Larval retention versus larval reception: Marine connectivity patterns within and around the Hawaiian Archipelago

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ABSTRACT: Metapopulation connectivity in the Hawaiian Archipelago is poorly understood, which hinders effective management and assessment of living marine resources in the region. This study addresses potential connectivity among geographically separated areas via the pelagic egg and larval life-history phases based on the assumption that propagules are passive prior to the settlement phase. Pelagic transport was investigated using high-resolution ocean current data and computer simulation. Connectivity measures between 25 geographic strata are presented for a suite of pelagic larval durations. Adjacent strata in the archipelago were well connected via pelagic larval transport regardless of larval duration, while connectivity of more distant strata was clearly mediated by larval duration. Retention, i.e., the return of natal propagules, is contrasted with reception, i.e., the influx of propagules from other sources. These two processes appear to be decoupled based on examination of archipelago-wide patterns. Single-generation and multigeneration effects of connectivity are considered using a simple population dynamics model driven by the dispersal kernel probability estimates. The Papahānaumokuākea Marine National Monument appears to be largely self-sustaining based on these results, with differential input to certain inhabited islands further southward in the archipelago depending on the pelagic larval duration.

KEY WORDS: Recruitment • Settlement • Oceanography • Larval Transport • Northwestern Hawaiian Islands

INTRODUCTION

Many animal and plant populations are structured as relatively isolated geographic units as a result of patchy habitat distributions or other ecological constraints. This phenomenon was termed the 'metapopulation concept' initially in a terrestrial arthropod system (Levins 1969), in which the original definition of a metapopulation required periodic extinctions and recolonization events. Following the approach of Hanski (1999) and others, Kritzer & Sale (2004) define marine metapopulations as a "system of discrete local populations, each of which determines its own internal dynamics to a large extent, but with a degree of identifiable and nontrivial demographic influence from other local populations through dispersal of individuals." Many marine populations fall into this category because of relatively sessile, adult life-history stages and dispersive egg/larval propagules. These propagules are pelagic for many species and are capable of long-distance transport as a result of both passive, planktonic drift in ocean currents (Hare et al. 2002) and active swimming and orientation of the older pelagic life-history stages (Leis & Carson-Ewart 2003, Fisher, 2004). These same mechanisms may also be important for natal retention (Sponaugle et al. 2002). The degree of connection between metapopulations is often termed connectivity, and includes both the dispersal of early life-history stages and the directed movements of adults, i.e., emigration/immigration and migration. For benthic marine species inhabiting island systems, connectivity during the early life-history stages is thought to be most important with regard to population dynamics (Barlow 1981). There are a large number of such geographically separated islands, coral atolls, seamounts, and banks throughout the Hawaiian Archipelago (Fig. 1). Most of the benthic or islandassociated species in this region do not routinely cross the large expanses of deep ocean among habitats as adults; however pelagic egg and larval stages can easily traverse these boundaries and even longer distances (Robertson et al. 2004). Despite the importance of this issue towards understanding population dynamics and effectively managing these species or areas (e.g. Crowder et al. 2000, Valles et al. 2001), larval connectivity in this region is relatively unknown. The uniquely endemic fish and other marine faunas of the Hawaiian Archipelago (Hourigan & Reese 1987) and the extreme expression of endemism in the Northwestern Hawaiian Islands (DeMartini & Friedlander 2004) make such information critically important for the Hawaiian Archipelago. Such information will also be extremely important towards understanding the ecological impact of the recently established Papahānaumokuākea Marine National Monument[1] as well as for understanding the source/sink dynamics of marine protected areas established for bottomfish, the Humpback Whale sanctuaries, the military-related closure around Kahoolawe, the Fish Replenishment Areas of west Hawaii, and various other areal closures in the state. The purpose of this study is to examine patterns of larval connectivity among a large number of geographic strata in and around the Hawaiian Archipelago using high-resolution ocean current data and computer simulation. Ocean drifter data are compared to the ocean current data used in this study for ground-truthing.

[1] June 15, 2006 proclamation by President George W. Bush.

MATERIALS AND METHODS

Ocean current data. This study uses the same U.S. Naval Research Laboratory (NRL) ocean current data as used in Kobayashi (2006) for a study on Johnston Atoll connectivity. The NRL Layered Ocean Model (NLOM) is a global, six-layered ocean circulation model that is operated by the NRL. The NLOM operates at a resolution of 1/16° (0.0625°) latitude by 45/512° (0.0879°) longitude (Rhodes et al. 2002, Wallcraft et al. 2003). This mesoscale model is eddy-resolving and thermodynamic, meaning that the density structure of the modeled ocean can be modified by physical processes. The NLOM is atmospherically forced using data from the Navy Operational Global Atmospheric Prediction System (NOGAPS). It also assimilates remotely sensed, sea surface height data (GFO, JASON-1, and ERS-2 satellites) and sea surface temperature data (NRL/MODAS SST). Daily NLOM output is an operational product by NRL that is available from many cooperating data servers. One of these is the Asia-Pacific Data-Research Center (UH/SOEST/IPRC/APDRC — http://apdrc.soest.hawaii.edu/). One of the daily output layers routinely archived is the upper 100 m, henceforth termed 'surface layer.' For this study, 365 days of daily surface layer data (31 January 2003 to 30 January 2004, these exact dates were not chosen but reflected data availability at the time) spanning the region 170°E to 150°W longitude, 10°N to 35°N latitude were obtained from the APDRC. The daily surface layer data included estimates of *u* (zonal East-West) component and *v* (meridional North-South) component for current vectors. The spatial grid (Fig. 1) covered 457 x 401 pixels.

Geographic location. The Hawaiian Archipelago spans from SE Hancock Seamount in the northwest to the Island of Hawaii in the southeast. Locations and sizes of the 25 primary geographic features used in this study are presented in Table 1. Several subregions of the archipelago are recognized. The main Hawaiian Islands (MHI) are mostly larger populated islands in the southern portion of the chain but also include some submerged and/or uninhabited islands. The Northwestern Hawaiian Islands (NWHI) includes all areas recently designated as a Papahānaumokuākea Marine National Monument[1] but is also further divided for some fishery management purposes. In the Bottomfish and Seamount Groundfish Fishery Management Plan implemented by the Western Pacific Regional Fishery Management Council, the lower portion of the NWHI is referred to as the Mau Zone (Necker and Nihoa Islands) and the larger region further north is referred to as the Hoomalu Zone (French Frigate Shoals and northward). The commercial NWHI spiny lobster fishery is currently closed, but this fishery, with primary fishing grounds located at Maro Reef and Necker Island, was managed on a bank-specific basis since 1998. Aside from a short-lived black coral fishery north of Midway there are no other extractive activities of nearshore resources in the NWHI. Conversely, the nearshore resources of the MHI are relatively heavily fished by recreational, subsistence, and commercial activities; hence, connectivity to more pristine areas is of extreme concern. Although geographically separated from the archipelago, Johnston Atoll was examined as part of the spatial matrix that was used in this study considering its proximity to the archipelago and its ability to provide larval exchange (Kobayashi 2006). Understanding connectivity among these larger strata as well as the individual islands, banks, seamounts, and coral atolls is important towards effective management and scientific understanding of population dynamics in a metapopulation context.

The spawning event. The spatiotemporal pattern of propagule release is a key part of this study. For the spatial component, spawning output was assumed proportional to the amount of shallow-water habitat identified through the 2-minute pixel analysis of the Smith & Sandwell (1997) bathymetric database, as described below. This does not take into consideration substratum composition, habitat type, habitat quality, population size, spawning biomass, fecundity or propagule viability. This approach further assumes that the shallow-water habitat is either fully saturated or equally so across strata. For the purposes of this study, the target organism (plant, invertebrate or fish) is assumed to be an insular species residing uniformly from 0 to 100 m depth throughout the archipelago. Forthcoming analyses will be tailored toward particular species using specific release locations as available. Spawning output was assumed to be uniform throughout the year for the temporal component. While many marine species in Hawaii are known to display seasonal spawning patterns (e.g. Walsh 1987), these patterns are not clearly unimodal nor are they likely to be similar even across ecologically similar species (Reese 1968). The target organisms (plant, invertebrate or fish) are assumed to spawn continually throughout the year or with sufficient variability which dampens pronounced seasonality for the purposes of this study.

Modeling of transport. The movement of larvae was simulated using the individual-based, Lagrangian modeling techniques identical to that used in Kobayashi (2006). These are also known as biased random-walk models (Codling et al. 2004). The daily NLOM data was used to advect larvae horizontally. A detection radius of 25 km from suitable settlement habitat at the end of the pelagic larval duration (PLD) was used as an indicator of settlement. Suitable settlement habitat was defined from a 2-minute resolution bathymetric database (Smith & Sandwell 1997) by screening to only include 2-minute pixels ranging in depth from 0 to 100 m. A summary of these habitat pixels is presented in Table 1. An eddy-diffusivity coefficient of 500 $m^2 s^{-1}$ was used, which was qualitatively based on drifter buoy observations (Polovina et al. 1999).

Fisher & Wilson (2004) found that sustainable swimming speeds were on the order of 30 cm s^{-1} for large, ready-to-settle fish larvae. The 25 km radius used in this study could be traversed in 1 day at these speeds, assuming continuous swimming and directional orientation were accomplished. Invertebrate larval swimming speeds of this magnitude have also been observed in the late larval stage of spiny lobster called the "peurulus" (Philips & Olsen 1975), and in the late larval stage of crabs called the "megalops" (Fernández et al. 1994). While the cues available on the high seas are poorly understood, the "Island Mass Effect" (Gilmartin & Revelante 1974) can have significant, visually detectable effects out to this radius (e.g. Palacios 2004). Elevated levels of chlorophyll a, because of proximity to islands, banks, and seamounts, are also apparent at this spatial scale in the Hawaiian Archipelago (Kobayashi, unpublished data). Olfactory and auditory cues may also be functional many kilometers from shore (Atema et al. 2002, Leis &

Lockett 2005, Wright et al. 2005). Some larvae do not have well-developed swimming abilities and appear to behave as passive drifters (coral planula, lobster phyllosomes, etc.), or may exhibit “behavioral drifting” despite being able to swim capably (Hogan & Mora 2005). These larvae may require a more accurate “hit” on suitable substrate for successful settlement to occur. However, the 25 km radius was used in all simulations as a compromise to yield some settlement at a manageable level of larval release magnitude; i.e., the radius could be reduced but would require more releases to attain nonzero settlement.

