depth simulations for settlement windows of ≥ 15-60 days were very inconsistent compared to other parameters. There was no release depth (including averaged current layers) that consistently had more or fewer predicted import events into the Hawaiian Archipelago or Johnston Atoll across 15-60-, 15-90-, and 15–180-day settlement windows. Particles in the surface layers may have different transport patterns from the other layers since flow in the surface layers is influenced more heavily by winds [85,86]. However, increasing the number of particles released and including horizontal diffusivity mitigated some of the uncertainties associated with release depth, especially for shallow depths (5-10m) (Figure S2). Unfortunately, a knowledge gap exists for spawning depths for many species and whether larvae can change depth through buoyancy changes or swimming behavior. Because the model was very sensitive to release depth for both larval transport and dispersal, our results suggest that understanding the depth distribution of larval production is important for minimizing uncertainty in larval transport and dispersal output.

For simulations testing diffusivity, release interval, and number of particles, larval import estimates appeared more consistent at shorter settlement windows (15-30 days) compared to longer settlement windows (15-90+ days). Longer settlement windows likely provided more opportunity for rare larval connections. Larvae were released from archipelagos very distant from the Hawaiian Archipelago and Johnston Atoll. When the upper range of the settlement window was 30 days, larvae never reached the Hawaiian Archipelago or Johnston from other archipelagos. The only larval connection that occurred across all simulations with a settlement window of 15-30 days was self-seeding of Johnston Atoll and the NWHI. However, with a settlement window of 15-60+

days, larval connections from other archipelagos emerged allowing us to evaluate the model sensitivity using larval import metrics. When testing sensitivity of each parameter, differences in larval import were driven by rare connections.

Diffusivity is an important parameter to encapsulate random and sub-grid scale processes (i.e., processes that cannot be adequately resolved within the numerical simulation due to scaling and/or uncertainties) but is difficult to quantify. Additionally, model diffusivity randomly displaces particles relative to *in situ* eddy diffusivity which is unknown for the majority of model systems. Values in previous studies ranged from 0.01 m^2/s [33] to 250 m^2/s [36] and 1000 m^2/s [35]. Here we found that incorporating diffusivity led to substantial changes in larval transport, allowing for more connections whether it was set to 10 m^2/s or 50 m^2/s. Larval import was not sensitive to changes in diffusivity between 10 m^2/s and 50 m^2/s, so either value can likely be used without greatly changing larval import estimates. However, two rare connections were predicted when diffusivity was set to 50 m^2/s at 90 and 180 days. Since some rare connections were not predicted in all simulation runs (Table S3), increasing the number of particles released could help saturate the model and make the rare connections more consistent across repeated runs.

Frequency and quantity of particle release are important for identifying the balance between model saturation and reducing the need for computational resources. For our model, saturation was reached at 250 particles released at a daily interval. Within these parameters, much of the sensitivity is due to relatively rare connections with the Hawaiian Archipelago and Johnston Atoll. Although relatively rare connections may not create any demographic or ecological connectivity, they could be important for genetic connectivity [20,87,88] given that as few as 10 migrants per generation can create evolutionary connectivity between populations [89]. Therefore, depending on the goals of a connectivity study, any alteration in larval connections in model output could change the interpretation of results. However, releasing 250 particles daily is computationally expensive, especially when models are run across multiple years. If dominant trends are of interest, such as when studying ecological connectivity relevant for stock assessments in the Hawaiian Archipelago, our analyses suggest that a release interval of 4 days and 100 particles released per time point would be sufficient in this scenario. Overall, to optimize the parameterization of large-scale oceanographic models, our results suggest it is important to define what type of connectivity the model is trying to estimate and how the assumptions of that model impacts sensitivity testing.

