# Modeled larval connectivity of a multi-species reef fish and invertebrate assemblage off the coast of Moloka'i, Hawai'i

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We use a novel individual-based model (IBM) to simulate larval dispersal around the island of Moloka'i in the Hawaiian Archipelago. Our model uses ocean current output from the Massachusetts Institute of Technology general circulation model (MITgcm) as well as biological data on four invertebrate and seven fish species of management relevance to produce connectivity maps among sites around the island of Moloka'i. These 11 species span the range of life history characteristics of Hawaiian coral reef species and show different spatial and temporal patterns of connectivity as a result. As expected, the longer the pelagic larval duration (PLD), the greater the proportion of larvae that disperse longer distances, but regardless of PLD (3 – 270d) most successful dispersal occurs either over short distances within an island (<30 km) or to adjacent islands (50-125km). Again, regardless of PLD, around the island of Moloka'i, connectivity tends to be greatest among sites along the same coastline and exchange between northward, southward, eastward and westward-facing shores is limited. Using a graph-theoretic approach to visualize the data, we highlight that the eastern side of the island tends to show the greatest out-degree and betweenness centrality, which indicate important larval sources and connectivity pathways for the rest of the island. The marine protected area surrounding Kalaupapa National Historical Park emerges as a potential source for between-island larval connections, and the west coast of the Park is one of the few regions on Moloka'i that acts as a net larval source across all species. Using this IBM and visualization approach reveals patterns of exchange between habitat regions and highlights critical larval sources and multi-generational pathways to indicate priority areas for marine resource managers.

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## Abstract:

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17   island of Molokaʻi in the Hawaiian Archipelago. Our model uses ocean current output from the
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24   days) most successful dispersal occurs either over short distances within an island (<30 km) or to
25   adjacent islands (50-125 km). Again, regardless of PLD, around the island of Molokaʻi,
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27   northward, southward, eastward and westward-facing shores is limited. Using a graph-theoretic
28   approach to visualize the data, we highlight that the eastern side of the island tends to show the
29   greatest out-degree and betweenness centrality, which indicate important larval sources and
30   connectivity pathways for the rest of the island. The marine protected area surrounding
31   Kalaupapa National Historical Park emerges as a potential source for between-island larval
32   connections, and the west coast of the Park is one of the few regions on Molokaʻi that acts as a
33   net larval source across all species. This IBM approach reveals patterns of exchange between
34   habitat regions and highlights critical larval sources and multi-generational pathways to indicate
35   priority areas for marine resource managers.

## Introduction:

37      Knowledge of population connectivity is necessary for effective management in marine
38   environments (Mitarai, Siegel, & Winters, 2008; Botsford et al., 2009; Toonen et al., 2011). For
39   many species of marine invertebrate and reef fish, dispersal is mostly limited to the pelagic larval
40   life stage. Therefore, an understanding of larval dispersal patterns is critical for studying
41   population dynamics, connectivity, and conservation in the marine environment (Jones,
42   Srinivasan, & Almany, 2007; Lipcius et al., 2008; Gaines et al., 2010; Toonen et al., 2011).
43   Many coastal and reef species have a bi-phasic life history in which adults display limited
44   geographic range and high site fidelity, while larvae are pelagic and highly mobile (Thorson,
45   1950; Scheltema, 1971; Strathmann, 1993; Marshall et al., 2012). This life history strategy is not
46   only common to sessile invertebrates such as corals or limpets; many reef fish species have been
47   shown to have a home range of <1 km as adults (Meyer et al., 2000; Meyer, Papastamatiou, &
48   Clark, 2010). Depending on species, the mobile planktonic stage can last from hours to months
49   and has the potential to transport larvae up to hundreds of kilometers away from a site of origin
50   (Scheltema, 1971; Richmond, 1987; Shanks, 2009). Knowledge of larval dispersal patterns can
51   be used to inform effective management, such as marine spatial management strategies that
52   sustain source populations of breeding individuals capable of dispersing offspring to other areas.
53      Both biological and physical factors impact larval dispersal, although the relative
54   importance of these factors is likely variable among species and sites and remains debated
55   (Levin, 2006; Paris, Chérubin, & Cowen, 2007; Cowen & Sponaugle, 2009; White et al., 2010).
56   In situ data on pelagic larvae are sparse; marine organisms at this life stage are difficult to
57   capture and identify, and are typically found in low densities across large areas of the open ocean
58   (Clarke, 1991; Wren & Kobayashi, 2016). A variety of genetic and chemistry techniques have

59  therefore been developed to estimate larval connectivity (Gillanders 2005; Leis et al., 2011;
60  Toonen et al., 2011; Johnson et al., 2018). Computer models informed by field and laboratory
61  data have also become a valuable tool for estimating larval dispersal and population connectivity
62  (Paris, Chérubin, & Cowen, 2007; Botsford et al., 2009; Sponaugle et al., 2012; Kough, Paris, &
63  Butler, 2013; Wood et al., 2014). Individual-based models, or IBMs, can incorporate both
64  biological and physical factors known to influence larval movement. Pelagic larval duration
65  (PLD), for example, is the amount of time a larva spends in the water column before settlement
66  and can vary widely among or even within species (Toonen & Pawlik, 2001). PLD affects how
67  far an individual can be successfully transported by ocean currents, and so is expected to directly
68  affect connectivity patterns (Siegel et al., 2003; Shanks, 2009; Dawson et al., 2014). In addition
69  to PLD, adult reproductive strategy and timing (Carson et al., 2010; Portnoy et al., 2013),
70  fecundity (Castorani et al., 2017), larval mortality (Vikebø et al., 2007), and larval
71  developmental, morphological, and behavioral characteristics (Paris, Chérubin, & Cowen, 2007)
72  may all play a role in shaping connectivity patterns. Physical factors such as temperature,
73  bathymetry, and current direction can also substantially influence connectivity (Cowen &
74  Sponaugle, 2009). In this study, we incorporated both biotic and abiotic components in an IBM
75  coupled with an oceanographic model to predict fine-scale patterns of larval exchange around the
76  island of Moloka'i in the Hawaiian archipelago.
77      The main Hawaiian Islands are located in the middle of the North Pacific Subtropical
78  Gyre, and are bordered by the North Hawaiian Ridge current along the northern coasts of the
79  islands and the Hawaii Lee Current along the southern coasts, both of which run east to west and
80  are driven by the prevailing easterly trade winds (Lumpkin, 1998, Friedlander et al., 2005). The
81  Hawai'i Lee Countercurrent, which runs along the southern perimeter of the chain, flows west to
82  east (Lumpkin, 1998). The pattern of mesoscale eddies around the islands is complex and varies
83  seasonally (Friedlander et al., 2005; Vaz et al., 2013).
84      Hawaiian marine communities face unprecedented pressures, including coastal
85  development, overexploitation, disease, and increasing temperature and acidification due to
86  climate change (Smith, 1993; Lowe, 1995; Coles & Brown, 2003; Friedlander et al., 2003;
87  Friedlander et al., 2005; Aeby, 2006). Declines in Hawaiian marine resources argue for
88  implementation of a more holistic approach than traditional single-species maximum sustainable
89  yield techniques, which have proven ineffective (Goodyear, 1996; Hilborn, 2011). There is a
90  general movement toward the use of ecosystem-based management, which requires knowledge
91  of ecosystem structure and connectivity patterns to establish and manage marine spatial planning
92  areas (Slocombe, 1993; Browman et al., 2004; Pikitch et al., 2004; Arkema, Abramson, &
93  Dewsbury, 2006). Kalaupapa National Historical Park is a federal marine protected area (MPA)
94  located on the north shore of Moloka'i, an island in the Maui Nui complex of the Hawaiian
95  archipelago, that includes submerged lands and waters up to ¼ mile offshore (NOAA, 2009). At
96  least five IUCN red-listed coral species have been identified within this area (Kenyon, Maragos,
97  & Fenner, 2011), and in 2010 the Park showed the greatest fish biomass and species diversity out
98  of four Hawaiian National Parks surveyed (Beets, Brown, & Friedlander, 2010). One of the
99  major benefits expected of MPAs is that the protected waters within the area provide a source of
100  larval spillover to other sites on the island, seeding these areas for commercial, recreational, and
101  subsistence fishing (McClanahan & Mangi, 2000; Halpern & Warner, 2003; Lester et al., 2009).
102      In this study, we used a Lagrangian particle-tracking IBM (Wong-Ala et al., 2018) to
103  simulate larval dispersal around Moloka'i and to estimate the larval exchange among sites at the
104  scale of an individual island. We have parameterized our model with biological data for eleven