For each of the 2238 pixels of shallow-water habitat, 100 simulated larvae were released on each of the 365 calendar days in the NLOM current data and tracked for pelagic larval durations (PLDs) of 15, 30, 60, 90, 180, and 365 days. The sample size of 100 was chosen as a compromise because of computational speed and data storage concerns. Given 27 habitat units, this works out to approximately 8289 larvae released per habitat unit per 365 days per 6 PLDs. The range of PLDs encompasses the known values for a wide variety of vertebrate and invertebrate species in the Hawaiian Archipelago, including commercially important species such as deepwater bottomfish and lobster, as well as coral reef inhabitants. Among some of the more commercially important or conspicuous fauna, the spiny lobster has approximately a 12-month PLD (Kittaka & Kimura 1989), the various slipper lobsters range from 2- to 9-month PLDs (Booth et al. 2005); the deepwater snappers and grouper have approximately 1–3 month PLDs (Leis 1987); and most coral reef fishes typically have 0.5–3 month PLDs (Victor & Wellington 2000). Because the data spanned a discrete 365-day time block, data were allowed to "wrap around" for simulations initiated in the latter portions of the data. In other words, any larvae still at large during their PLD on 30 January 2004 would next encounter currents from 31 January 2003 and carry on from that point forward. This would allow a symmetrical analysis of possible seasonal effects. One undesirable consequence of this approach is that it imposes a discrete "jump" in the data stream at the end of January; however, this approach was used to make best use of all available data for the widest range of PLDs possible. Operationally, the location of larvae in Cartesian space was calculated with the following equations:

$$
\begin{aligned}
x_{t+\Delta t} &= x_t + \left[u_{(x_t, y_t, t)} \Delta t + \varepsilon \sqrt{D \Delta t} \right] / \cos(y_t) \\
y_{t+\Delta t} &= y_t + \left[v_{(x_t, y_t, t)} \Delta t + \varepsilon \sqrt{D \Delta t} \right]
\end{aligned}
$$

where x represents longitude in degrees, y represents latitude in degrees, t represents time in days, u represents the zonal East-West component of the current speed in degrees day^{-1}, v represents the meridional North-South component of the current speed in degrees day^{-1}, ε is a normal random variate (mean 0 and standard deviation 1), $\cos(y_t)$ adjusts longitudinal distance by latitude to account for the spherical coordinate system, and D is the diffusivity coefficient (500 m^2 s^{-1}, 0.0035 degrees^2 d^{-1}, Polovina et al. 1999). The full-resolution, daily 1/16° latitude by 45/512° longitude *u* and *v* arrays were sampled depending on the location in time and space of individual simulated larvae. Simulated larvae at the end of the PLD and in the 25 km radius of any habitat pixel were scored as settled. Orientation and swimming were not implicitly part of the model structure nor was the capability of early or delayed settlement/metamorphosis. However, it was assumed that competent larvae were able to successfully navigate the last 25 km at the end of the pelagic duration, loosely based on the 30 cm s^{-1} of Fisher & Wilson (2004) for some fish larvae and coupled with 24 hours of continuous directional swimming. The tabulation of settled larvae includes a range of individuals from directly on the habitat pixel up to 25 km distant; therefore, the actual mean PLD within this grouping may slightly exceed the index value PLD based on variable final transit time among individuals.

Evaluating connectivity. Successful settlement was cross-tabulated into matrices defined by source site (larval release site) and sink site (larval settlement site). Data for individual pixels were collapsed into the 25 strata presented in Table 1. Since the raw counts of settlement are a function of release sample size it is desirable to standardize the counts into meaningful indices. Settlement was standardized by source site across all sink sites; in other words, calculating what proportion of a batch of larvae released from a particular source site settled at a particular sink site. When summed across all sink sites this would add up to 1. These data are presented in tabular form and graphically for particular subsets of the data such as examining retention as a function of PLD or geography. Retention, i.e., the return of natal propagules, is contrasted with reception, i.e., the influx of propagules from other sources, realizing that both processes are important towards population dynamics. All settlement data were pooled across 365 days for a coarse examination of retention and reception geographic patterns.

Multigeneration dynamics. A simple metapopulation simulator was parameterized with the connectivity measures and forecast for many generations. An initial baseline condition was defined by the spatial distribution of habitat and propagule releases. The baseline condition began with 100% natal composition; i.e., all residents were considered to be derived from retention. The total initial number of propagules released per habitat stratum was used as a cap in subsequent generations as a simple means of density-dependence. In other words, after each generation was tabulated with respect to retention and reception from all sources, the overall population at each geographic strata was trimmed until it was equivalent to the starting population size at that strata while preserving the relative metapopulation structure contained therein. This stabilized the overall archipelagic population to a constant level for the purposes of examining the source composition within each habitat strata over time. For each generation, the connectivity measures were used to drive retention and reception at each of the strata, followed by a leveling-down process to achieve the initial metapopulation size. This was repeated for 1000 generations for each of the 6 PLDs, keeping careful track of lineages of all propagules. This number of generations was observed to be adequate for achieving source composition stability. Quasi-equilibrium was quickly achieved within 30–40 generations depending on the PLD. It is realized that the number of propagules released will determine this time to equilibrium, but this exercise was undertaken to examine the resulting equilibrium structure, not the absolute time trajectory to reach said equilibrium. A technique called nonmetric multidimensional scaling (NMDS) was used to examine spatial affinities among equilibrium metapopulation structure across all geographic strata and PLDs. NMDS is an iterative ordination approach that is also useful to assess dimensionality in a data set. It is considered the method of choice for ordination of most ecological data (McCune & Grace 2002). NMDS of the metapopulation structure across all geographic strata and PLDs was accomplished using the commercial software package PC-ORD. The NMDS output is a two-dimensional scatterplot of points, each representing a particular combination of geographic strata and PLD. Similarity or dissimilarity is assessed from visual examination of the relative location of points in Cartesian space.

Ground-truthing with drifter buoys. Drifter buoy data are publicly available from the NOAA Global Drifter Program (http://www.aoml.noaa.gov/phod/dac/gdp.html). NOAA research platforms and vessels of opportunity deploy these drifters, which have their drogues at 15 m depth and communicate daily with Argos, an American-French satellite data network (Lumpkin & Pazos 2006). For the spatial and temporal window of NLOM data used in this study there were 64 individual drifters with some level of intersection representing a total of 29,750 records at 6-hour kriged (smoothed) data resolution (Table 2). This represents an average of approximately 116 days of information per drifter buoy in this area at this time. The aggregated tracks are shown in Figure 2. Each drifter buoy data record was matched to a corresponding NLOM daily current at its location and the differences were tabulated for statistical analyses. Four components were examined separately: the *u* component, *v* component, magnitude, and direction. NLOM observations were binned at 1 cm sec^{-1} or 1° intervals of drifter values. Simple linear regressions were used to characterize the relationships between modeled and observed current components, applying the regression to the portion of the data range where sample size was high (n ≥ 100 per 1 cm sec^{-1} binned mean).

How representative is 2003–2004 data? The results presented here reflect modeled processes during the 2003–2004 calendar years. Temporal variability in the oceanographic processes clearly exists, including interannual variability, decadal variability, regime shifts, climate change, global warming, etc. Such changes in oceanography and resulting current patterns are principally driven by large-scale climate events. Two commonly used indices of temporal variability in the Hawaiian Archipelago climate and oceanography are the Southern Oscillation Index (SOI) and the Pacific Decadal Oscillation (PDO). The former is thought to capture interannual variability around the equatorial regions related to El Niño and La Niña, while the latter is thought to capture dynamics related to decadal variability in the higher latitudes north of 20°N. Monthly time series of these two oceanographic indices were obtained from NOAA Physical Sciences Division of the Earth System Research Laboratory (http://www.cdc.noaa.gov/ClimateIndices/) over the 1980–2007 time period. Monthly values from the 2003–2004 time period were compared to monthly values from this larger 28-year span of data using a Student's *t*-test. The results of this test are used to judge the applicability of the findings of this study to other time periods.

RESULTS

The overall geographic patterns of retention and reception are tabulated in Table 1. This aggregated all settlement data for the 365 daily releases. Retention rate (as a fraction of propagules released) ranged from a low of 0.39% at Middle Bank and Lanai, to a high of 17.24% for the island of Maui. This is not an artifact of stratum size since this measure is scaled by the amount of propagules released, which is directly proportional to shallow-water habitat area; therefore, the retention rate is "per area." When retention and reception were pooled to estimate total settlement per unit of habitat, settlement ranged from a low of 6,288 settlers per pixel at Kure Atoll to a high of 149,192 settlers per pixel at Northampton. The high settlement rate at the relatively small Northampton is attributed mostly to reception (Table 1).

The connectivity results were converted to probabilities and tabulated into transition matrices; these are also often referred to as "dispersal kernels." This standardized settlement by source site spans across all sink sites for each PLD. The dispersal kernel probabilities are presented in Appendix 1 (Appendix Tables 1A–F).

The metapopulation simulation was performed for each of the PLDs for 1000 generations. Starting from a purely natal population, the composition at each habitat strata was allowed to change over time as determined by the dispersal kernel probabilities. An example of time trajectory of this process is shown in Figure 3 for Maro Reef. Predictably, at longer PLDs, the equilibrium condition consisted of fewer of natal origin, corresponding to more mixing between metapopulations. At shorter PLDs the equilibrium condition was primarily composed of individuals of natal origin. The NMDS ordination graphically shows the strong impact of PLD on metapopulation structure (Fig. 4). As PLD increases the NMDS coalesces into a nearly uniform pattern of metapopulation structure.

NLOM currents were found to be in good correspondence to drifter data over the time interval and location studied (Fig. 5). The three regression slopes clearly depart from the 1:1 relationship which might be expected if the currents were exactly synchronized. The *u* component, *v* component, and resultant magnitude of the NLOM currents were consistently lower in value than the corresponding drifter data. There was also a slight rightward deflection in direction when comparing NLOM currents to drifter data. The NLOM currents reflect an average water flow over the 0–100m layer, loosely termed the "mixed layer," while the drifters are measuring water movement at a drogued 15 m depth. These two measurements of water movement are theoretically expected to be different based on the Coriolis Effect and resulting Ekman Spiral pattern of circulation in which successive vertical layers of water move at a lesser velocity and at a slight offset to each other. The magnitude of dampening and the overall deflection qualitatively match what would be predicted with Ekman Spiral dynamics in the Northern hemisphere (rightward deflection).

Examination of the SOI and PDO monthly time series (Fig. 6) indicated that the 2003–2004 time period was nonanomalous, both for short term interannual events and longer term events. The majority of this time interval has been classified as neither "warm" nor "cool" by the NOAA National Weather Service Climate Prediction Center. The SOI and PDO values for the months of NLOM data used in this study were not significantly different when compared to all other months spanning 1980–2007 using a Student's *t*-test (SOI *t*-value = 0.37, df = 329, $p = 0.71$; PDO *t*-value = –1.33, df = 324, $p = 0.18$), suggesting that the connectivity findings presented here may be of general applicability.

DISCUSSION

This paper presents the first complete series of connectivity measures for the Hawaiian Archipelago. These measures are used in a metapopulation simulation to provide insight into population structure and between-stratum dependencies. The distinction between larval *retention* and larval *reception* is put forth here since this critical difference in larval source is often overlooked. Field studies of settlement and recruitment often lump these two distinctly different processes together because of the inherent difficulty in sourcing incoming propagules. The findings presented here advance our understanding of population dynamics in this region and will assist in posing useful hypotheses for future research, both for purely scientific questions as well as applied issues such as spatial closures and other fishery management and conservation measures.