Model caveats

In this study, we simplified our approach by treating larvae as passive particles in a 2D environment since Parcels cannot implement diffusivity in a 3D environment. By using a 2D model, we reduced computational requirements at the cost of testing for model

sensitivity to vertical movement and swimming behavior. In the field, larvae may experience buoyancy changes, movement with pycnocline changes, swimming behavior, or upwelling or downwelling currents that could change the depth at which larvae are transported [90–94]. The majority of shallow reef dwelling organisms are data poor so these changes including diel vertical migration and ontogenetic changes are unknown and therefore difficult to parameterize in models [24]. Although our model did not include vertical movement, our sensitivity analysis provides a baseline for modeling connectivity in the North Central Pacific Ocean because it describes some of the uncertainty inherent in Lagrangian particle tracking models of this large region.

While sensitivity testing is beneficial for assessing the effects of parameters on a model, the results of sensitivity testing are inevitably case-specific. Our study focused on the North Central Pacific, a large region for which low resolution HYCOM circulation models are available. Thus, the extent to which our results from the sensitivity analysis could be applied to other regions with different circulation models is limited. However, the North Central Pacific is a region of key interest for many species as it contains many isolated islands, including the Hawaiian Archipelago [62]. Previous studies using genetic analyses have investigated the nature of connectivity between the Hawaiian Archipelago and the rest of the North Central Pacific [58,88,95]. However, genetic estimates of connectivity do not necessarily represent contemporary exchange because signatures of past connectivity can remain for many generations after a barrier has formed [19,96–98]. Biophysical models that take advantage of contemporary circulation models are a useful tool for investigating present-day connectivity in the North Central Pacific.

Conclusion

Here we found that larval transport and import within our particle tracking model were sensitive to release interval, number of particles, diffusivity, and release depth each to varying degrees. Sensitivity differences depended on the input parameters, the output metric tested (transport vs dispersal), and PLD/settlement window.

The sensitivity analysis revealed the minimum computational power to saturate the model and estimate long-distance connections to the Hawaiian Archipelago and Johnston Atoll for 2013. The model demonstrated that the diffusivity constant and depth layers added a large amount of uncertainty to the model. Choosing the diffusivity constant and depth layers in future modeling therefore requires careful consideration. There is considerable concern given that the behavior and depth distribution of pelagic larvae in the field are not well understood for most taxa. In order to increase the accuracy of biophysical models, better *in situ* measurements are needed for both of these parameters. Until then, the results of this study suggest that these issues can be somewhat mitigated by testing across multiple depths and diffusivity values to understand the range of dispersal potential.

Data availability

Example code and tables are available on GitHub (https://github.com/taylorely/LAPS).

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Appendix

Supplemental Tables

Table S1. Region-level larval imports for release interval sensitivity test. We defined a source as any successful larva imported from an island in the study domain to regions of the Hawaiian Archipelago (main Hawaiian Islands: MHI, Northwest Hawaiian Islands: NWHI, Johnston Atoll). Successful larval imports occurred if a particle's closest distance to an island in each region of the Hawaiian Archipelago was ≤10km during the settlement window. The settlement window had a constant pre-competency period of 15 days and a maximum PLD of either 30, 60, 90, or 180 days. Maximum PLD is color coded in table. Sensitivity runs tested across parameters (release interval) of daily, every 4 days, and every 7 days. For each region, any successful larval import from a source island is listed under MHI, NWHI, or Johnston Atoll.

Parameter	Maximum PLD	MHI	NWHI	Johnston_Atoll
daily	30	None	Lalo	Johnston
every 4 days	30	None	Lalo	Johnston
every 7 days	30	None	Lalo	Johnston
daily	60	None	Lalo	Johnston
every 4 days	60	None	Lalo	Johnston
every 7 days	60	None	Lalo	Johnston
daily	90	None	Lalo,Johnston	Johnston
every 4 days	90	None	Lalo,Johnston	Johnston
every 7 days	90	None	Lalo,Johnston	Johnston
daily	180	None	Lalo,Johnston, Wake*	Johnston
every 4 days	180	None	Lalo,Johnston	Johnston
every 7 days	180	None	Lalo,Johnston	Johnston

* Indicates island of origin did not occur in run with 7 days release interval within the same PLD.