105    species covering a breadth of Hawaiian reef species life histories (e.g. habitat preferences, larval
106    behaviors, and pelagic larval durations, Table 1), and of interest to both the local community and
107    resource managers. Our goals were to examine patterns of species-specific connectivity,
108    characterize the location and relative magnitude of connections around Moloka'i, describe sites
109    of potential management relevance, and address the question of whether Kalaupapa National
110    Historical Park provides larval spillover for adjacent sites on Moloka'i, or connections to the
111    adjacent islands of Hawai'i, Maui, O'ahu, Lana'i, and Kaho'olawe.

## Methods:

### I) Circulation model

114        We selected the hydrodynamic model MITgcm, which is designed for the study of
115    dynamical processes in the ocean on a horizontal scale. This model solves incompressible
116    Navier-Stokes equations to describe the motion of viscous fluid on a sphere, discretized using a
117    finite-volume technique (Marshall et al., 1997). The 1-km resolution MITgcm domain for this
118    study extends from 198.2°E to 206°E and from 17°N to 22.2°N, an area that includes the islands
119    of Moloka'i, Maui, Lana'i, Kaho'olawe, O'ahu, and Hawai'i. While Ni'ihau and southern Kauai
120    also fall within the domain, we discarded connectivity to these islands because they lie within the
121    0.5° boundary zone of the current model. Boundary conditions are enforced over 20 grid points
122    on all sides of the model domain. Vertically, the model is divided into 50 layers that increase in
123    thickness with depth, from 5 m at the surface (0.0 – 5.0 m) to 510 m at the base (4470 – 4980 m).
124    Model variables were initialized using the output of a Hybrid Coordinate Ocean Model
125    (HYCOM) at a horizontal resolution of 0.04° (~ 4 km) configured for the main Hawaiian Islands,
126    using the General Bathymetric Chart of the Oceans database (GEBCO, 1/60°) (Jia et al., 2011).
127        The simulation runs from March 31$^{st}$, 2011 to July 30$^{th}$, 2013 with a temporal resolution
128    of 24 hours and shows seasonal eddies as well as persistent mesoscale features (Fig. S1). We do
129    not include tides in the model due to temporal resolution. Our model period represents a neutral
130    ocean state; no El Niño or La Niña events occurred during this time period. To ground-truth the
131    circulation model, we compared surface current output to real-time trajectories of surface drifters
132    from the GDP Drifter Data Assembly Center (Fig. S2) (Elipot et al., 2016), as well as other
133    current models of the area (Wren et al., 2016; Storlazzi et al., 2017).

### II) Biological model

135        To simulate larval dispersal, we used a modified version of the Wong-Ala et al. (2018)
136    IBM, a 3D Lagrangian particle-tracking model written in the R programming language (R Core
137    Team, 2017). The model takes the aforementioned MITgcm current products as input, as well as
138    shoreline shapefiles extracted from the full resolution NOAA Global Self-consistent Hierarchical
139    High-resolution Geography database, v2.3.0 (Wessel & Smith, 1996). Our model included 65
140    land masses within the geographic domain, the largest being the island of Hawai'i and the
141    smallest being Pu'uki'i Island, a 1.5-acre islet off the eastern coast of Maui. To model depth, we
142    used the one arc-minute-resolution ETOPO1 bathymetry, extracted using the R package
143    'marmap' (Amante & Eakins, 2009; Pante & Simon-Bouhe, 2013).
144        Each species was simulated with a separate model run. Larvae were modeled from
145    spawning to settlement and were transported at each timestep ($t$=2 hours) by advection-diffusion
146    transport. This transport consisted of (1) advective displacement caused by water flow,
147    consisting of east ($u$) and north ($v$) velocities read from daily MITgcm files, and (2) additional

148  random-walk displacement, using a diffusion constant of 0.2 m²/s⁻¹ (Lowe et al., 2009). Vertical
149  velocities (*w*) were not implemented by the model; details of vertical larval movement are
150  described below. Advection was interpolated between data points at each timestep using an
151  Eulerian 2D barycentric interpolation method. We chose this implementation over a more
152  computationally intensive interpolation method (i.e. 4ᵗʰ-order Runge-Kutta) because we did not
153  observe a difference at this timestep length. Biological processes modeled include PLD,
154  reproduction timing and location, mortality, and ontogenetic changes in vertical distribution;
155  these qualities were parameterized via species-specific data obtained from previous studies and
156  from the local fishing and management community (Table 1).
157        Larvae were released from habitat-specific spawning sites and were considered settled if
158  they fell within a roughly 1-km contour around reef or intertidal habitat at the end of their
159  pelagic larval duration. Distance from habitat was used rather than water depth because Penguin
160  Bank, a relatively shallow bank to the southwest of Moloka'i, does not represent suitable habitat
161  for reef-associated species. PLD for each larva was a randomly assigned value between the
162  minimum and maximum PLD for that species, and larvae were removed from the model if they
163  had reached their PLD and were not within a settlement zone. No data on pre-competency period
164  were available for our study species, so this parameter was not included. Mortality rates were
165  calculated as larval half-lives; e.g., one-half of all larvae were assumed to have survived at one-
166  half of the maximum PLD for that species (following Holstein, Paris, & Mumby, 2014). Since
167  our focus was on potential connectivity pathways, reproductive rates were calibrated to allow for
168  saturation of possible settlement sites, equating from ~900,000 to ~1,7000,000 larvae released
169  depending on species. Fecundity is therefore derived not from biological data, but from
170  computational minimums.
171        Development, and resulting ontogenetic changes in behavior, is specific to the life history
172  of each species. Broadcast-spawning species with weakly-swimming larvae (*P. meandrina* and
173  *Cellana* spp., Table 1) were transported as passive particles randomly distributed between 0-5m
174  depth (Storlazzi, Brown, & Field, 2006). Previous studies have demonstrated that fish larvae
175  have a high degree of control over their vertical position in the water column (Irisson et al.,
176  2010; Huebert, Cowen, & Sponaugle, 2011). Therefore, we modeled broadcast-spawning fish
177  species with a 24-hour passive buoyant phase to simulate eggs pre-hatch, followed by a pelagic
178  larval phase with a species-specific depth distribution. For *C. ignoblis, C. melampygus, P.*
179  *porphyreus, C. perspicillatus,* and *S. rubroviolaceus,* we used genus-level depth distributions
180  (Fig. S3) obtained from the 1996 NOAA ichthyoplankton vertical distributions data report
181  (Boehlert & Mundy, 1996). *P. sexfilis* and *C. strigosus* larvae were randomly distributed between
182  50-100 m (Boehlert et al., 1992). Benthic brooding species (*O. cyanea* and *Panulirus* spp.) do
183  not have a passive buoyant phase, and thus were released as larvae randomly distributed between
184  50-100 m. At each time step, a larva's depth was checked against bathymetry, and was assigned
185  to the nearest available layer if the species-specific depth was not available at these coordinates.
186        For data-poor species, we used congener-level estimates for PLD (see Table 1). For
187  example, there is no estimate of larval duration for *Caranx* species, but in Hawai'i peak
188  spawning occurs in May-July and peak recruitment in August-December (Sudekum, 1984;
189  Longenecker et al., 2010). In consultation with resource managers and community members, a
190  PLD of 140 days was chosen pending future data that indicates a more accurate pelagic period.