The biological significance of the Papahānaumokuākea Marine National Monument to the entire Hawaiian Archipelago can be examined from the connectivity probabilities and the metapopulation analysis. The equilibrium metapopulation composition predicted after many generations can be useful in understanding the importance of adjacent or even nonadjacent geographic strata. Three such examples are graphically presented for comparison, with PLDs of 15 days (Fig. 7A), 90 days (Fig. 7B), and 365 days (Fig. 7C). The importance of retention for the briefer PLD is apparent. A relatively narrow transitional region including Nihoa, Middle Bank, Niihau, and Kauai are composed of settlers from both the Papahānaumokuākea Marine National Monument and

MHI regions. Areas further north and south have negligible crossover. However, at longer PLDs, nearly all regions throughout the MHI have some component of Papahānaumokuākea Marine National Monument-derived settlers, whereas most of the Papahānaumokuākea Marine National Monument is self-seeding until approximately Necker is reached. For extremely long PLDs, the entire archipelago is connected nearly uniformly after many generations (Fig. 7C). This process is easily visualized in the NMDS ordination (Fig. 4). Briefer PLDs are scattered widely over the two-dimensional ordination space, but coalescence of the pattern is seen as the PLD increases. At a 365-day PLD, the patterns are most clustered yet still not entirely identical. The abrupt shift in Johnston Atoll position from 30-day PLD to 60-day PLD is consistent with the results of Kobayashi (2006) suggesting a threshold PLD of 50 days for significant colonization from Johnston Atoll to the Hawaiian Archipelago. A similar threshold PLD likely operates in the reverse direction based on the NMDS results of Johnston Atoll metapopulation structure (Fig. 4). The equilibrium composition is somewhat driven by the spatial pattern in spawning magnitude, which is a function of habitat size in this analysis. A breakdown of habitat size by area is shown in Figure 8. While the effects of Maro and Gardner can be attributed to their relatively large reproductive output in the simulations, other large areas do not contribute similarly to the equilibrium composition, which is a consequence of dispersal kernel probabilities operating over many generations. When the effect of habitat size is removed by scaling total retention and reception by habitat pixel counts, this yields evidence of a decoupling of retention and reception processes (Fig. 9). This implies that there is very little, if any, physical (geographic or oceanographic) relationship between factors which promote effective natal larval retention and factors which promote influx of outside larval reception. Settlement and recruitment studies which ignore propagule origins may have difficulty in relating observed patterns to oceanographic features for this very reason. Since neither measure is a strong proxy for the other (Fig. 9), the futility of understanding transport dynamics given the single aggregated measure is readily apparent. The need for additional genetics studies and other stock identification markers for sourcing of incoming propagules is urgent (e.g. Bernardi et al. 2002, Schultz et al. 2007).

It should be noted that the raw connectivity measures presented in this study (Appendix 1) are a product of examining the single-generation effects of connectivity, i.e., a “snapshot” of pair-wise connectivity values rather than the cumulative effects of many generations. Clearly since the connectivity measures are high for adjacent habitats, over evolutionary time the genetic connectivity will be more pronounced than inferred here. This could be particularly important at the southern boundary of the Papahānaumokuākea Marine National Monument, with a protected spawning source able to effectively seed areas to the south over time via a “stepping stone” effect, not immediately apparent from examining the pair-wise connectivity values. This gradual diffusive process could lead to much more connectivity than that described by a single generation. Previous studies that have relied on the “snapshot” approach should be revisited with a multigenerational approach to better understand metapopulation dynamics. The simple metapopulation model used in this study is a useful start; however, much more can be accomplished with a better understanding of habitat, target species density, and reproductive output patterns. A demographic model linked to an ocean circulation model is an ambitious undertaking but will be necessary to understand population dynamics in a complex source/sink marine environment.

Clearly, these results can be improved for specific target organisms with a better understanding of their spatial and temporal reproductive output patterns, their pelagic larval ecology, and their settlement behavior when competent. This approach can be tailored to model dispersal of invasive or introduced species, and can be a useful tool towards establishing effective closed areas for population recovery and conservation.

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Table captions

Table 1. Listing of geographic strata utilized in connectivity simulations. Inclusion criteria was presence of at least one 2' pixel in the Smith & Sandwell bathymetric database. Also presented are locations, sizes, and summary of releases/retentions/receptions per strata aggregated over all simulations performed.

Table 2. Listing of NOAA drifter buoys intersecting the NLOM region over the studied time interval. Number of datapoints used represents the number of 6-hour resolution data available.

Figure captions

Figure 1. Map of Hawaiian Archipelago study region showing location of primary habitat strata used in the larval transport simulations. Bathymetry is from the Smith & Sandwell (1997) 2-minute database.

Figure 2. NOAA drifter buoy trajectories in the Hawaiian Archipelago region over the time interval 31 January 2003 – 30 January 2004.

Figure 3. Trajectories of Maro Reef percent natality using metapopulation simulation driven by NLOM derived dispersal kernels. Different lines correspond to different PLDs. Generations beyond 50 were not appreciably different from simulation endpoints at generation 1000.

Figure 4. NMDS ordination of metapopulation structure. Circle size is scaled linearly as a function of PLD, smallest circle representing 15-day PLD and largest circle representing 365-day PLD. Each geographic strata is color-coded in a gradient which approximately follows the geographic layout of the archipelago (Northwest to Southeast and lastly Johnston Atoll).

Figure 5. Comparison of NLOM currents and NOAA drifter data, for *u* component (A), *v* component (B), resultant speed (C), and direction (D). Histogram bars in panels A–C indicate sample size of drifter observations at each 1 cm sec^{-1} bin; error bars are 95% parametric confidence intervals about each mean (points). Dotted vertical lines represent limits of data span used in regression where $n \geq 100$ per bin. The fitted regression line is shown as a solid line. The angular displacement is tabulated in panel D as a polar histogram showing the departure of NLOM from drifter observations. Northward

represents complete agreement between NLOM and drifter observations, with other directions indicating the offset of NLOM from drifter observations.

Figure 6. Monthly time series of SOI and PDO climate indices over the time interval 1980–2007. Shaded region delineates the 2003–2004 time interval of NLOM data used in this study.

Figure 7A. Equilibrium metapopulation composition for 15-day PLD after 1000 generations of simulation using NLOM dispersal kernel probabilities. Red bars indicate natal origin. Each subplot *y*-axis is scaled independently to maximize data display.

Figure 7B. Equilibrium metapopulation composition for 90-day PLD after 1000 generations of simulation using NLOM dispersal kernel probabilities. Red bars indicate natal origin. Each subplot *y*-axis is scaled independently to maximize data display.

Figure 7C. Equilibrium metapopulation composition for 365-day PLD after 1000 generations of simulation using NLOM dispersal kernel probabilities. Red bars indicate natal origin. Each subplot *y*-axis is scaled independently to maximize data display.

Figure 8. Pixel counts of 0–100m habitat from Smith & Sandwell (1997) bathymetric database. Spawning output in simulations was proportional to these counts. Johnston Atoll has a pixel count of 1.

Figure 9. Scatterplot of retention per pixel of habitat (*x*-axis) versus reception per pixel of habitat (*y*-axis). Each point represents 1 of the 25 habitat strata listed in Table 1. Solid line is nonsignificant linear regression.

Table 1. Listing of geographic strata utilized in connectivity simulations. Inclusion criteria was presence of at least one 2' pixel in the Smith and Sandwell bathymetric database. Also presented are locations, sizes, and summary of releases/retentions/receptions per strata aggregated over all simulation performed.

Index #	Location	Longitude E	Latitude N	2' pixels 0-100m	Total releases	Total retention	Retention per release	Total reception	Total settlement	Settlement per pixel
1	Kure	181.66	28.41	11	2409000	30747	1.28%	38426	69173	6288
2	Midway	182.62	28.21	9	1971000	38579	1.96%	89336	127915	14213
3	Pearl & Hermes	184.17	27.86	24	5256000	176189	3.35%	131800	307989	12833
4	Salmon	183.57	26.93	2	438000	3072	0.70%	92505	95577	47789
5	Lisianski	186.07	26.05	24	5256000	258803	4.92%	217695	476498	19854
6	Pioneer	186.57	26.00	29	6351000	91598	1.44%	288039	379637	13091
7	Laysan	188.26	25.82	27	5913000	189576	3.21%	556023	745599	27615
8	Northampton	187.85	25.38	4	876000	24289	2.77%	572478	596767	149192
9	Maro	189.30	25.48	91	19929000	1335332	6.70%	400380	1735712	19074
10	Raita	190.57	25.64	14	3066000	88058	2.87%	414671	502729	35909
11	Gardner	191.96	24.88	143	31317000	1822490	5.82%	363624	2186114	15288
12	St. Rogatien	192.86	24.33	19	4161000	26880	0.65%	375485	402365	21177
13	Brooks	193.10	24.16	5	1095000	10549	0.96%	308981	319530	63906
14	French Frigate Shoals	193.80	23.79	51	11169000	319006	2.86%	343052	662058	12982
15	Necker	195.50	23.44	66	14454000	1176951	8.14%	399529	1576480	23886
16	Nihoa	197.89	23.11	37	8103000	277273	3.42%	377511	654784	17697
17	Middle	198.93	22.73	3	657000	2593	0.39%	137013	139606	46535
18	Niihau	199.84	21.91	21	4599000	67025	1.46%	220240	287265	13679
19	Kauai	200.45	22.09	36	7884000	628720	7.97%	504455	1133175	31477
20	Oahu	202.21	21.28	92	20148000	2125237	10.55%	1373999	3499236	38035
21	Molokai	202.95	21.01	84	18396000	2759697	15.00%	2521814	5281511	62875
22	Lanai	203.28	20.57	4	876000	3399	0.39%	178743	182142	45536
23	Maui	203.58	20.76	63	13797000	2378704	17.24%	2601584	4980288	79052
24	Hawaii	204.32	19.64	99	21681000	3490738	16.10%	1628482	5119220	51709
25	Johnston	190.45	16.75	1	219000	1241	0.57%	7850	9091	9091

Table 2. Listing of NOAA drifter buoys intersecting the NLOM region over the studied time interval. Number of datapoints used represents the number of 6 hour resolution data available.

Drifter ID	Start-end dates	Number of datapoints used
13519	5/21/2001-10/17/2003	1033
13575	7/3/2001-4/19/2003	310
17956	4/24/2001-4/18/2003	96
18288	4/4/2001-2/4/2003	15
19241	7/7/2001-7/11/2003	21
20098	6/20/2001-8/29/2003	302
21532	7/1/2001-9/2/2003	155
22936	3/21/2001-10/10/2005	1092
23122	12/12/2001-8/7/2003	159
23173	6/30/2001-3/16/2003	175
24014	6/6/2001-7/28/2003	711
24097	7/1/2001-5/11/2003	254
24443	1/13/1996-4/6/2003	255
25764	1/1/1996-11/27/2004	869
25770	3/15/2001-6/24/2003	575
25929	3/15/2001-3/14/2004	246
26035	3/11/2001-12/31/2004	1391
27465	9/6/2001-12/24/2003	364
33862	5/17/2002-1/12/2005	403
33866	6/22/2002-8/31/2003	525
33867	6/23/2002-11/11/2003	212
33920	10/5/2001-11/25/2004	469
33922	10/6/2001-10/30/2005	152
33997	2/26/2002-5/4/2004	81
34000	6/6/2002-4/13/2004	236
34009	12/19/2001-10/20/2003	1047
34021	7/4/2002-2/16/2004	756
34026	7/17/2002-11/4/2003	147
34042	7/24/2002-2/10/2004	401
34051	8/14/2002-9/27/2004	1460
34052	8/15/2002-3/1/2003	113
34061	7/1/2002-7/19/2003	642
34071	6/20/2002-7/7/2004	701
34102	1/29/2002-8/12/2003	596
34108	2/10/2002-7/22/2004	588
34131	11/4/2002-11/2/2004	157
34319	11/16/2002-6/17/2003	124
34320	6/30/2003-1/10/2005	255
34325	11/17/2002-3/31/2004	1448
34332	5/31/2002-4/15/2003	292
34333	6/6/2002-9/29/2003	213
34334	6/22/2002-7/22/2004	1453
36009	9/9/2002-6/8/2004	224
36907	11/11/2002-11/8/2004	440
36909	9/29/2002-1/28/2004	471
36911	9/17/2002-1/23/2005	999
36914	10/17/2002-11/5/2004	487
36919	9/15/2002-2/1/2006	1140
36920	9/16/2002-2/1/2006	716
36924	9/10/2002-1/2/2006	1197
36925	9/28/2002-4/1/2004	93
36948	1/18/2003-4/1/2004	94
36956	2/1/2003-1/31/2006	324
36957	2/3/2003-6/23/2004	389
36958	2/3/2003-1/13/2006	218
36960	1/17/2003-1/15/2005	466
36961	1/16/2003-2/1/2006	1111
39092	1/12/2003-2/28/2004	107
39099	2/15/2003-6/24/2004	138
39109	1/15/2003-1/13/2004	24
39155	4/30/2003-8/11/2004	262
39167	7/25/2003-3/14/2004	151
39602	6/24/2003-2/1/2006	187
39631	8/1/2003-2/1/2006	18
		29750 total

Figure 1.