Table S2. Region-level larval imports for number of particles released per event sensitivity test. We defined a source as any successful larval import from an island in the study domain to regions of the Hawaiian Archipelago (main Hawaiian Islands: MHI, Northwest Hawaiian Islands: NWHI, and Johnston Atoll). Successful larval imports occurred if a particle's closest distance to an island in each region of the Hawaiian Archipelago was ≤10km during the settlement window. The settlement window had a constant pre-competency period of 15 days and a maximum PLD of either 30, 60, 90, or 180 days. Maximum PLD is color coded in table. Sensitivity runs tested across parameters (number of particles released per event) of 100, 250, repeat run of 250, 500, 750, and 1000. For each region, any successful larval import from a source island is listed under MHI, NWHI, or Johnston Atoll.

Parameter	Maximum PLD	Transported to MHI	Transported to NWHI	Transported to Johnston
100	30	None	Lalo	Johnston
250	30	None	Lalo	Johnston
250 repeat	30	None	Lalo	Johnston
500	30	None	Lalo	Johnston
750	30	None	Lalo	Johnston
1000	30	None	Lalo	Johnston
100	60	Lalo	Lalo	Johnston
250	60	Lalo	Lalo, Johnston*	Johnston
250 repeat	60	Lalo	Lalo, Johnston*	Johnston
500	60	Lalo	Lalo, Johnston*	Johnston
750	60	Lalo	Lalo, Johnston*	Johnston
1000	60	Lalo	Lalo, Johnston*	Johnston
100	90	Lalo	Lalo, Johnston	Johnston
250	90	Lalo	Lalo, Johnston	Johnston
250 repeat	90	Lalo	Lalo, Johnston	Johnston
500	90	Lalo	Lalo, Johnston	Johnston
750	90	Lalo	Lalo, Johnston	Johnston
1000	90	Lalo	Lalo, Johnston	Johnston
100	180	Lalo, Johnston, Kiritimati	Lalo, Johnston, Wake	Johnston, Lalo, Kiritimati
250	180	Lalo, Johnston, Kiritimati	Lalo, Johnston, Wake, Kiritimati*, Okinawa*	Johnston, Lalo, Kiritimati
250 repeat	180	Lalo, Johnston, Kiritimati	Lalo, Johnston, Wake, Kiritimati*	Johnston, Lalo, Kiritimati
500	180	Lalo, Johnston,	Lalo, Johnston, Wake,	Johnston, Lalo,

Parameter	Maximum PLD	Transported to MHI	Transported to NWHI	Transported to Johnston
		Kiritimati	Kiritimati*	Kiritimati
750	180	Lalo, Johnston, Kiritimati	Lalo, Johnston, Wake, Kiritimati*	Johnston, Lalo, Kiritimati
1000	180	Lalo, Johnston, Kiritimati	Lalo, Johnston, Wake, Kiritimati*	Johnston, Lalo, Kiritimati

* Indicates island of origin did not occur in run with 100 particles within the same PLD.

Table S3. Region-level larval imports for eddy diffusivity sensitivity test. We defined a source as any successful larval import from an island in the study domain to regions of the Hawaiian Archipelago (main Hawaiian Islands: MHI, Northwest Hawaiian Islands: NWHI, and Johnston Atoll). Successful larval exchange occurred if a particle's closest distance to an island in each region of the Hawaiian archipelago was ≤10km during the settlement window. The settlement window had a constant pre-competency period of 15 days and a maximum PLD of either 30, 60, 90, or 180 days. Maximum PLD is color coded in table. Sensitivity runs tested across parameters (eddy diffusivity) of 0 m^2/s, 10 m^2/s, 50 m^2/s, and 50 m^2/s repeat run. For each region, any successful larval import from a source island is listed under MHI, NWHI, or Johnston Atoll.