### III) Habitat selection

192        Spawning sites were generated using data from published literature and modified after
193  input from Native Hawaiian cultural practitioners and the Moloka'i fishing community (Fig. 1).

194 Species-specific habitat suitability was inferred from the 2013-2016 Marine Biogeographic
195 Assessment of the Main Hawaiian Islands (Costa & Kendall, 2016). We designated coral habitat
196 as areas with 5 – 90% coral cover, or >=1 site-specific coral species richness, for a total of 127
197 spawning sites on Molokaʻi. Habitat for reef invertebrates followed coral habitat, with additional
198 sites added after community feedback for a total of 136 sites. Areas with a predicted reef fish
199 biomass of 58 – 1,288 g/m$^2$ were designated as reef fish habitat (Stamoulis et al., 2016), for a
200 total of 109 spawning sites. Sand habitat was designated as 90 – 100% uncolonized for a total of
201 115 sites. Intertidal habitat was designated as any rocky shoreline area not covered by sand or
202 mud, for a total of 87 sites. Number of adults was assumed equal at all sites. For regional
203 analysis, we pooled sites into groups of 2 to 11 sites based on benthic habitat and surrounding
204 geography (Fig. 1A). Adjacent sites were grouped if they shared the same benthic habitat
205 classification and prevailing wave direction, and/or were part of the same reef tract.

### IV) Source-sink dynamics and local retention

207 Dispersal distance was measured via the *distm* function in the R package 'geosphere',
208 which calculates distance between geographical points via the Haversine formula (Hijmans
209 2016). This distance, measured between spawn and settlement locations, was used to calculate
210 dispersal kernels to examine and compare species-specific distributions. We also measured local
211 retention, or the percentage of successful settlers from a site that were retained at that site (i.e.
212 settlers at site *A* that originated from site *A* / total successful settlers that originated from site *A*).
213 To estimate the role of specific sites around Molokaʻi, we also calculated a source-sink index for
214 each species (Holstein, Paris, & Mumby, 2014; Wren et al., 2016). This index defines sites as
215 either a source, in which a site's successful export to other sites is greater than its import, or a
216 sink, in which import from other sites is greater than successful export. It is calculated by
217 dividing the difference between number of successfully exported and imported larvae by the sum
218 of all successfully exported and imported larvae. A value <0 indicates that a site acts as a net
219 sink, while a value >0 indicates that a site acts as a net source. While we measured successful
220 dispersal to adjacent islands, we did not spawn larvae from them, and therefore these islands
221 represent exogenous sinks. For this reason, settlement to other islands was not included in
222 source-sink index calculations.
223 We also calculated settlement proportion between different regions for each species
224 (Calabrese & Fagan, 2004). We calculated the forward settlement proportion, i.e. the proportion
225 of settlers from a specific settlement site (*s*) originating from an observed origin site (*o*), by
226 scaling the number of successful settlers from site *o* settling at site *s* to all successful settlers
227 originating from site *o*. Forward proportion can be represented as $P_{so} = S_{os} / \sum S_o$. We also
228 calculated rearward settlement proportion, or the proportion of settlers from a specific origin site
229 (*o*) observed at settlement site (*s*), by scaling the number of settlers observed at site *s* originating
230 from site *o* to all settlers observed at site *s*. Rearward proportion can be represented as $P_{os} = S_{os} /$
231 $\sum S_s$.

### V) Graph-theoretic analysis

233 To quantify connections between sites, we applied graph theory to population
234 connectivity (Treml et al., 2008; Holstein, Paris, & Mumby, 2014). Graph theoretic analysis is
235 highly scalable and can be used to examine fine-scale networks between reef sites up to broad-
236 scale analyses between islands or archipelagos, mapping to both local and regional management
237 needs. It also allows for both network- and site-specific metrics, enabling the comparison of
238 connectivity between species and habitat sites as well as highlighting potential multi-

239   generational dispersal corridors. Graph theory also provides a powerful tool for spatial
240   visualization, allowing for rapid, intuitive communication of connectivity results to researchers,
241   managers, and the public alike. This type of analysis can be used to model pairwise relationships
242   between spatial data points by breaking down individual-based output into a series of nodes
243   (habitat sites) and edges (directed connections between habitat sites). We then used these nodes
244   and edges to examine the relative importance of each site and dispersal pathway to the greater
245   pattern of connectivity around Moloka'i, as well as differences in connectivity patterns between
246   species (Treml et al., 2008; Holstein, Paris, & Mumby, 2014). We used the R package 'igraph' to
247   examine several measures of within-island connectivity (Csardi & Nepusz, 2006). Edge density,
248   or the proportion of realized edges out of all possible edges, is a multi-site measure of
249   connectivity. Areas with a higher edge density have more direct connections between habitat
250   sites, and thus are more strongly connected. We measured edge density along and between the
251   north, south, east, and west coasts of Moloka'i to examine possible population structure and
252   degree of exchange among the marine resources of local communities.
253        The distribution of shortest path length is also informative for comparing overall
254   connectivity. In graph theory, a shortest path is the minimum number of steps needed to connect
255   two sites. For example, two sites that exchange larvae in either direction are connected by a
256   shortest path of one, whereas if they both share larvae with an intermediate site but not with each
257   other, they are connected by a shortest path of two. In a biological context, shortest path can
258   correspond to number of generations needed for exchange: sites with a shortest path of two
259   require two generations to make a connection. Average shortest path, therefore, is a descriptive
260   statistic to estimate connectivity of a network. If two sites are unconnected, it is possible to have
261   infinite-length shortest paths; here, these infinite values were noted but not included in final
262   analyses.
263        Networks can also be broken in connected components (Csardi & Nepusz, 2006). A
264   weakly connected component (WCC) is a subgraph in which all nodes are not reachable by other
265   nodes. A network split into multiple WCCs indicates separate populations that do not exchange
266   any individuals, and a large number of WCCs indicates a low degree of island-wide connectivity.
267   A strongly connected component (SCC) is a subgraph in which all nodes are directly connected
268   and indicates a high degree of connectivity. A region with many small SCCs can indicate high
269   local connectivity but low island-wide connectivity. Furthermore, component analysis can
270   identify cut nodes, or nodes that, if removed, break a network into multiple WCCs. Pinpointing
271   these cut nodes can identify potential important sites for preserving a population's connectivity,
272   and could inform predictions about the impact of site loss (e.g. a large-scale coral bleaching
273   event) on overall connectivity.
274        On a regional scale, it is important to note which sites are exporting larvae to, or
275   importing larvae from, other sites. To this end, we examined in-degree and out-degree for each
276   region. In-degree refers to the number of inward-directed edges to a specific node, or how many
277   other sites provide larvae into site 'A'. Out-degree refers to the number of outward-directed
278   edges from a specific node, or how many sites receive larvae from site 'A'. Habitat sites with a
279   high out-degree seed a large number of other sites, and indicate potentially important larval
280   sources, while habitat sites with a low in-degree rely on a limited number of larval sources and
281   may therefore be dependent on connections with these few other sites to maintain population
282   size. Finally, betweenness centrality (BC) refers to the number of shortest paths that pass through
283   a given node, and may therefore indicate connectivity pathways or 'chokepoints' that are
284   important to overall connectivity on a multigenerational timescale. BC was weighted with the