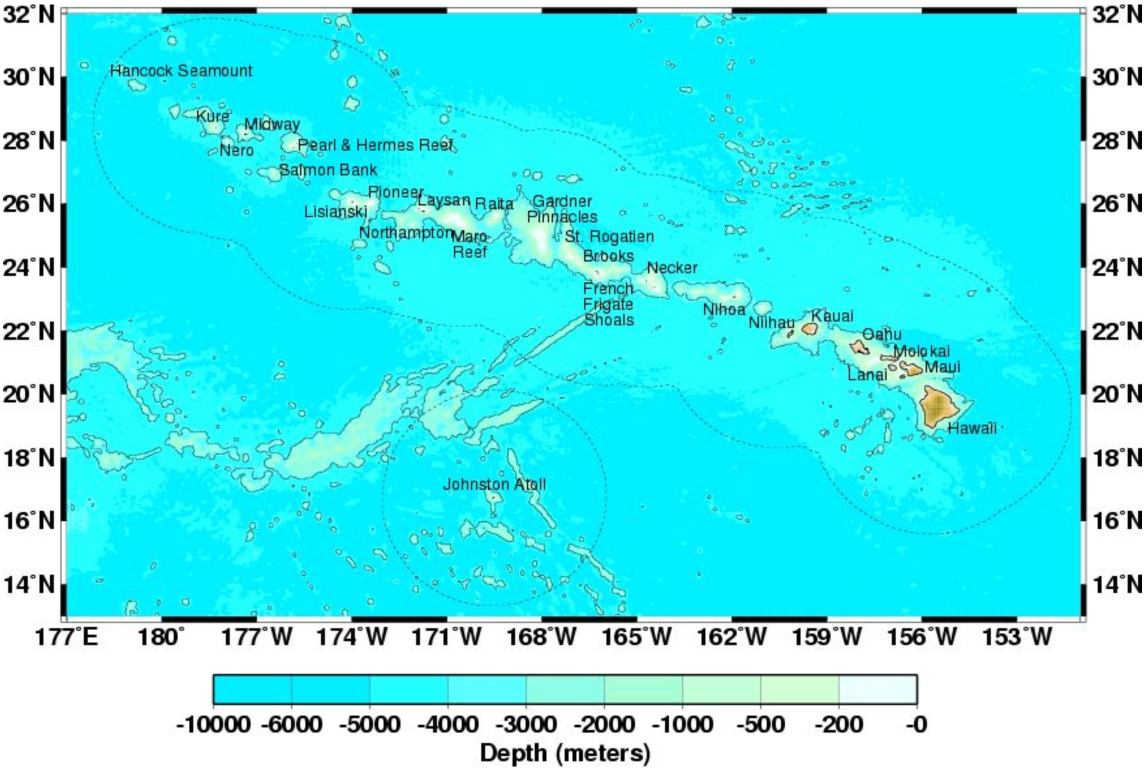

Hancock Seamount
Kure
Midway
Nero
Pearl & Hermes Reef
Salmon Bank
Pioneer
Laysan
Raita
Lisianski
Northampton
Maro Reef
Gardner Pinnacles
St. Rogatien
Brooks
Necker
French Frigate Shoals
Nihoa
Niihau
Kauai
Oahu
Molokai
Maui
Lanai
Hawaii
Johnston Atoll
32°N
30°N
28°N
26°N
24°N
22°N
20°N
18°N
16°N
14°N
177°E
180°
177°W
174°W
171°W
168°W
165°W
162°W
159°W
156°W
153°W
-10000 -6000 -5000 -4000 -3000 -2000 -1000 -500 -200 -0
Depth (meters)

Figure 2.

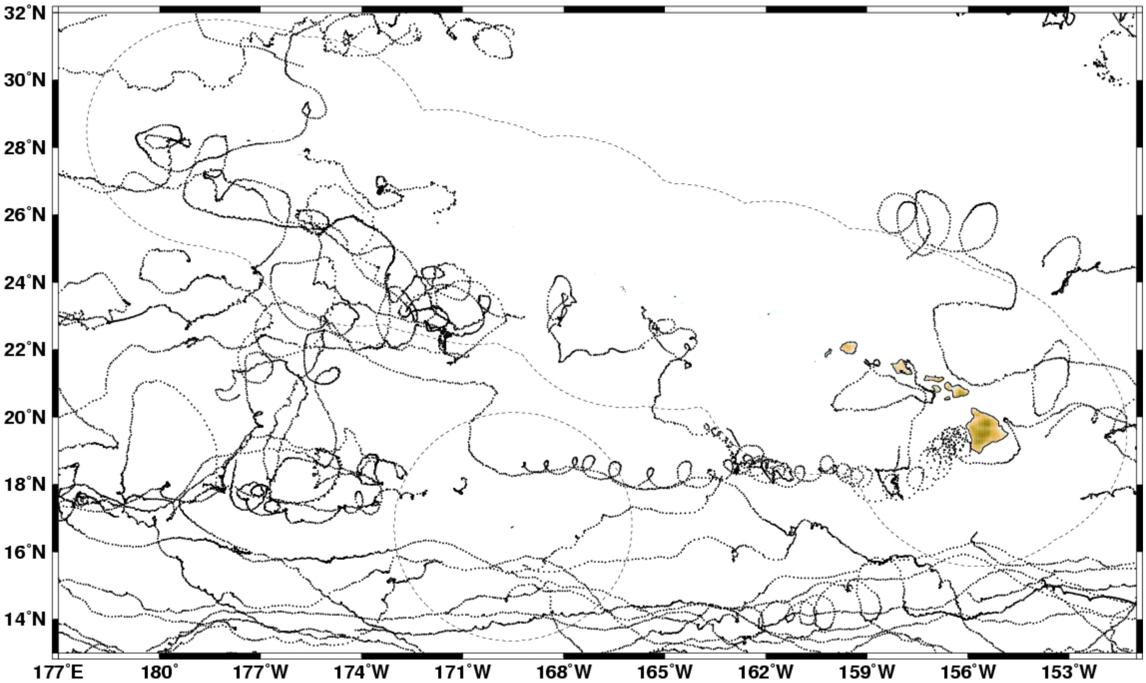

32°N
30°N
28°N
26°N
24°N
22°N
20°N
18°N
16°N
14°N
177°E
180°
177°W
174°W
171°W
168°W
165°W
162°W
159°W
156°W
153°W

Figure 3.

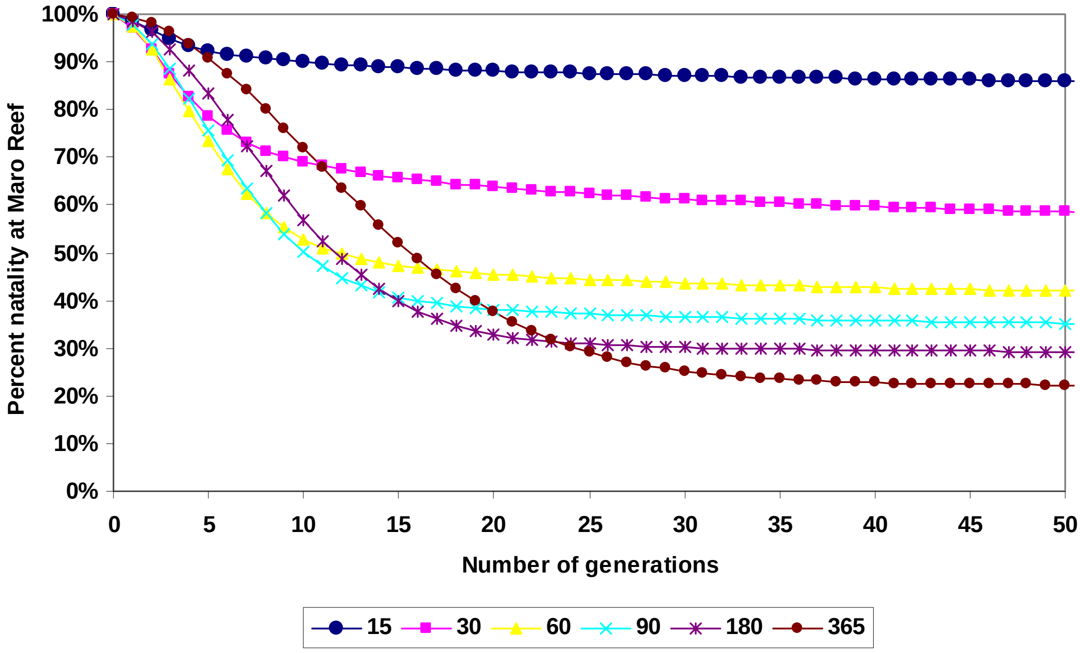

Percent natality at Maro Reef
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
0
5
10
15
20
25
30
35
40
45
50
Number of generations
15
30
60
90
180
365

Figure 4.