Parameter	Maximum PLD	Transported to MHI	Transported to NWHI	Transported to Johnston
0	30	None	Lalo	Johnston
10 Run 1	30	None	Lalo	Johnston
50 Run 1	30	None	Lalo	Johnston
10 Run 2	30	None	Lalo	Johnston
50 Run 2	30	None	Lalo	Johnston
10 Run 3	30	None	Lalo	Johnston
50 Run 3	30	None	Lalo	Johnston
0	60	None	Lalo	Johnston
10 Run 1	60	Lalo*	Lalo	Johnston
50 Run 1	60	Lalo*	Lalo, Johnston*	Johnston
10 Run 2	60	Lalo*	Lalo, Johnston*	Johnston
50 Run 2	60	Lalo*	Lalo, Johnston*	Johnston
10 Run 3	60	Lalo*	Lalo, Johnston*	Johnston
50 Run 3	60	Lalo*	Lalo, Johnston*	Johnston
0	90	None	Lalo, Johnston	Johnston
10 Run 1	90	Lalo*	Lalo, Johnston	Johnston
50 Run 1	90	Lalo*	Lalo, Johnston	Johnston
10 Run 2	90	Lalo*	Lalo, Johnston	Johnston
50 Run 2	90	Lalo*	Lalo, Johnston	Johnston
10 Run 3	90	Lalo*	Lalo, Johnston	Johnston
50 Run 3	90	Lalo*	Lalo, Johnston	Johnston
0	180	None	Lalo, Johnston, Wake	Johnston
10 Run 1	180	Lalo, Johnston, Kiritimati	Lalo, Johnston, Wake	Johnston, Kiritimati*, Lalo*

Parameter	Maximum PLD	Transported to MHI	Transported to NWHI	Transported to Johnston
50 Run 1	180	Lalo, Johnston, Kiritimati	Lalo, Johnston, Kiritimati*, Wake	Johnston, Kiritimati*, Lalo*
10 Run 2	180	Lalo, Johnston, Kiritimati	Lalo, Johnston, Kiritimati*, Wake	Johnston, Kiritimati*, Lalo*
50 Run 2	180	Lalo, Johnston, Kiritimati	Lalo, Johnston, Kiritimati*, Wake	Johnston, Kiritimati*, Lalo*
10 Run 3	180	Lalo, Johnston, Kiritimati	Lalo, Johnston, Wake	Johnston, Kiritimati*, Lalo*
50 Run 3	180	Lalo, Johnston, Kiritimati	Lalo, Johnston, Wake	Johnston, Kiritimati*, Lalo*

* Indicates island of origin did not occur in run with 0 m^2/s within the same PLD.

Table S4. Region-level larval imports for depth sensitivity test. We defined a source as any successful larval import from an island in the study domain to regions of the Hawaiian Archipelago (Main Hawaiian Islands: MHI, Northwest Hawaiian Islands: NWHI, and Johnston Atoll). Successful larval imports occurred if a particle's closest distance to an island in each region of the Hawaiian Archipelago was ≤10km during the settlement window. The settlement window had a constant pre-competency period of 15 days and a maximum PLD of either 30, 60, 90, or 180 days. Maximum PLD is color coded in table. Sensitivity runs tested across parameters (depth) of 0 m, 5 m, 10 m, 20 m, 30 m, 50 m, 0-25 m averaged, and 0-50 m averaged. For each region, any successful larval import from a source island is listed under MHI, NWHI, or Johnston Atoll.