285  proportion of dispersal as described in the preceding section. We calculated in-degree, out-
286  degree, and weighted betweenness centrality for each region in the network for each species.
287      As with the source-sink index, we did not include sites on islands other than Moloka'i in
288  our calculations of edge density, shortest paths, connected components, cut nodes, in- and out-
289  degree, or betweenness centrality in order to focus on within-island patterns of connectivity.

## Results

290

### I) Effects of biological parameters on fine-scale connectivity patterns

291

292      The species-specific parameters that were available to parameterize the dispersal models
293  substantially influenced final output (Fig. 2). The proportion of successful settlers (either to
294  Moloka'i or to neighboring islands) varied widely by species, from 2% (*Panulirus* spp.) to 25%
295  (*Cellana* spp.). Minimum pelagic duration and settlement success were negatively correlated
296  (e.g. an estimated -0.79 Pearson correlation coefficient). Species modeled with batch spawning at
297  a specific moon phase and/or time of day (*Cellana* spp., *P. meandrina,* and *C. ignoblis*)
298  displayed slightly higher settlement success than similar species modeled with constant
299  spawning over specific months. On a smaller scale, we also examined average site-scale local
300  retention, comparing only retention to the spawning site versus other sites on Moloka'i (Fig. 2).
301  Local retention was lowest for *Caranx* spp. (<1%) and highest for *O. cyanea* and *P. sexfilis*
302  (8.1% and 10%, respectively).
303      We measured network-wide connectivity via distribution of shortest paths, or the
304  minimum number of steps between a given two nodes in a network, only including sites on
305  Moloka'i (Fig. 2). *O. cyanea* and *P. sexfilis* showed the smallest shortest paths overall, meaning
306  that on average, it would take fewer generations for these species to demographically bridge any
307  given pair of sites. Using maximum shortest path, it could take these species three generations at
308  most to connect sites. *Cellana* spp. and *P. meandrina,* by comparison, could take as many as five
309  generations. Other medium- and long-dispersing species showed relatively equivalent shortest-
310  path distributions, with trevally species showing the highest mean path length and therefore the
311  lowest island-scale connectivity.
312      The number and size of weakly-connected and strongly-connected components in a
313  network is also an informative measure of connectivity (Fig. 2). No species in our study group
314  was broken into multiple weakly-connected components; however, there were species-specific
315  patterns of strongly connected sites. *O. cyanea* and *P. sexfilis* were the most strongly connected,
316  with all sites in the network falling into a single SCC. *Cellana* spp. and *P. meandrina* each had
317  approximately 60% of sites included in a SCC, but both show fragmentation with 7 and 6 SCCs
318  respectively, ranging in size from 2-22 sites. This SCC pattern suggests low global connectivity
319  but high local connectivity for these species. Medium and long dispersers showed larger
320  connected components; 70% of parrotfish sites fell within two SCCs; 40% of *P. porphyreus* sites
321  fell within two SCCs; 70% of *C. strigosus* sites, 55% of *C. melampygus* sites, and 40% of
322  *Panulirus* sites fell within a single SCC. In contrast, only 26% of *C. ignoblis* sites fell within a
323  single SCC. It is also important to note that the lower connectivity scores observed in long-
324  dispersing species likely reflect a larger scale of connectivity. Species with a shorter PLD are
325  highly connected at reef and island levels but may show weaker connections between islands.
326  Species with a longer PLD, such as trevally or spiny lobster, are likely more highly connected at
327  inter-island scales which reflects the lower connectivity scores per island shown here.

328         Minimum PLD was positively correlated with mean dispersal distance (e.g. an estimated
329    0.88 Pearson correlation coefficient with minimum pelagic duration $\log_e$-transformed to linearize
330    the relationship), and dispersal kernels differed between species that are short dispersers (3-25
331    days), medium dispersers (30-50 days), or long dispersers (140-270 days) (Fig. 3). Short
332    dispersers travelled a mean distance of 24.06 ± 31.33 km, medium dispersers travelled a mean
333    distance of 52.71 ± 40.37 km, and long dispersers travelled the farthest, at a mean of 89.41 ±
334    41.43 km. However, regardless of PLD, there were essentially two peaks of mean dispersal: a
335    short-distance peak of <30 km, and a long-distance peak of roughly 50-125 km (Fig. 3). The
336    short-distance peak largely represents larvae that settle back to Moloka'i, while the long-distance
337    peak largely represents settlement to other islands; the low point between them corresponds to
338    deep-water channels between islands, i.e. unsuitable habitat for settlement. Median dispersal
339    distance for short dispersers was substantially less than the mean at 8.85 km, indicating that most
340    of these larvae settled relatively close to their spawning sites, with rare long-distance dispersal
341    events bringing up the average. Median distance for medium (54.22 km) and long (91.57 km)
342    dispersers was closer to the mean, indicating more even distance distributions and thus a higher
343    probability of long-distance dispersal for these species. Maximum dispersal distance varied
344    between ~150-180 km depending on species, except for the spiny lobster *Panulirus* spp., with a
345    PLD of 270 d and a maximum dispersal distance of approximately 300 km.

### II) Settlement to Moloka'i and other islands in the archipelago

347         Different species showed different forward settlement proportion to adjacent islands (Fig.
348    4), although every species in the study group successfully settled back to Moloka'i. *P.*
349    *meandrina* showed the highest percentage of island-scale local retention (82%), while *C. ignoblis*
350    showed the lowest (7%). An average of 74% of larvae from short-dispersing species settled back
351    to Moloka'i, as compared to an average of 41% of medium dispersers and 9% of long dispersers.
352    A large proportion of larvae also settled to O'ahu, with longer PLDs resulting in greater
353    proportions, ranging from 14% of *O. cyanea* to 88% of *C. ignoblis*. Moloka'i and O'ahu were the
354    most commonly settled islands by percentage. Overall, settlement from Moloka'i to Lana'i,
355    Maui, Kaho'olawe, and Hawai'i was somewhat lower. Larvae of every species settled to Lana'i,
356    and settlement to this island made up less than 5% of settled larvae across all species. Likewise,
357    settlement to Maui made up less than 7% of settlement across species, with *P. meandrina* as the
358    only species that had no successful paths from Moloka'i to Maui. Settlement to Kaho'olawe and
359    Hawai'i was less common, with the exception of *Panulirus* spp., which had 16% of all settled
360    larvae on Hawai'i.
361         We also examined coast-specific patterns of rearward settlement proportion to other
362    islands, discarding connections with a very low proportion of larvae (<0.1% of total larvae of
363    that species settling to other islands). Averaged across species, 83% of larvae settling to O'ahu
364    from Moloka'i were spawned on the north shore of Moloka'i, with 12% spawned on the west
365    shore (Fig S4). Spawning sites on the east and south shores contributed <5% of all larvae settling
366    to O'ahu from Moloka'i. The east and south shores of Moloka'i had the highest average
367    percentage of larvae settling to Lana'i from Moloka'i, at 78% and 20% respectively, and to
368    Kaho'olawe from Moloka'i at 63% and 34%. Of the species that settled to Maui from Moloka'i,
369    on average most were spawned on the east (53%) or north (39%) shores, as were the species that
370    settled to Hawai'i Island from Moloka'i (22% east, 76% north). These patterns indicate that
371    multiple coasts of Moloka'i have the potential to export larvae to neighboring islands.
372         Temporal settlement profiles also varied by species (Fig. 5). Species modeled with moon-
373    phase spawning and relatively short settlement windows (*Cellana* spp. and *C. ignoblis*) were