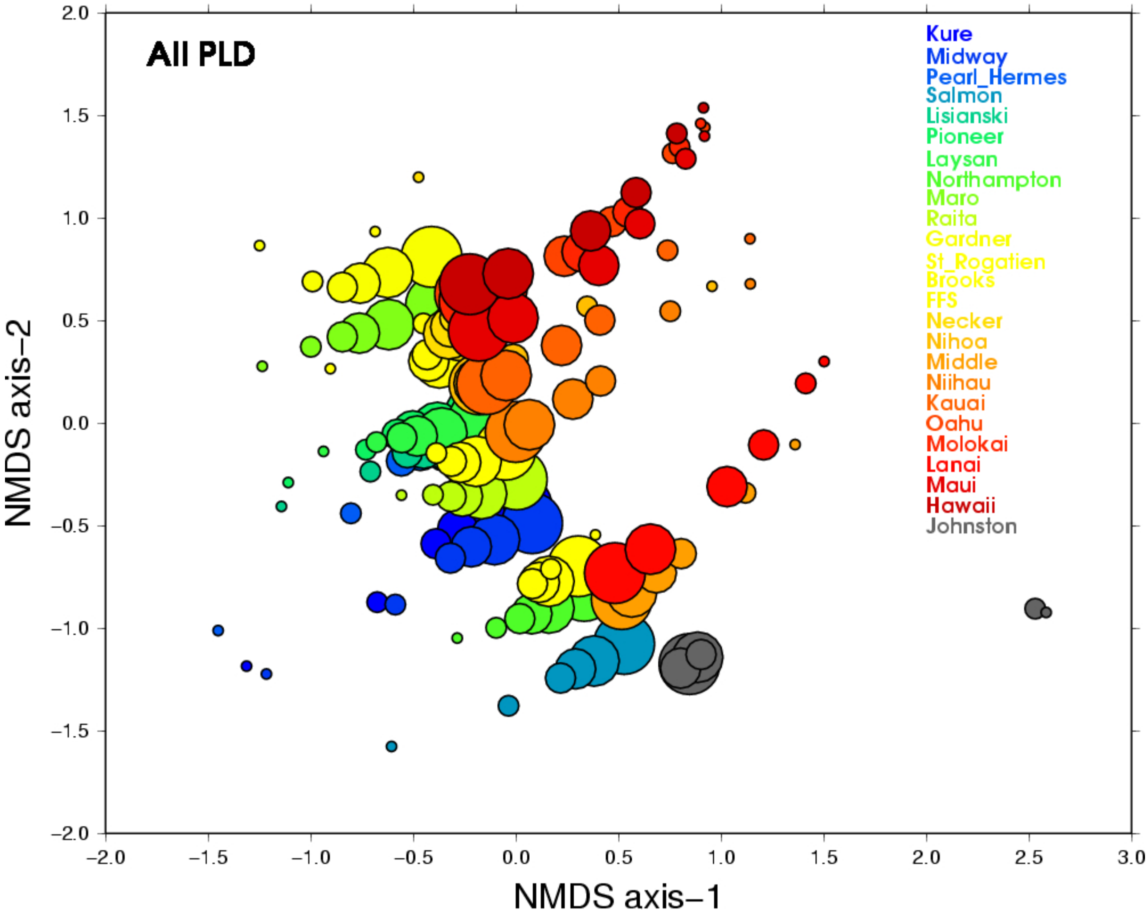
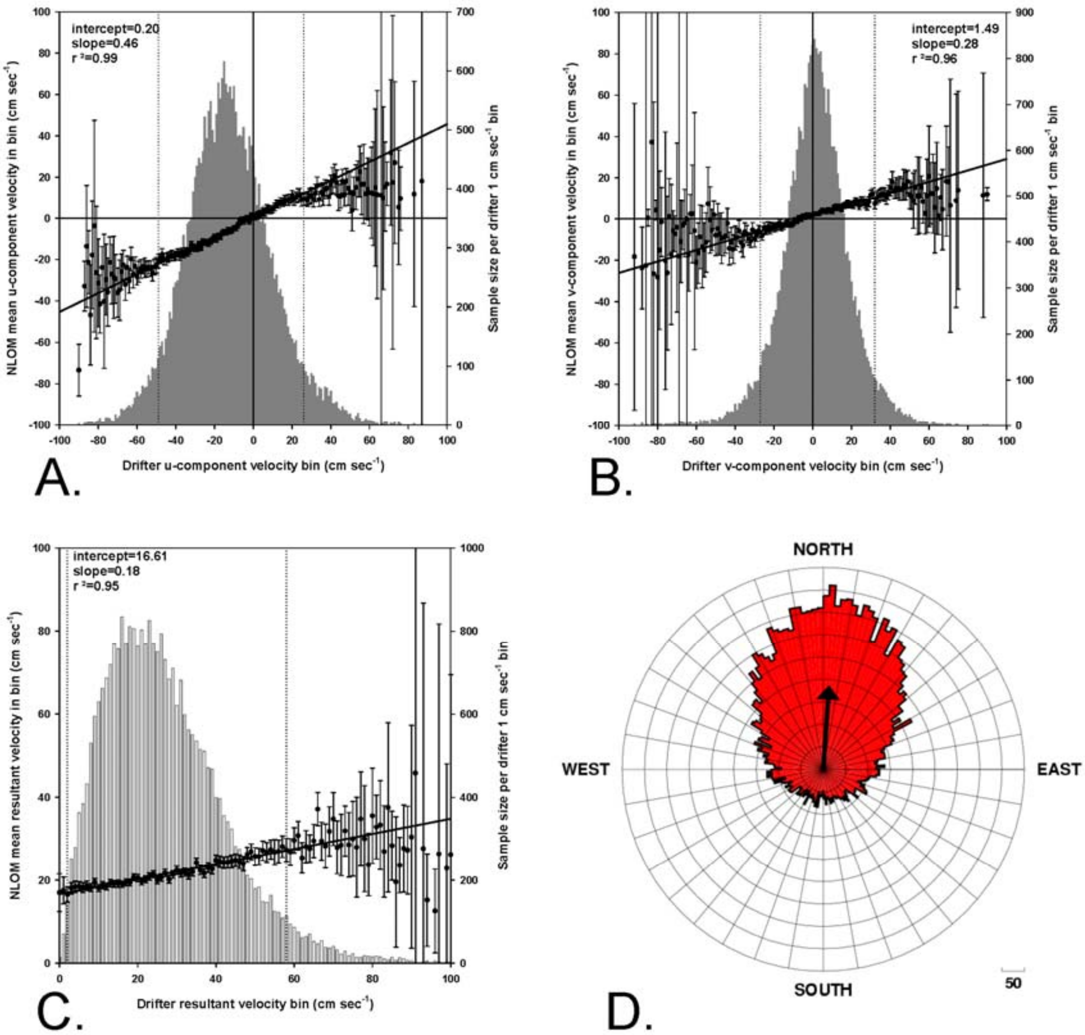
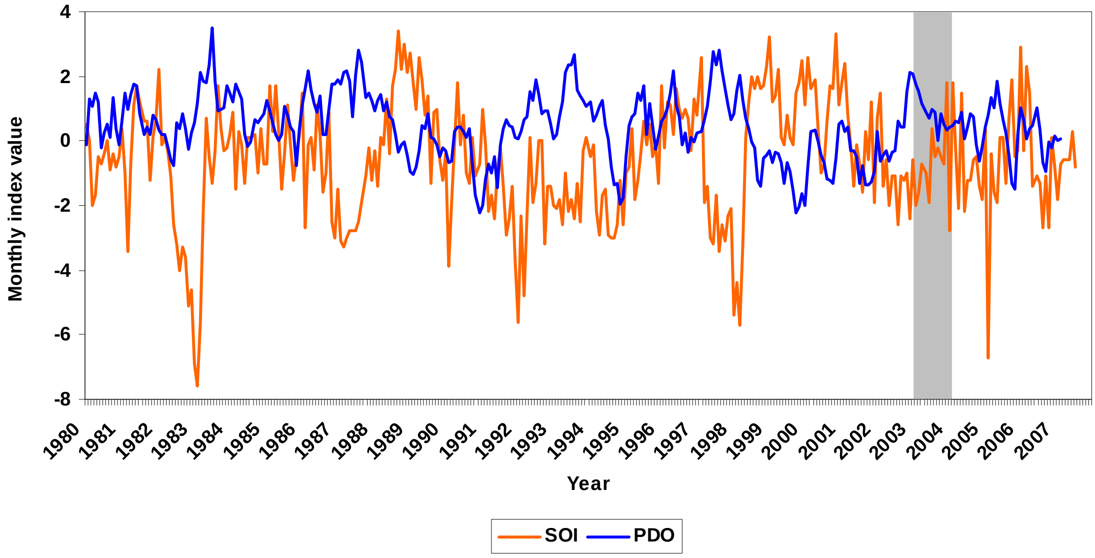

All PLD
NMDS axis–1
NMDS axis–2
−2.0
−1.5
−1.0
−0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Kure
Midway
Pearl_Hermes
Salmon
Lisianski
Pioneer
Laysan
Northampton
Maro
Raita
Gardner
St_Rogatien
Brooks
FFS
Necker
Nihoa
Middle
Niihau
Kauai
Oahu
Molokai
Lanai
Maui
Hawaii
Johnston

Figure 5.



intercept=0.20
slope=0.46
r ²=0.99
NLOM mean u-component velocity in bin (cm sec⁻¹)
Sample size per drifter 1 cm sec⁻¹ bin
Drifter u-component velocity bin (cm sec⁻¹)
A.
intercept=1.49
slope=0.28
r ²=0.96
NLOM mean v-component velocity in bin (cm sec⁻¹)
Sample size per drifter 1 cm sec⁻¹ bin
Drifter v-component velocity bin (cm sec⁻¹)
B.
intercept=16.61
slope=0.18
r ²=0.95
NLOM mean resultant velocity in bin (cm sec⁻¹)
Sample size per drifter 1 cm sec⁻¹ bin
Drifter resultant velocity bin (cm sec⁻¹)
C.
NORTH
WEST
EAST
SOUTH
50
D.

Figure 6.



4
2
0
-2
-4
-6
-8
Monthly index value
1980
1981
1982
1983
1984
1985
1986
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
Year
SOI
PDO

Figure 7A.