Parameter	Maximum PLD	Transported to MHI	Transported to NWHI	Transported to Johnston
0m	30	None	Lalo	Johnston
5m	30	None	Lalo	Johnston
10m	30	None	Lalo	Johnston
20m	30	None	Lalo	Johnston
30m	30	None	Lalo	Johnston
50m	30	None	Lalo	Johnston
25m avg	30	None	Lalo	Johnston
50m avg	30	None	Lalo	Johnston
0m	60	None	Lalo	Johnston
5m	60	None	Lalo	Johnston
10m	60	Lalo*	Lalo, Johnston*	Johnston
20m	60	Johnston*	Lalo	Johnston
30m	60	None	Lalo	Johnston
50m	60	None	Lalo	Johnston
25m avg	60	None	Lalo	Johnston
50m avg	60	None	Lalo	Johnston
0m	90	None	Lalo, Johnston*	Johnston
5m	90	None	Lalo, Johnston*	Johnston
10m	90	Lalo*	Lalo, Johnston*	Johnston
20m	90	Lalo*, Johnston*	Lalo, Johnston*	Johnston
30m	90	Lalo*	Lalo	Johnston
50m	90	None	Lalo	Johnston
25m avg	90	Lalo*	Lalo, Johnston*	Johnston

Parameter	Maximum PLD	Transported to MHI	Transported to NWHI	Transported to Johnston
50m avg	90	Lalo*, Johnston*	Lalo	Johnston
0m	180	None	Lalo, Johnston*	Johnston
5m	180	None	Lalo, Johnston*, Wake*	Johnston
10m	180	Lalo*, Johnston*	Lalo, Johnston*, Wake*	Johnston
20m	180	Lalo*, Johnston*	Lalo, Johnston*, Wake*	Johnston
30m	180	Lalo*, Johnston*	Lalo	Johnston
50m	180	Lalo*	Lalo	Johnston, Lalo*
25m avg	180	Lalo*, Johnston*	Lalo, Johnston*, Wake*	Johnston
50m avg	180	Lalo*, Johnston*	Lalo, Johnston*, Wake*	Johnston

* Indicates source island did not occur in all runs within the same PLD.

Table S5. Full depth comparison of PDDs. All combinations of depth layers and the PDDs at each PLD (i.e., 30, 60, 90, 180 days).

RUNS	D_30	D_60	D_90	D_180
0 x 5	0.023637027	0.04839196	0.06369119	0.07580051
0 x 10	0.046200634	0.08817646	0.10136566	0.15615309
0 x 20	0.089467864	0.17097049	0.18215933	0.22336854
0 x 30	0.112841543	0.23792546	0.23501909	0.32689863
0 x 50	0.141181643	0.27260222	0.26921665	0.37592121
0 x 0-25	0.049153241	0.10074798	0.11860587	0.12288228
0 x 0-50	0.084813068	0.175598002	0.20122209	0.24677444
5 x 10	0.006668449	0.0154574	0.02726948	0.06974423
5 x 20	0.038186144	0.08908711	0.12486128	0.19445256
5 x 30	0.062283639	0.16983126	0.20225111	0.31342077
5 x 50	0.091272997	0.22056796	0.25864337	0.38366998
5 x 0-25	0.011242333	0.03030844	0.04652895	0.08857342
5 x 0-50	0.038498333	0.103554276	0.15160521	0.2664432
10 x 20	0.016217897	0.04698086	0.09165233	0.19873357
10 x 30	0.035288818	0.1144397	0.15827713	0.27495841
10 x 50	0.058518487	0.15568633	0.19680915	0.28151756
10 x 0-25	0.002025248	0.0119263	0.03451078	0.12900235
10 x 0-50	0.017631915	0.059037014	0.11820435	0.30697979
20 x 30	0.005945353	0.02754854	0.04825098	0.06842016
20 x 50	0.02291793	0.0758265	0.12909607	0.18245429
20 x 0-25	0.00938649	0.02342988	0.03302086	0.05489038
20 x 0-50	0.001329303	0.005793415	0.0154516	0.04721543
30 x 50	0.009664093	0.03036165	0.05538304	0.09211128
30 x 0-25	0.024700345	0.07762022	0.09579672	0.14278937
30 x 0-50	0.004322974	0.021856117	0.03913498	0.09123607
50 x 0-25	0.046975422	0.12855185	0.16073154	0.25650593
50 x 0-50	0.018501101	0.057575476	0.10418202	0.21311958
0-25 x 0-50	0.009694949	0.029983776	0.05014586	0.08729718