374  characterized by discrete settlement pulses, whereas other species showed settlement over a
375  broader period of time. Some species also showed distinctive patterns of settlement to other
376  islands; our model suggests specific windows when long-distance dispersal is possible, as well as
377  times of year when local retention is maximized (Fig. 5).

378  **III) Regional patterns of connectivity in Molokaʻi coastal waters**
379         Within Molokaʻi, our model predicts that coast-specific population structure is likely;
380  averaged across all species, 84% of individuals settled back to the same coast on which they
381  were spawned rather than a different coast on Molokaʻi. Excluding connections with a very low
382  proportion of larvae (<0.1% of total larvae of that species that settled to Molokaʻi), we found that
383  the proportion of coast-scale local retention was generally higher than dispersal to another coast,
384  with the exception of the west coast (Fig 6A). The north and south coasts had a high degree of
385  local retention in every species except for the long-dispersing *Panulirus* spp., and the east coast
386  also had high local retention overall. Between coasts, a high proportion of larvae that spawned
387  on the west coast settled on the north coast, and a lesser amount of larvae were exchanged from
388  the east to south and from the north to east. With a few species-specific exceptions, larval
389  exchange between other coasts of Molokaʻi was negligible.
390         We also calculated edge density, including all connections between coasts on Molokaʻi
391  regardless of settlement proportion (Fig. 6B). The eastern coast was particularly well-connected,
392  with an edge density between 0.14 and 0.44, depending on species. The southern shore showed
393  high edge density for short and medium dispersers (0.16-0.39) but low for long dispersers
394  (<0.005). The north shore also showed relatively high edge density (0.20 on average), although
395  these values were smaller for long dispersers. The west coast showed very low edge density,
396  with the exceptions of *O. cyanea* (0.37) and *P. sexfilis* (0.13). Virtually all networks that
397  included two coasts showed lower edge density. One exception was the east/south shore
398  network, which had an edge density of 0.10-0.65 except for *Cellana* spp. Across species, edge
399  density between the south and west coasts was 0.12 on average, and between the east and west
400  coasts was 0.04 on average. Edge density between north and south coasts was particularly low
401  for all species (<0.05), a divide that was especially distinct in *Cellana* spp. and *P. meandrina*,
402  which showed zero realized connections between these coasts. Although northern and southern
403  populations are potentially weakly connected by sites along the eastern (*P. meandrina*) or
404  western (*Cellana* spp.) shores, our model predicts very little, if any, demographic connectivity.
405         To explore patterns of connectivity on a finer scale, we pooled sites into regions (as
406  defined in Fig. 1) in order to analyze relationships between these regions. Arranging model
407  output into node-edge networks clarified pathways and regions of note, and revealed several
408  patterns which did not follow simple predictions based on PLD (Fig. 7). *Cellana* spp. and *P.
409  meandrina* showed the most fragmentation, with several SCCs and low connectivity between
410  coasts. Connectivity was highest in *O. cyanea* and *P. sexfilis*, which had a single SCC containing
411  all regions. Medium and long dispersers generally showed fewer strongly connected regions on
412  the south shore than the north shore, with the exception of *C. strigosus*. *P. porphyreus* showed
413  more strongly connected regions east of Kalaupapa but lower connectivity on the western half of
414  the island.
415         Region-level networks showed both species-specific and species-wide patterns of
416  connectivity (Fig. 8). With a few exceptions, sites along the eastern coast - notably, Cape Halawa
417  and Pauwalu Harbor – showed relatively high betweenness centrality, and may therefore act as
418  multigenerational pathways between north-shore and south-shore populations. In *Cellana* spp.,
419  Leinapapio Point and Mokio Point had the highest BC, while in high-connectivity *O. cyanea* and

420    *P. sexfilis,* regions on the west coast had high BC scores. *P. meandrina* and *C. strigosus* showed
421    several regions along the south shore with high BC. For *Cellana* spp. and *P. meandrina,* regions
422    in the northeast had the highest out-degree, and therefore seeded the greatest number of other
423    sites with larvae (Fig. 8). Correspondingly, regions in the northwest (and southwest in the case of
424    *P. meandrina*) showed the highest in-degree. For *O. cyanea* and *P. sexfilis*, regions on the
425    western and southern coasts showed the highest out-degree. For most species, both out-degree
426    and in-degree were generally highest on the northern and eastern coasts, suggesting higher
427    connectivity in these areas.
428          Several species-wide hotspots of local retention emerged, particularly East Kalaupapa
429    Peninsula/Leinaopapio Point, the northeast corner of Molokaʻi, and the middle of the south
430    shore. Some species also showed some degree of local retention west of Kalaupapa Peninsula.
431    While some local retention was observed in the long-dispersing *Caranx* spp. and *Panulirus* spp.,
432    this amount was essentially negligible. In terms of source-sink dynamics, Kiʻokoʻo, Puʻukaoku
433    Point, and West Kalaupapa Peninsula, all on the north shore, were the only sites that consistently
434    acted as a net source, exporting more larvae than they import (Fig. 8). Kaunakakai Harbor, Lono
435    Harbor, and Mokio Point acted as net sinks across all species. Pukoʻo, Pauwalu Harbor, and
436    Cape Halawa were either weak net sources or neither sources nor sinks, which corresponds to the
437    high levels of local retention observed at these sites. Palaʻau and Moʻomomi acted as either weak
438    sinks or sources for short dispersers and as sources for long dispersers.
439          Only four networks showed regional cut-nodes, or nodes that, if removed, break a
440    network into multiple weakly-connected components (Fig. S5). *Cellana* spp. showed two cut-
441    nodes: Mokio Point in northwest Molokaʻi and Laʻau Point in southwest Molokaʻi, which if
442    removed isolated Small Bay and Lono Harbor, respectively. *C. perspicillatus,* and *S.*
443    *rubroviolaceus* showed a similar pattern in regards to Mokio Point; removal of this node isolated
444    Small Bay in this species as well. In *C. ignoblis,* loss of Pauwalu Harbor isolated Lono Harbor,
445    and loss of Palaʻau isolated Ilio Point on the northern coast. Finally, in *Panulirus* spp., loss of
446    Leinaopapio Point isolated Papuhaku Beach, since Leinapapio Point was the only larval source
447    from Molokaʻi for Papuhaku Beach in this species.