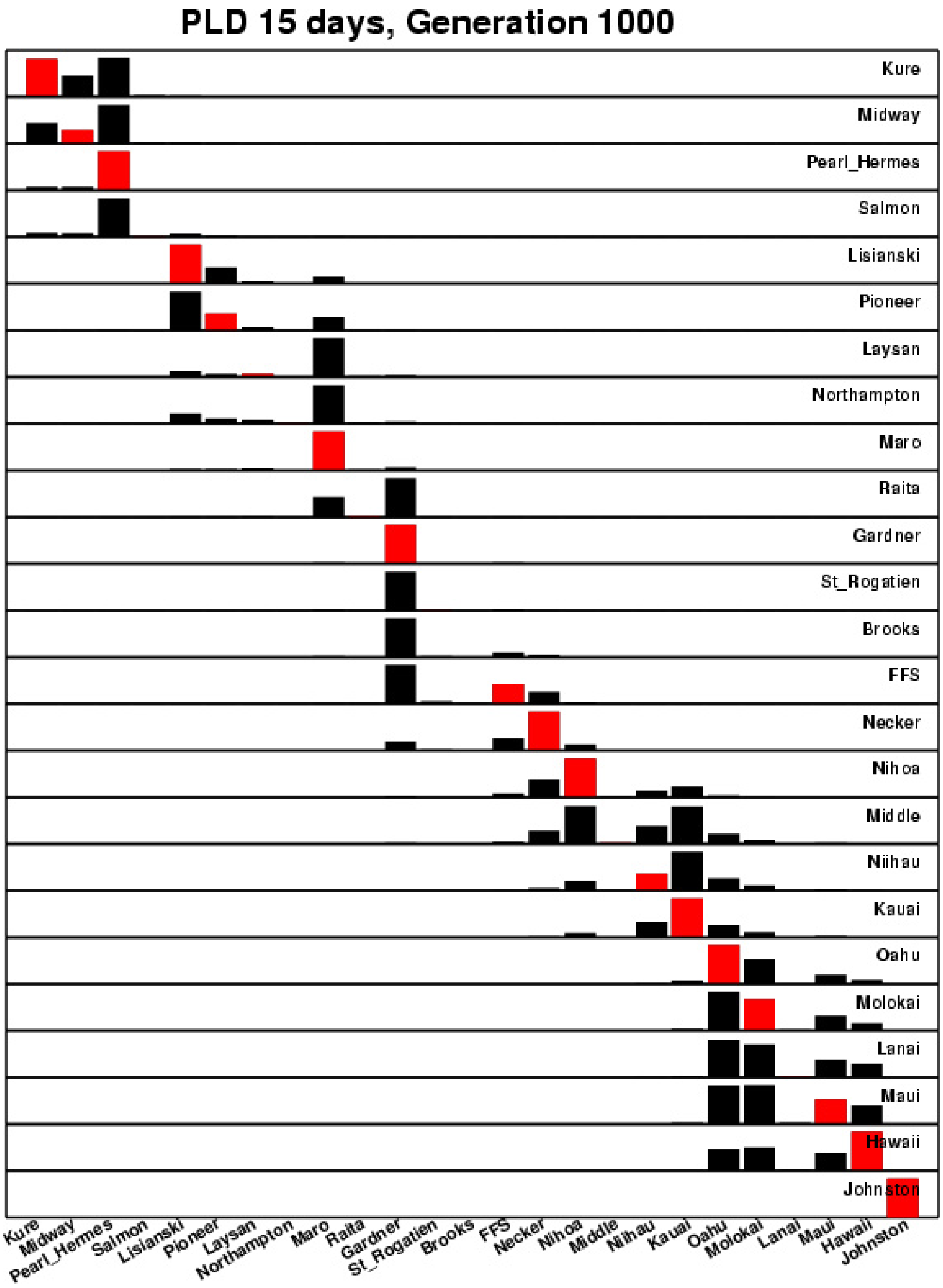
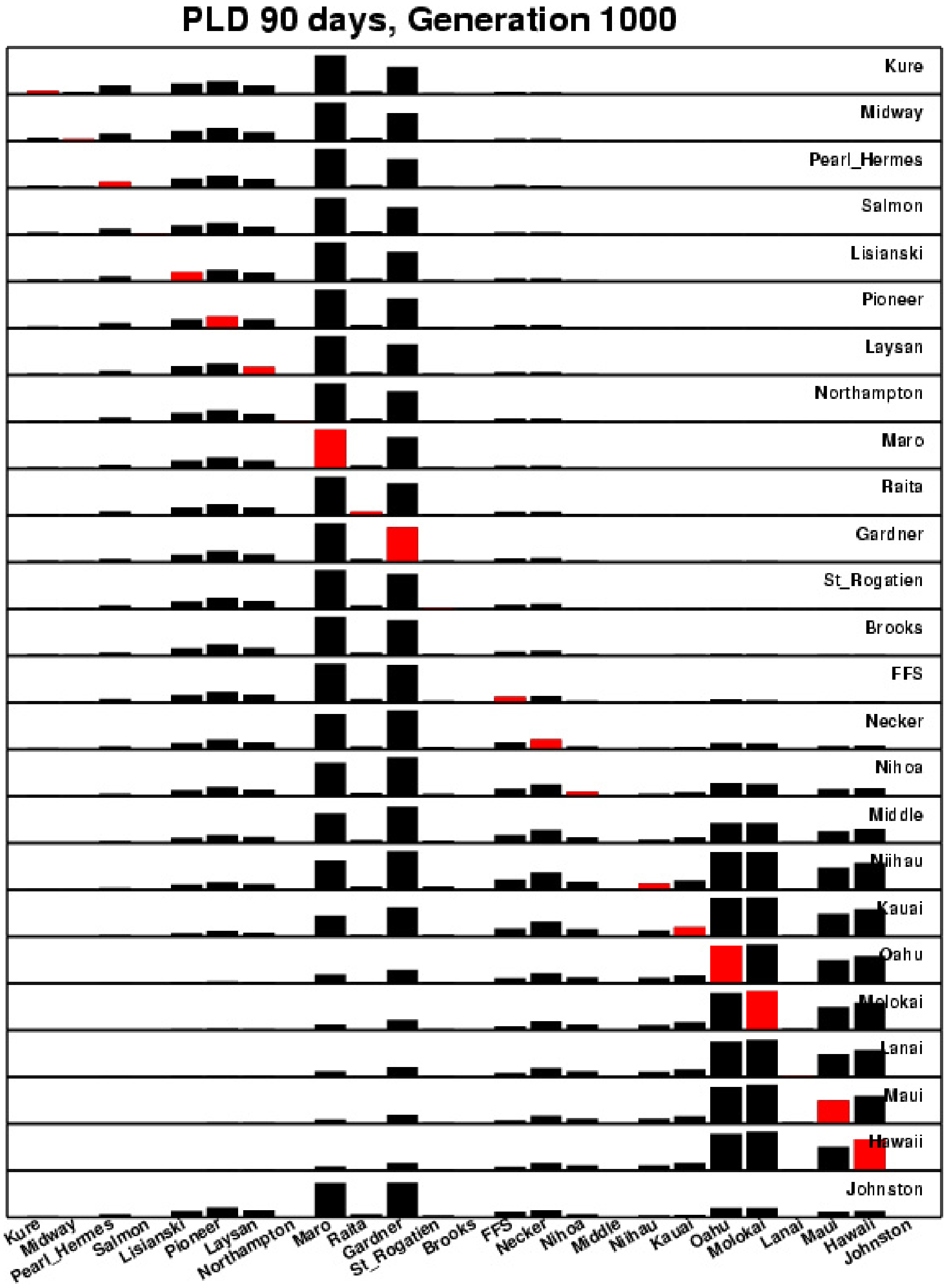

PLD 15 days, Generation 1000
Kure
Midway
Pearl_Hermes
Salmon
Lisianski
Pioneer
Laysan
Northampton
Maro
Raita
Gardner
St_Rogatien
Brooks
FFS
Necker
Nihoa
Middle
Niihau
Kauai
Oahu
Molokai
Lanai
Maui
Hawaii
Johnston

Figure 7B.



PLD 90 days, Generation 1000
Kure
Midway
Pearl_Hermes
Salmon
Lisianski
Pioneer
Laysan
Northampton
Maro
Raita
Gardner
St_Rogatien
Brooks
FFS
Necker
Nihoa
Middle
Niihau
Kauai
Oahu
Molokai
Lanai
Maui
Hawaii
Johnston

Figure 7C.

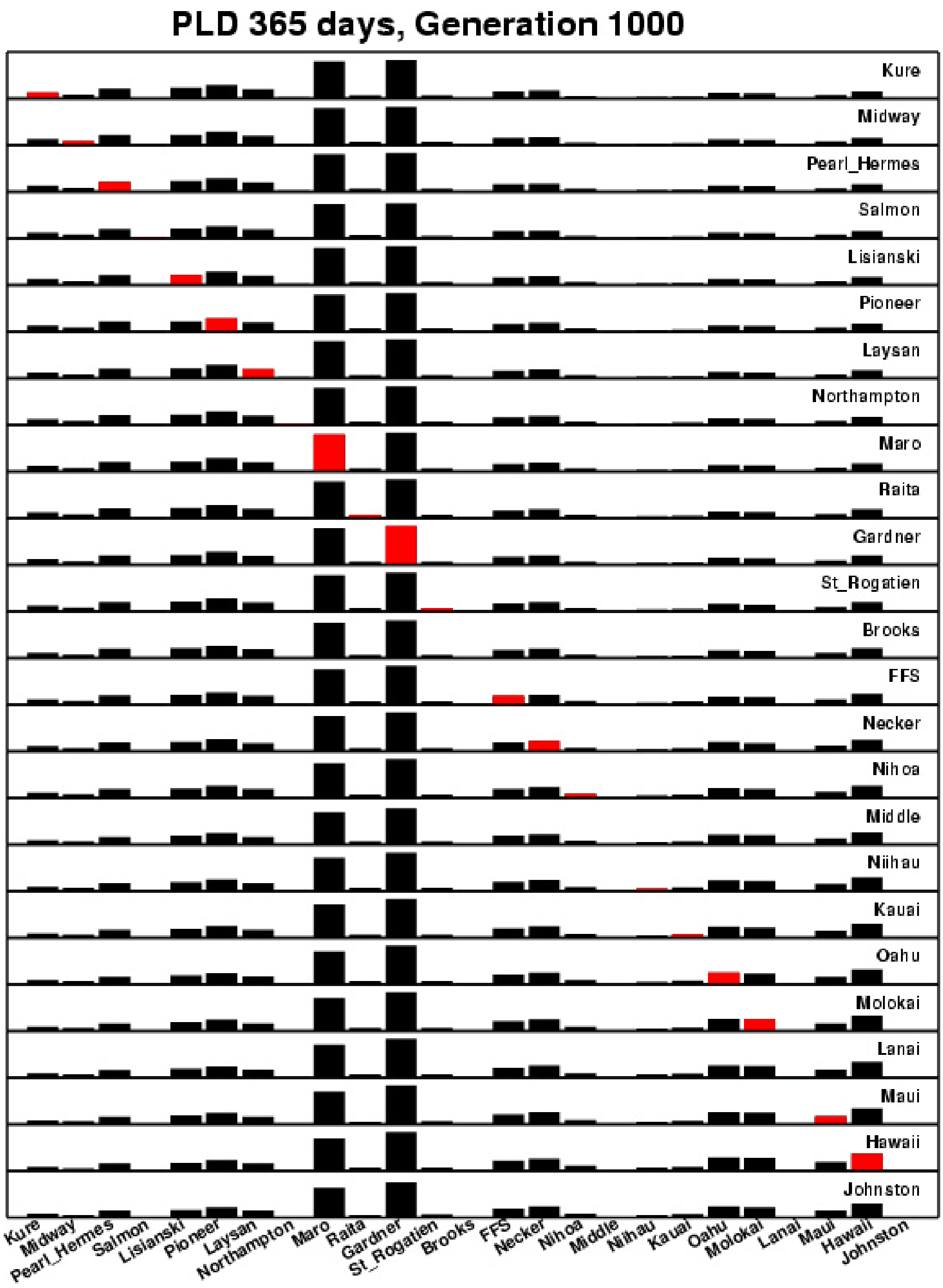

PLD 365 days, Generation 1000
Kure
Midway
Pearl_Hermes
Salmon
Lisianski
Pioneer
Laysan
Northampton
Maro
Raita
Gardner
St_Rogatien
Brooks
FFS
Necker
Nihoa
Middle
Niihau
Kauai
Oahu
Molokai
Lanai
Maui
Hawaii
Johnston

Figure 8.