Supplemental Figures

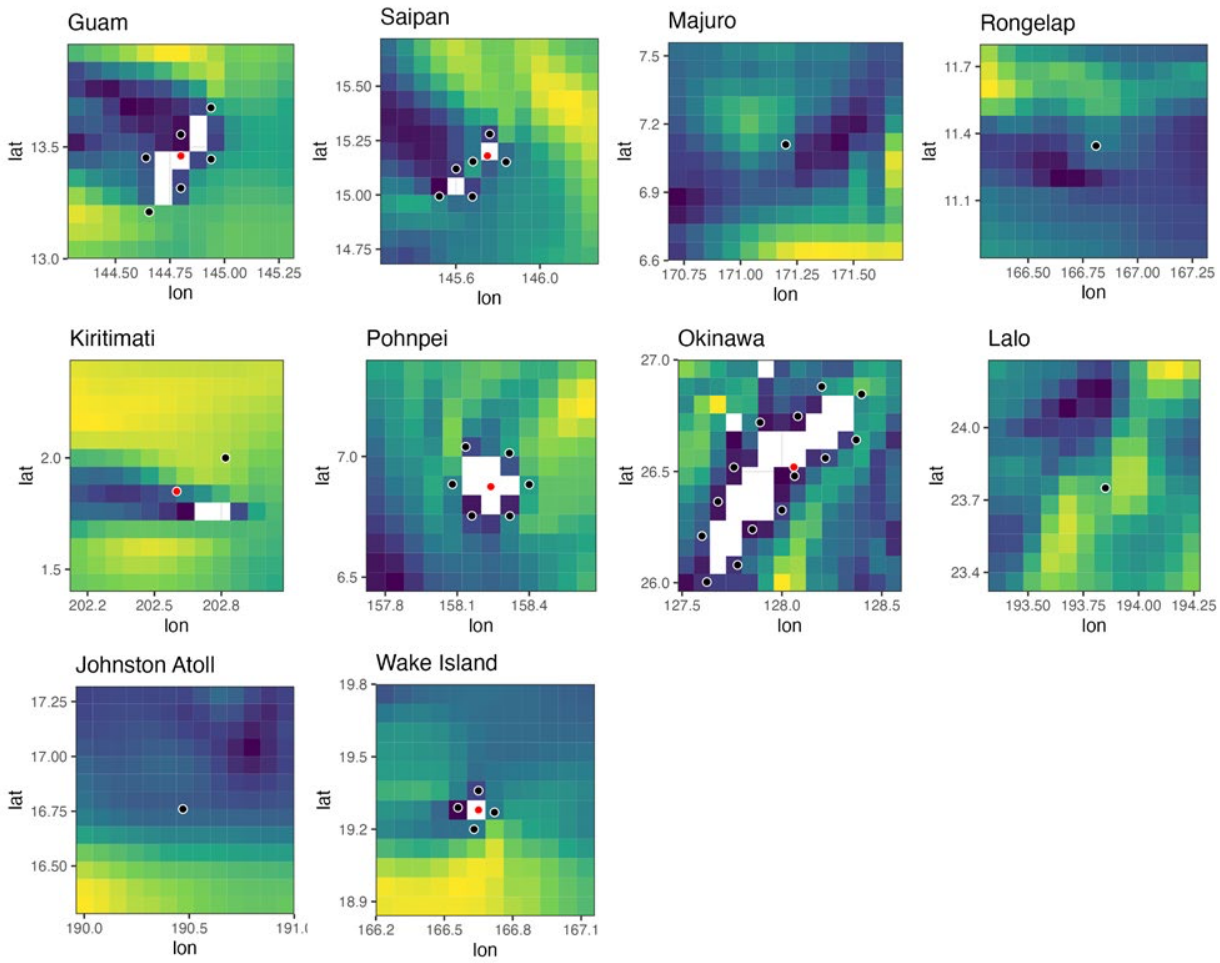

Figure S1. Release points for each island. The location of each release point (black points) per island (red point) included in our model is overlaid on HYCOM surface current speeds at 0.08° resolution. White boxes indicate land. Each box is 0.08° x 0.08°.