448    **IV) The role of Kalaupapa Peninsula in inter- and intra-island connectivity**
449    Our model suggests that Kalaupapa National Historical Park may play a role in inter-island
450    connectivity, especially in terms of long-distance dispersal. Out of all regions on Molokaʻi, East
451    Kalaupapa Peninsula was the single largest exporter of larvae to Hawaiʻi Island, accounting for
452    19% of all larvae transported from Molokaʻi to this island; West Kalaupapa Peninsula accounted
453    for another 10%. The Park also contributed 22% of all larvae exported from Molokaʻi to Oʻahu,
454    and successfully exported a smaller percentage of larvae to Maui, Lanaʻi, and Kahoʻolawe (Fig.
455    9). Kalaupapa was not marked as a cut-node for any species, meaning that full population breaks
456    are not predicted in the case of habitat or population loss in this area. Nevertheless, in our model
457    Kalaupapa exported larvae to multiple regions along the north shore in all species, as well as
458    regions along the east, south, and/or west shores in most species networks (Fig. 9 and Fig. 10).
459    The Park may play a particularly important role for long-dispersing species; settlement from
460    Kalaupapa made up 18% - 29% of all successful settlement in *Caranx* spp. and *Panulirus* spp.,
461    despite making up only 12% of spawning sites included in the model. In *C. strigosus, S.*
462    *rubroviolaceus,* and *C. strigosus,* Kalaupapa showed a particularly high out-degree, or number of
463    outgoing connections to other regions, and West Kalaupapa was also one of the few regions on
464    Molokaʻi that acted as a net larval source across all species (Fig. 8). Our study has also
465    demonstrated that different regions of a marine protected area can potentially perform different

466   roles, even in a small MPA such as Kalaupapa. Across species, the east coast of Kalaupapa
467   showed a significantly higher betweenness centrality than the west (p=0.028), while the west
468   coast of Kalauapapa showed a significantly higher source-sink index than the east (p=2.63e-9).

## Discussion:

### I) Effects of biological and physical parameters on connectivity

471       We incorporated the distribution of suitable habitat, variable reproduction, variable PLD,
472   and ontogenetic changes in swimming ability and empirical vertical distributions of larvae into
473   our model to increase biological realism, and assess how such traits impact predictions of larval
474   dispersal. The Wong-Ala et al. (2018) IBM provides a highly flexible model framework that can
475   easily be modified to incorporate either additional species-specific data or entirely new
476   biological traits. In this study, we included specific spawning seasons for all species, as well as
477   spawning by moon phase for *Cellana* spp., *P. meandrina,* and *C. ignoblis* because such data was
478   available for these species. It proved difficult to obtain the necessary biological information to
479   parameterize the model, but as more data about life history and larval behavior become available,
480   such information can be easily added for these species and others. Some potential additions to
481   future iterations of the model might include density of reproductive-age adults within each
482   habitat patch, temperature-dependent pelagic larval duration (Houde, 1989), ontogenetic-
483   dependent behavioral changes such as orientation and diel vertical migration (Fiksen et al., 2007;
484   Paris, Chérubin, & Cowen, 2007), pre-competency period, and larval habitat preferences as such
485   information becomes available.
486       In this study, we have demonstrated that patterns of fine-scale connectivity around
487   Moloka‘i are largely species-specific and can vary with life history traits, even in species with
488   identical pelagic larval duration. For example, the parrotfish *S. rubroviolaceus* and *C.
489   perspicillatus* show greater connectivity along the northern coast, while the goatfish *P.
490   porphyreus* shows higher connectivity along the eastern half of the island. These species have
491   similar PLD windows, but vary in dispersal depth and spawning season. Spawning season and
492   timing altered patterns of inter-island dispersal (Fig. 5) as well as overall settlement success,
493   which was slightly higher in species that spawned by moon phase (Fig. 2). While maximum PLD
494   did appear play a role in the probability of rare long-distance dispersal, minimum PLD appears to
495   be the main driver of average dispersal distance (Fig. 2). Overall, species with a shorter
496   minimum PLD had higher settlement success, shorter mean dispersal distance, higher local
497   retention, and higher local connectivity as measured by the amount and size of strongly
498   connected components.
499       The interaction of biological and oceanographic factors also influenced connectivity
500   patterns. Because mesoscale current patterns can vary substantially over the course of the year,
501   the timing of spawning for certain species may be critical for estimating settlement (Wren et al.,
502   2016; Wong-Ala et al. 2018). Intermittent ocean processes may influence the probability of local
503   retention versus long-distance dispersal; a large proportion of larvae settled to O‘ahu, which is
504   somewhat surprising given that in order to settle from Moloka‘i to O‘ahu, larvae must cross the
505   Kaiwi Channel (approx. 40 km). However, the intermittent presence of mesoscale gyres may act
506   as a stabilizing pathway across the channel, sweeping larvae up either the windward or leeward
507   coast of O‘ahu depending on spawning site. Likewise, in our model long-distance dispersal to
508   Hawai‘i Island was possible at certain times of the year due to a gyre to the north of Maui; larvae

509   were transported from Kalaupapa to this gyre, where they were carried to the northeast shore of
510   Hawaiʻi (Fig. S6). Preliminary analysis also suggests that distribution of larval depth influenced
511   edge directionality and size of connected components (Fig. 7); surface currents are variable and
512   primarily wind-driven, giving positively-buoyant larvae different patterns of dispersal than
513   species that disperse deeper in the water column (Fig. S7).

514   **II) Model limitations and future perspectives**
515         Our findings have several caveats. Because fine-scale density estimates are not available
516   for our species of interest around Molokaʻi, we assumed that fecundity is equivalent at all sites.
517   This simplification may lead us to under- or over-estimate the strength of connections between
518   sites. Lack of adequate data also necessitated estimation or extrapolation from congener
519   information for larval traits such as larval dispersal depth and PLD. Since it is difficult if not
520   impossible to identify larvae to the species level without genetic analysis, we used genus-level
521   larval distribution data (Boehlert & Mundy 1996), or lacking that, an estimate of 50-100m as a
522   depth layer that is generally more enriched with larvae (Boehlert et al., 1992, Wren &
523   Kobayashi, 2016). We also estimated PLD in several cases using congener-level data (see Table
524   1). While specificity is ideal for making informed management decisions about a certain species,
525   past sensitivity analysis has shown that variation in PLD length does not greatly impact patterns
526   of dispersal in species with a PLD of >40 days (Wren & Kobayashi, 2016).
527         Although our MITgcm current model shows annual consistency, it only spans two and a
528   half years chosen as neutral state 'average' ocean conditions. It does not span any El Niño or La
529   Niña (ENSO) events, which cause wide-scale sea-surface temperature anomalies and may
530   therefore affect patterns of connectivity during these years. El Niño can have a particularly
531   strong impact on coral reproduction, since the warm currents associated with these events can
532   lead to severe temperature stress (Glynn & D'Croz, 1990; Wood et al., 2016). While there has
533   been little study to date on the effects of ENSO on fine-scale connectivity, previous work has
534   demonstrated increased variability during these events. For example, Wood et al. (2016) showed
535   a decrease in eastward Pacific dispersal during El Niño years, but an increase in westward
536   dispersal, and Treml et al. (2008) showed unique connections in the West Pacific as well as an
537   increase in connectivity during El Niño. While these effects are difficult to predict, especially at
538   such a small scale, additional model years would increase confidence in long-term connectivity
539   estimations. Additionally, with a temporal resolution of 24 hours, we could not adequately
540   address the role of tides on dispersal, and therefore did not include them in the MITgcm.
541   Storlazzi et al. (2017) showed that tidal forces did affect larval dispersal in Maui Nui,
542   underlining the importance of including both fine-scale, short-duration models and coarser-scale,
543   long-duration models in final management decisions.
544         We also limit our model's scope geographically. Our goal was to determine whether we
545   could resolve predictive patterns at this scale relevant to management. Interpretation of
546   connectivity output can be biased by spatial resolution of the ocean model, since complex coastal
547   processes can be smoothed and therefore impact larval trajectories. To limit this bias, we focused
548   mainly on coastal and regional connectivity on scales greater than the current resolution. We also
549   used the finest-scale current products available for our study area, and our results show general
550   agreement with similar studies of the region that use a coarser resolution (Wren et al., 2016) and
551   a finer resolution (Storlazzi et al., 2018). Also, while knowledge of island-scale connectivity is
552   important for local management, it does disregard potential connections from other islands. In
553   our calculations of edge density, betweenness centrality, we included only settlement to
554   Molokaʻi, discarding exogenous sinks that would bias our analysis. Likewise, we cannot predict