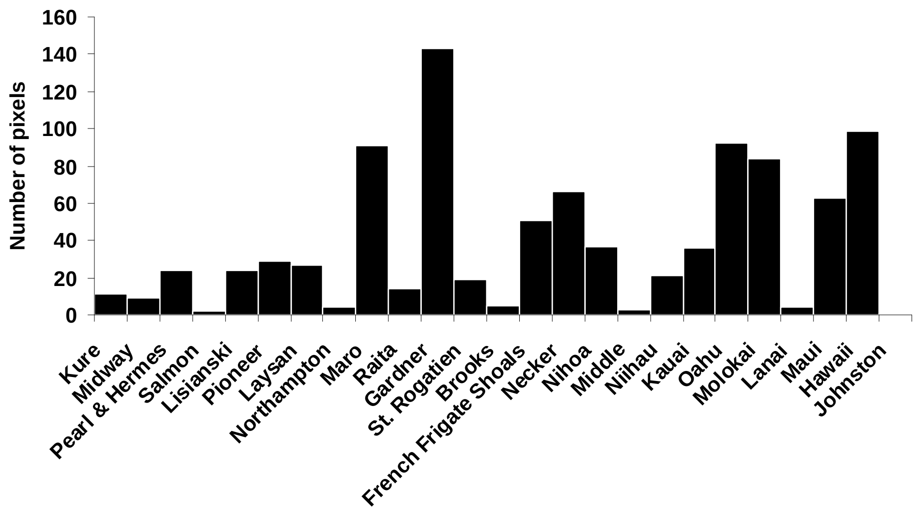
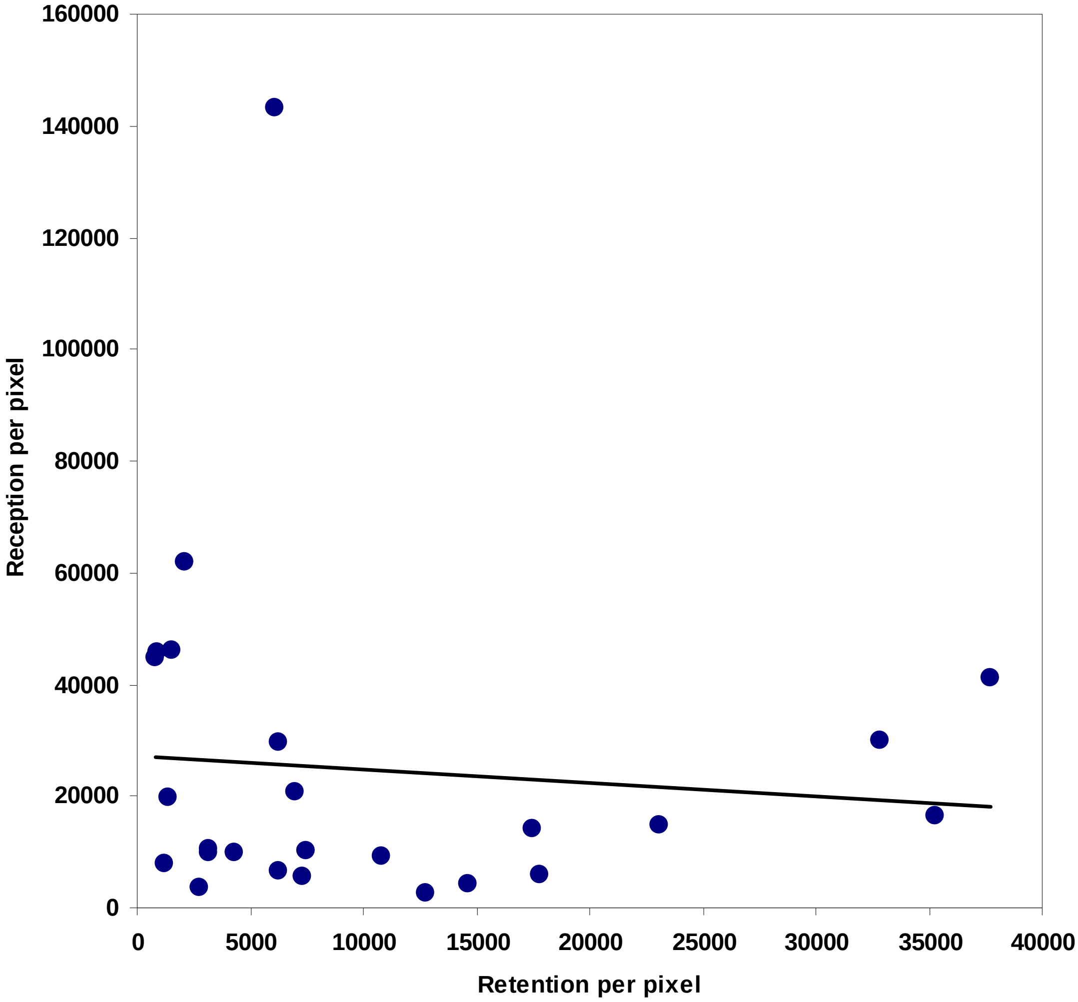

Number of pixels
0
20
40
60
80
100
120
140
160
Kure
Midway
Pearl & Hermes
Salmon
Lisianski
Pioneer
Laysan
Northampton
Maro
Raita
Gardner
St. Rogatien
Brooks
French Frigate Shoals
Necker
Nihoa
Middle
Niihau
Kauai
Oahu
Molokai
Lanai
Maui
Hawaii
Johnston

Figure 9.



Reception per pixel
160000
140000
120000
100000
80000
60000
40000
20000
0
0
5000
10000
15000
20000
25000
30000
35000
40000
Retention per pixel

Appendix Table 1A. Dispersal kernel matrix for 15 day PLD. Each cell represents probability of a larva leaving source location and arriving at sink location using 2003-2004 NLOM daily currents. Highlighted diagonal cells represent natal retention.

Source

Sink	Kure	Midway	Pearl & Hermes	Salmon	Lisianski	Pioneer	Laysan	Northampton	Maro	Raita	Gardner	St Rogatien	Brooks	French Frigate Shoals	Necker	Nihoa	Middle	Niihau	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii	Johnston
Kure	0.043	0.019	0.001	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Midway	0.033	0.078	0.011	0.026	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pearl & Hermes	0.003	0.011	0.128	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Salmon	0.000	0.006	0.024	0.022	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lisianski	0.000	0.000	0.000	0.004	0.201	0.046	0.001	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pioneer	0.000	0.000	0.000	0.001	0.095	0.051	0.013	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Laysan	0.000	0.000	0.000	0.000	0.002	0.024	0.118	0.073	0.048	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northampton	0.000	0.000	0.000	0.000	0.009	0.040	0.057	0.104	0.030	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Maro	0.000	0.000	0.000	0.000	0.000	0.006	0.032	0.034	0.250	0.029	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Raita	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.001	0.011	0.122	0.012	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Gardner	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.018	0.224	0.018	0.012	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
St Rogatien	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.021	0.025	0.024	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Brooks	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.010	0.036	0.043	0.011	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
French Frigate Shoals	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.029	0.045	0.131	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Necker	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.005	0.033	0.326	0.017	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nihoa	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.132	0.035	0.010	0.003	0.000	0.000	0.000	0.000	0.000	0.000
Middle	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.011	0.014	0.004	0.000	0.000	0.000	0.000	0.000	0.000
Niihau	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.018	0.061	0.034	0.001	0.000	0.000	0.000	0.000	0.000
Kauai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.023	0.102	0.306	0.007	0.000	0.000	0.000	0.000	0.000
Oahu	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.015	0.344	0.084	0.028	0.008	0.002	0.000
Molokai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.147	0.463	0.136	0.128	0.005	0.000
Lanai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.009	0.013	0.010	0.002	0.000
Maui	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.152	0.240	0.502	0.044	0.000
Hawaii	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.024	0.146	0.064	0.384	0.000
Johnston	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.024
Lost	0.921	0.886	0.836	0.925	0.691	0.833	0.777	0.762	0.660	0.826	0.727	0.888	0.871	0.818	0.657	0.833	0.910	0.810	0.638	0.468	0.268	0.436	0.288	0.563	0.976

Appendix Table 1B. Dispersal kernel matrix for 30 day PLD. Each cell represents probability of a larva leaving source location and arriving at sink location using 2003-2004 NLOM daily currents. Highlighted diagonal cells represent natal retention.

Sink \ Source	Kure	Midway	Pearl & Hermes	Salmon	Lisianski	Pioneer	Laysan	Northampton	Maro	Raita	Gardner	St Rogatien	Brooks	French Frigate Shoals	Necker	Nihoa	Middle	Niihau	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii	Johnston
Kure	0.020	0.014	0.003	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Midway	0.017	0.023	0.014	0.019	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pearl & Hermes	0.012	0.016	0.042	0.017	0.006	0.002	0.003	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Salmon	0.003	0.007	0.014	0.008	0.004	0.001	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lisianski	0.000	0.001	0.005	0.006	0.063	0.020	0.008	0.013	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pioneer	0.000	0.000	0.003	0.005	0.040	0.018	0.016	0.012	0.006	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Laysan	0.000	0.000	0.000	0.000	0.009	0.024	0.046	0.039	0.034	0.007	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northampton	0.000	0.000	0.001	0.000	0.016	0.023	0.033	0.037	0.025	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Maro	0.000	0.000	0.000	0.000	0.003	0.018	0.037	0.041	0.098	0.031	0.005	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Raita	0.000	0.000	0.000	0.000	0.000	0.002	0.004	0.005	0.017	0.033	0.013	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Gardner	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.003	0.010	0.028	0.084	0.011	0.009	0.005	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
St Rogatien	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.003	0.006	0.013	0.006	0.005	0.003	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Brooks	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.004	0.008	0.007	0.008	0.005	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
French Frigate Shoals	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.005	0.006	0.013	0.017	0.028	0.012	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Necker	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.008	0.012	0.031	0.119	0.015	0.008	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000
Nihoa	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.003	0.010	0.038	0.025	0.019	0.010	0.002	0.000	0.000	0.000	0.000	0.000
Middle	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.006	0.006	0.006	0.004	0.001	0.000	0.000	0.000	0.000	0.000
Niihau	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.008	0.013	0.016	0.016	0.003	0.000	0.001	0.000	0.000	0.000
Kauai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.026	0.051	0.127	0.012	0.002	0.005	0.001	0.000	0.000
Oahu	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.012	0.026	0.181	0.077	0.033	0.017	0.007	0.000
Molokai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.004	0.004	0.118	0.264	0.102	0.116	0.012	0.000
Lanai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.003	0.006	0.005	0.006	0.002	0.000
Maui	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.004	0.002	0.033	0.146	0.167	0.314	0.038	0.000
Hawaii	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.009	0.001	0.018	0.035	0.111	0.067	0.264	0.000
Johnston	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007
Lost	0.948	0.938	0.919	0.937	0.856	0.892	0.852	0.846	0.803	0.876	0.870	0.950	0.947	0.925	0.852	0.922	0.913	0.874	0.808	0.631	0.469	0.577	0.478	0.676	0.993

Appendix Table 1C. Dispersal kernel matrix for 60 day PLD. Each cell represents probability of a larva leaving source location and arriving at sink location using 2003-2004 NLOM daily currents. Highlighted diagonal cells represent natal retention.