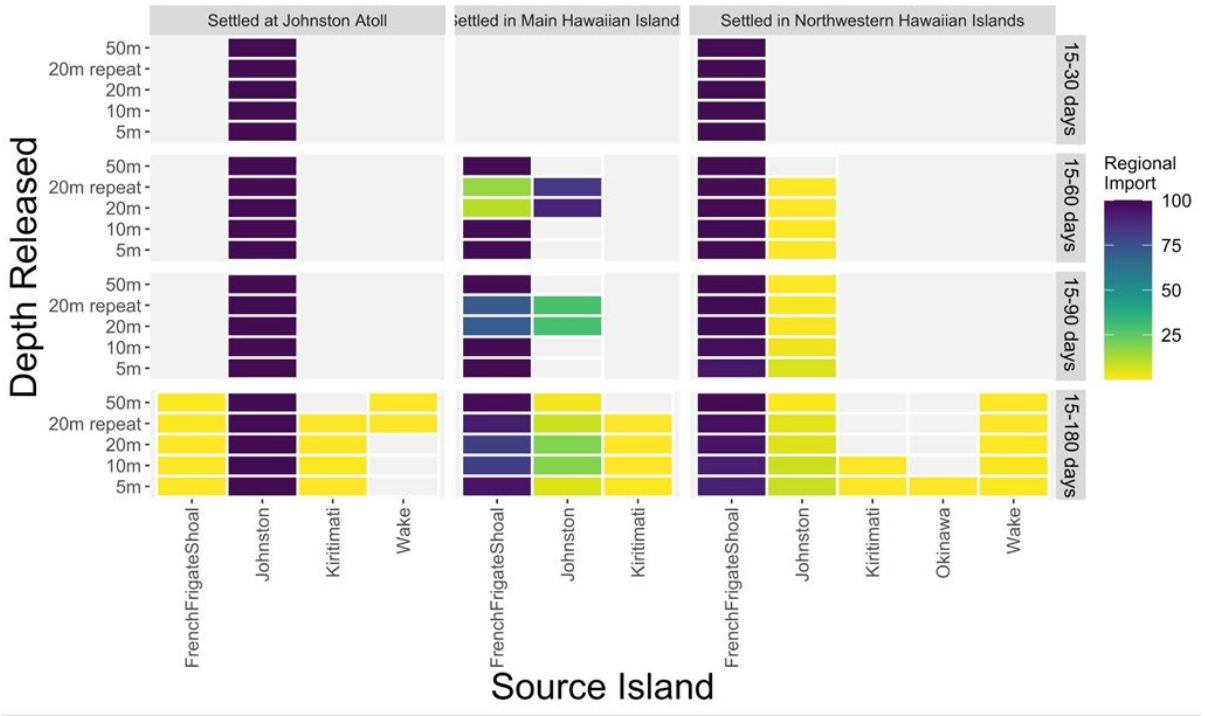

Figure S2. Estimated larval import across depth simulations with 250 particles released daily and 10 m^2/s diffusivity for each simulation across settlement windows. Predicted larval import is grouped by settlement window (15-30 days, 15-60 days, 15-90 days, and 15-180 days) vertically and by region (Johnston Atoll, MHI, NWHI) horizontally. Predicted regional larval import is a percentage defined by the number of particles imported to a region from a source island divided by the total number of particles imported to that region from all source islands. White indicates no connection.