555    the proportion of larvae settling to other islands that originated from Moloka'i, or the proportion
556    of larvae on Moloka'i that originated from other islands.
557          It is also important to note scale in relation to measures of connectivity; we expect that
558    long-dispersing species such as *Caranx* spp. and *Panulirus* spp. will show much higher measures
559    of connectivity when measured across the whole archipelago as opposed to a single island. The
560    cut-nodes observed in these species may not actually break up populations on a large scale due to
561    this inter-island connectivity. Nevertheless, cut-nodes in species with short- and medium-length
562    PLD may indeed mark important habitat locations, especially in terms of providing links
563    between two otherwise disconnected coasts. It may be that for certain species or certain regions,
564    stock replenishment relies on larval import from other islands, underscoring the importance of
565    MPA selection for population maintenance in the archipelago as a whole.

### III) Implications for management

567          Clearly, there is no single management approach that encompasses the breadth of life
568    history and behavior differences that impact patterns of larval dispersal and connectivity (Toonen
569    et al., 2011, Holstein, Paris, & Mumby, 2014). The spatial, temporal, and species-specific
570    variability suggested by our model stresses the need for multi-scale management, specifically
571    tailored to local and regional connectivity patterns and the suite of target species. Even on such a
572    small scale, different regions around the island of Moloka'i can play very different roles in the
573    greater pattern of connectivity (Fig. 8); sites along the west coast, for example, showed fewer
574    ingoing and outgoing connections than sites on the north coast, and therefore may be more at risk
575    of isolation. Seasonal variation should also be taken into account, as mesoscale current patterns
576    (and resulting connectivity patterns) vary over the course of a year. Our model suggests species-
577    specific temporal patterns of settlement (Fig. 5); even in the year-round spawner *O. cyanea,* local
578    retention to Moloka'i as well as settlement to O'ahu was maximized in spring and early summer,
579    while settlement to other islands mostly occurred in late summer and fall.
580          Regions that show similar network dynamics may benefit from similar management
581    strategies. Areas that act as larval sources either by proportion of larvae (high source-sink index)
582    or number of sites (high out-degree) should receive management consideration. On Moloka'i,
583    across all species in our study, these sources fell mostly on the northern and eastern coasts.
584    Maintenance of these areas is especially important for downstream areas that depend on
585    upstream populations for a source of larvae, such as those with a low source-sink index, low in-
586    degree, and/or low local retention. Across species, regions with the highest betweenness
587    centrality scores fell mainly in the northeast (Cape Halawa and Pauwalu Harbor). These areas
588    should receive consideration as potentially important intergenerational pathways, particularly as
589    a means of connecting north-coast and south-coast populations, which showed a lack of
590    connectivity both in total number of connections (edge density) and proportion of larvae. Both of
591    these connectivity measures were included because edge density includes all connections, even
592    those with a very small proportion of larvae, and may therefore include rare dispersal events that
593    are of little relevance to managers. Additionally, edge density comparisons between networks
594    should be viewed with the caveat that these networks do not necessarily have the same number
595    of nodes. Nevertheless, both edge density and proportion show very similar patterns, and include
596    both demographically-relevant common connections as well as rare connections that could
597    influence genetic connectivity.
598          Management that seeks to establish a resilient network of spatially managed areas should
599    also consider the preservation of both weakly-connected and strongly-connected components, as
600    removal of key cut-nodes (Fig. S5) breaks up a network. Sites within a SCC have more direct

601    connections and therefore may be more resilient to local population loss. Care should be taken to
602    preserve breeding populations at larval sources, connectivity pathways, and cut-nodes within a
603    SCC, since without these key sites the network can fragment into multiple independent SCCs
604    instead of a single stable network. This practice may be especially important for species for
605    which we estimate multiple small SCCs, such as *Cellana* spp. or *P. meandrina.*
606            Kalaupapa Peninsula emerged as an important site in Molokaʻi population connectivity,
607    acting as a larval source for other regions around the island. The Park seeded areas along the
608    north shore in all species, and also exported larvae to sites along the east and west shores in all
609    species except *P. meandrina* and *Cellana* spp. Additionally, it was a larval source for sites along
610    the south shore in the fishes *C. perspicillatus, S. rubroviolaceus,* and *C. strigosus* as well as
611    *Panulirus* spp. Western Kalaupapa Peninsula was one of only three regions included in the
612    analysis (the others being Kiʻokoʻo and Puʻukaoku Point, also on the north shore) that acted as a
613    net larval source across all species. Eastern Kalaupapa Peninsula was particularly highly
614    connected, and was part of a strongly connected component in every species. The Park also
615    emerged as a potential point of connection to adjacent islands, particularly to Oʻahu and Hawaiʻi.
616    Expanding the spatial scale of our model will further elucidate Kalaupapa's role in the greater
617    pattern of inter-island connectivity.
618            In addition to biophysical modeling, genetic analyses can be used to identify persistent
619    population structure of relevance to managers (Cowen et al., 2000; Casey et al., 2016). Our
620    finding that exchange among islands is generally low in species with a short- to medium-length
621    PLD agrees with population genetic analyses of marine species in the Hawaiian Islands (Bird et
622    al., 2007; Rivera et al., 2011; Toonen et al., 2011, Concepcion, Baums, & Toonen, 2014). On a
623    finer scale, we predict some level of shoreline-specific population structure for most species
624    included in the study (Fig. 6). Unfortunately, genetic analyses to date have been performed over
625    too broad a scale to effectively compare to these fine-scale connectivity predictions around
626    Molokaʻi or even among locations on adjacent islands. These model results justify such small
627    scale genetic analyses because there are species, such as the coral *P. meandrina*, for which the
628    model predicts clear separation of north-shore and south-shore populations which should be
629    simple to test using genetic data. To validate these model predictions with this technique, more
630    fine-scale population genetic analyses are needed.