Source

Sink	Kure	Midway	Pearl & Hermes	Salmon	Lisianski	Pioneer	Laysan	Northampton	Maro	Raita	Gardner	St Rogatien	Brooks	French Frigate Shoals	Necker	Nihoa	Middle	Niihau	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii	Johnston
Kure	0.007	0.008	0.004	0.007	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Midway	0.008	0.010	0.007	0.008	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pearl & Hermes	0.013	0.010	0.016	0.012	0.009	0.004	0.003	0.004	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Salmon	0.003	0.004	0.006	0.006	0.003	0.002	0.001	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lisianski	0.001	0.002	0.005	0.005	0.017	0.010	0.006	0.006	0.005	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pioneer	0.001	0.002	0.004	0.003	0.013	0.008	0.006	0.006	0.005	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Laysan	0.000	0.000	0.002	0.001	0.010	0.013	0.016	0.014	0.015	0.008	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northampton	0.000	0.000	0.003	0.002	0.011	0.011	0.013	0.012	0.012	0.007	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Maro	0.000	0.000	0.001	0.000	0.009	0.016	0.024	0.022	0.030	0.020	0.006	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Raita	0.000	0.000	0.000	0.000	0.002	0.005	0.007	0.006	0.011	0.009	0.006	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Gardner	0.000	0.000	0.000	0.000	0.001	0.004	0.007	0.009	0.015	0.018	0.025	0.008	0.007	0.005	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
St Rogatien	0.000	0.000	0.000	0.000	0.001	0.002	0.002	0.003	0.004	0.005	0.007	0.004	0.003	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Brooks	0.000	0.000	0.000	0.000	0.000	0.001	0.002	0.002	0.003	0.004	0.006	0.004	0.003	0.002	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
French Frigate Shoals	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.002	0.004	0.006	0.008	0.007	0.006	0.007	0.002	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Necker	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.003	0.009	0.012	0.017	0.027	0.009	0.008	0.004	0.003	0.000	0.000	0.000	0.000	0.000	0.001
Nihoa	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.005	0.006	0.008	0.016	0.020	0.015	0.010	0.009	0.002	0.001	0.000	0.000	0.000	0.000
Middle	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.002	0.004	0.003	0.003	0.003	0.001	0.000	0.000	0.000	0.000	0.000
Niihau	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.006	0.005	0.005	0.006	0.003	0.001	0.001	0.001	0.000	0.001
Kauai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.011	0.014	0.017	0.030	0.010	0.005	0.005	0.002	0.001	0.001
Oahu	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.007	0.013	0.018	0.025	0.067	0.049	0.025	0.022	0.009	0.000
Molokai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.007	0.012	0.012	0.065	0.108	0.059	0.073	0.014	0.000
Lanai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.002	0.003	0.003	0.003	0.001	0.000
Maui	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.004	0.011	0.008	0.039	0.098	0.088	0.136	0.029	0.000
Hawaii	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.004	0.013	0.007	0.024	0.038	0.076	0.058	0.164	0.000
Johnston	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002
Lost	0.967	0.964	0.952	0.957	0.919	0.922	0.912	0.913	0.895	0.917	0.935	0.958	0.959	0.956	0.933	0.934	0.924	0.906	0.897	0.786	0.697	0.742	0.704	0.781	0.994

Appendix Table 1D. Dispersal kernel matrix for 90 day PLD. Each cell represents probability of a larva leaving source location and arriving at sink location using 2003-2004 NLOM daily currents. Highlighted diagonal cells represent natal retention.

Sink \ Source	Kure	Midway	Pearl & Hermes	Salmon	Lisianski	Pioneer	Laysan	Northampton	Maro	Raita	Gardner	St Rogatien	Brooks	French Frigate Shoals	Necker	Nihoa	Middle	Niihau	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii	Johnston
Kure	0.004	0.004	0.004	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Midway	0.004	0.005	0.006	0.006	0.002	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pearl & Hermes	0.007	0.006	0.009	0.010	0.006	0.004	0.004	0.005	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Salmon	0.002	0.003	0.004	0.004	0.002	0.002	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lisianski	0.002	0.003	0.005	0.005	0.010	0.007	0.004	0.005	0.003	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pioneer	0.002	0.002	0.003	0.003	0.007	0.006	0.004	0.004	0.003	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Laysan	0.001	0.002	0.003	0.002	0.008	0.008	0.008	0.008	0.008	0.006	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northampton	0.001	0.001	0.003	0.002	0.009	0.008	0.008	0.008	0.007	0.005	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Maro	0.001	0.001	0.002	0.002	0.009	0.012	0.014	0.013	0.016	0.012	0.005	0.002	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Raita	0.000	0.000	0.001	0.000	0.003	0.005	0.005	0.005	0.007	0.005	0.003	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Gardner	0.000	0.000	0.000	0.000	0.003	0.006	0.008	0.009	0.012	0.012	0.011	0.006	0.005	0.004	0.003	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
St Rogatien	0.000	0.000	0.000	0.000	0.001	0.002	0.002	0.003	0.004	0.003	0.004	0.003	0.003	0.002	0.002	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Brooks	0.000	0.000	0.000	0.000	0.001	0.002	0.002	0.002	0.003	0.003	0.004	0.003	0.003	0.002	0.002	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
French Frigate Shoals	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.002	0.002	0.003	0.006	0.006	0.005	0.004	0.004	0.002	0.003	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.001
Necker	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.004	0.007	0.008	0.009	0.011	0.006	0.006	0.004	0.003	0.001	0.000	0.000	0.000	0.000	0.001
Nihoa	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.003	0.004	0.006	0.007	0.011	0.010	0.009	0.007	0.006	0.002	0.001	0.001	0.000	0.000	0.001
Middle	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.002	0.002	0.003	0.002	0.002	0.002	0.001	0.001	0.000	0.000	0.000	0.000
Niihau	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.002	0.004	0.003	0.004	0.003	0.002	0.001	0.001	0.001	0.001	0.001
Kauai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.002	0.005	0.009	0.009	0.010	0.011	0.007	0.005	0.004	0.003	0.002	0.002
Oahu	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.004	0.009	0.011	0.014	0.017	0.031	0.029	0.020	0.018	0.010	0.001
Molokai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.005	0.008	0.011	0.013	0.036	0.052	0.035	0.042	0.013	0.000
Lanai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.002	0.002	0.002	0.001	0.000
Maui	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.003	0.004	0.010	0.009	0.031	0.057	0.048	0.066	0.022	0.000
Hawaii	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.002	0.004	0.012	0.009	0.025	0.035	0.058	0.047	0.107	0.000
Johnston	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Lost	0.975	0.973	0.961	0.962	0.935	0.935	0.938	0.933	0.929	0.939	0.953	0.965	0.964	0.964	0.950	0.944	0.938	0.923	0.924	0.863	0.817	0.831	0.821	0.843	0.988

Appendix Table 1E. Dispersal kernel matrix for 180 day PLD. Each cell represents probability of a larva leaving source location and arriving at sink location using 2003-2004 NLOM daily currents. Highlighted diagonal cells represent natal retention.

Sink \ Source	Kure	Midway	Pearl & Hermes	Salmon	Lisianski	Pioneer	Laysan	Northampton	Maro	Raita	Gardner	St Rogatien	Brooks	French Frigate Shoals	Necker	Nihoa	Middle	Niihau	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii	Johnston
Kure	0.002	0.002	0.002	0.002	0.001	0.001	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Midway	0.002	0.002	0.002	0.002	0.002	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pearl & Hermes	0.004	0.005	0.004	0.005	0.003	0.003	0.002	0.003	0.002	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Salmon	0.001	0.002	0.001	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lisianski	0.003	0.003	0.003	0.003	0.004	0.003	0.003	0.003	0.002	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Pioneer	0.002	0.002	0.002	0.003	0.003	0.003	0.002	0.002	0.002	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Laysan	0.002	0.002	0.003	0.003	0.004	0.004	0.003	0.003	0.004	0.002	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Northampton	0.002	0.002	0.003	0.002	0.004	0.004	0.003	0.004	0.003	0.003	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Maro	0.003	0.003	0.004	0.004	0.006	0.006	0.006	0.006	0.006	0.004	0.003	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002
Raita	0.001	0.001	0.002	0.001	0.002	0.003	0.002	0.003	0.003	0.002	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Gardner	0.002	0.003	0.003	0.003	0.005	0.005	0.005	0.006	0.006	0.005	0.004	0.002	0.002	0.002	0.002	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.003
St Rogatien	0.001	0.001	0.001	0.001	0.002	0.002	0.002	0.002	0.002	0.002	0.001	0.001	0.001	0.001	0.001	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Brooks	0.000	0.000	0.001	0.001	0.001	0.002	0.001	0.002	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
French Frigate Shoals	0.000	0.000	0.001	0.000	0.001	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.001
Necker	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.002	0.003	0.003	0.003	0.003	0.003	0.002	0.002	0.002	0.002	0.001	0.001	0.000	0.000	0.000	0.002
Nihoa	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.002	0.002	0.003	0.003	0.003	0.004	0.004	0.004	0.003	0.003	0.002	0.001	0.001	0.001	0.001	0.003
Middle	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.001
Niihau	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.002	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Kauai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.002	0.002	0.002	0.003	0.004	0.004	0.004	0.003	0.003	0.003	0.003	0.003	0.003	0.002
Oahu	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.001	0.001	0.001	0.002	0.003	0.003	0.004	0.005	0.007	0.006	0.006	0.006	0.008	0.009	0.008	0.008	0.007	0.003
Molokai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.002	0.002	0.002	0.004	0.005	0.005	0.006	0.006	0.009	0.011	0.011	0.011	0.008	0.002
Lanai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.000
Maui	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.002	0.003	0.004	0.005	0.006	0.006	0.011	0.014	0.013	0.014	0.011	0.001
Hawaii	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.002	0.002	0.003	0.005	0.006	0.009	0.008	0.016	0.020	0.027	0.024	0.039	0.001
Johnston	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lost	0.973	0.971	0.970	0.968	0.958	0.958	0.962	0.959	0.959	0.967	0.971	0.972	0.971	0.971	0.965	0.962	0.962	0.960	0.962	0.948	0.939	0.933	0.938	0.928	0.971

Appendix Table 1F. Dispersal kernel matrix for 365 day PLD. Each cell represents probability of a larva leaving source location and arriving at sink location using 2003-2004 NLOM daily currents. Highlighted diagonal cells represent natal retention.

Sink \ Source	Kure	Midway	Pearl & Hermes	Salmon	Lisianski	Pioneer	Laysan	Northampton	Maro	Raita	Gardner	St Rogatien	Brooks	French Frigate Shoals	Necker	Nihoa	Middle	Niihau	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii	Johnston
Kure	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Midway	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pearl & Hermes	0.002	0.003	0.002	0.002	0.002	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Salmon	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lisianski	0.002	0.002	0.001	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Pioneer	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Laysan	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Northampton	0.001	0.001	0.001	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Maro	0.002	0.002	0.002	0.003	0.002	0.002	0.002	0.002	0.002	0.002	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002
Raita	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Gardner	0.002	0.002	0.002	0.002	0.003	0.002	0.002	0.002	0.002	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002
St Rogatien	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Brooks	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
French Frigate Shoals	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
Necker	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002
Nihoa	0.001	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002
Middle	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Niihau	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.001	0.000	0.000	0.000	0.001	0.000	0.001	0.001
Kauai	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.002
Oahu	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.003	0.002	0.003	0.003
Molokai	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.003	0.002	0.003	0.002
Lanai	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Maui	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.002	0.002	0.002	0.002	0.002	0.003	0.003	0.003	0.004	0.002
Hawaii	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.002	0.002	0.003	0.003	0.003	0.004	0.004	0.005	0.006	0.007	0.006	0.008	0.003
Johnston	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lost	0.981	0.980	0.980	0.979	0.978	0.978	0.981	0.979	0.980	0.983	0.984	0.984	0.984	0.984	0.983	0.984	0.984	0.984	0.985	0.983	0.982	0.979	0.982	0.976	0.971