## Conclusions:

631
632            The maintenance of demographically connected populations is important for
633    conservation. In this study, we contribute to the growing body of work in biophysical
634    connectivity modeling, focusing on a region and suite of species that are of relevance to resource
635    managers. Furthermore, we demonstrate the value of quantifying fine-scale relationships
636    between habitat sites via graph-theoretic methods. Multispecies network analysis revealed
637    persistent patterns that can help define region-wide practices, as well as species-specific
638    connectivity that merits more individual consideration. We demonstrate that connectivity is
639    influenced not only by PLD, but also by other life-history traits such as spawning season, moon-
640    phase spawning, and ontogenetic changes in larval depth. High local retention of larvae with a
641    short- or medium-length PLD is consistent with population genetic studies of the area. We also
642    identify regions of management importance, including West Kalaupapa Peninsula, which acts as
643    a consistent larval source across species; East Kalaupapa Peninsula, which is a strongly
644    connected region in every species network, and Pauwalu Harbor/Cape Halawa, which may act as

645 important multigenerational pathways. Connectivity is only one piece of the puzzle of MPA
646 effectiveness, which must also account for reproductive population size, long-term persistence,
647 and post-settlement survival (Burgess et al., 2014). That being said, our study provides a
648 quantitative roadmap of potential demographic connectivity, and thus presents an effective tool
649 for estimating current and future patterns of dispersal around Kalaupapa Peninsula and around
650 Moloka'i as a whole.

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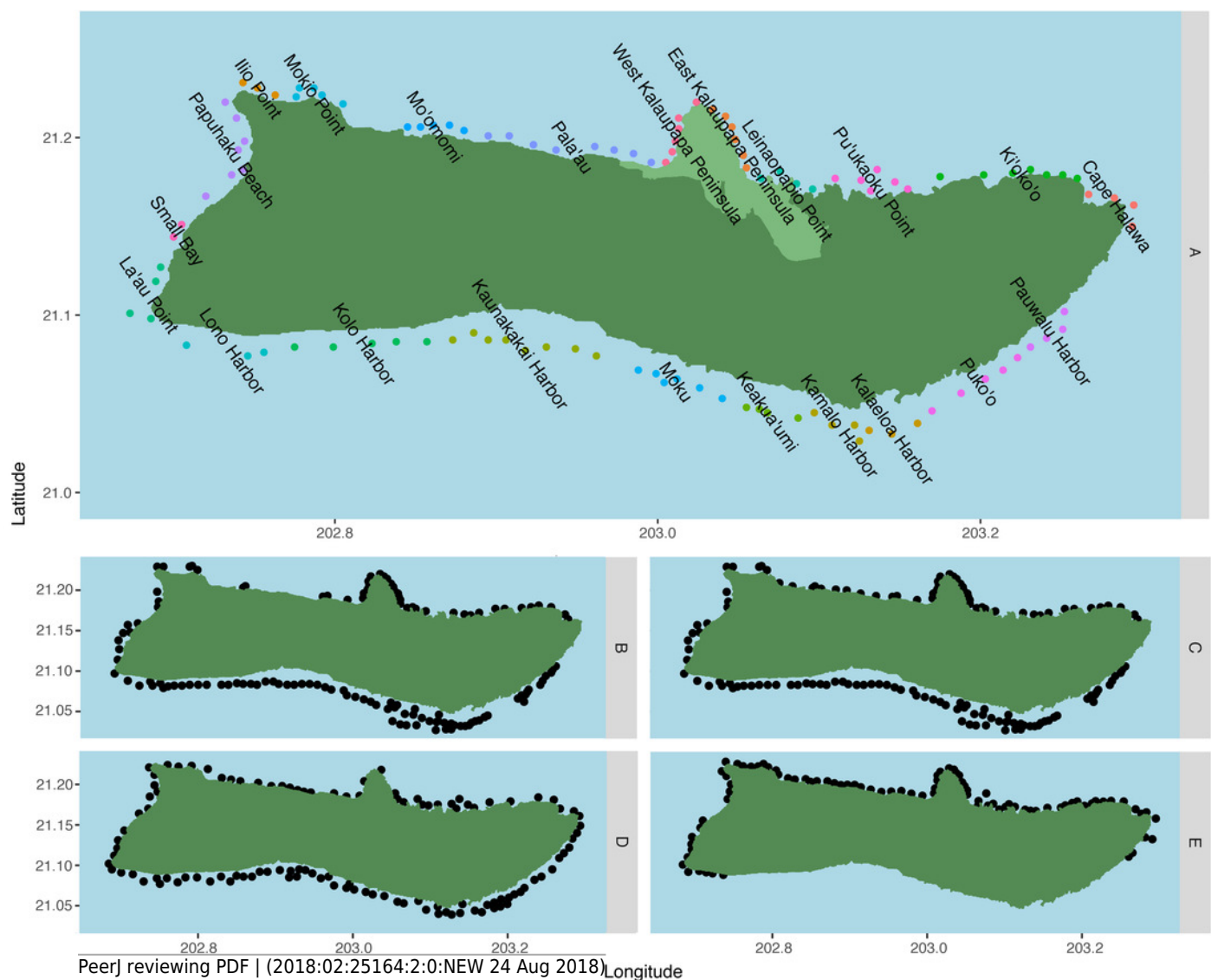
Target taxa selected for the study, based on cultural, ecological, and/or economic importance.

PLD = pelagic larval duration. Short dispersers (3-25 day minimum PLD) in white, medium dispersers (30-50 day minimum PLD) in light gray, and long dispersers (140-270 day minimum PLD) in dark gray. Spawn season and timing from traditional ecological knowledge shared by cultural practitioners on the island. Asterisk indicates that congener-level data was used. **(1)** Bird et al., 2007; **(2)** Corpuz, 1983; **(3)** Schmidt-Roach et al., 2012; **(4)** Storlazzi, Brown, & Field, 2006; **(5)** Richmond, 1987; **(6)** Heukelem, 1973; **(7)** Forsythe & Hanlon, 1997; **(8)** Boehlert et al., 1992; **(9)** Callan et al., 2012; **(10)** Mundy, 2005; **(11)** Boehlert & Mundy, 1996; **(12)** Luiz et al., 2013; **(13)** Sudekum, 1984; **(14)** Longenecker, Langston, & Barrett, 2010; **(15)** DeMartini, DiNardo, & Williams, 2003; **(16)** Polovina & Moffitt, 1995; **(17)** Phillips et al., 2006.

| Common name | Scientific name | Spawn type | # of larvae spawned | Spawning day of year | Spawning hour of day | Spawning moon phase | Larval depth (m) | PLD (days) | Habitat |
|---|---|---|---|---|---|---|---|---|---|
| 'Opihi/ Limpet | *Cellana* spp. | Broadcast[1] | 861,300 | 1-60 & 121-181 | - | New | 0-5 | 3-18[1,2] | Intertidal[1] |
| Ko'a / Cauliflower coral | *Pocillopora meandrina* | Broadcast[3] | 1,671,840 | 91-151 | 07:15-08:00 | Full | 0-5[4] | 5-90*[5] | Reef |
| He'e / Octopus | *Octopus cyanea* | Benthic[6] | 1,392,096 | 1-360 | - | - | 50-100 | 21[6] | Reef, rubble[7] |
| Moi / Pacific threadfin | *Polydactylus sexfilis* | Broadcast | 1,004,640 | 152-243 | - | - | 50-100[8] | 25[9] | Sand[10] |
| Uhu uliuli / Spectacled parrotfish | *Chlorurus perspicillatus* | Broadcast | 1,404,792 | 152-212 | - | - | 0-120*[11] | 30*[12] | Reef[10] |
| Uhu palukaluka / Reddlip parrotfish | *Scarus rubroviolaceus* | Broadcast | 1,404,792 | 152-212 | - | - | 0-120*[11] | 30*[12] | Rock, reef[10] |
| Kumu / Whitesaddle Goatfish | *Parupeneus porphyreus* | Broadcast | 1,071,252 | 32-90 | - | - | 0-50*[11] | 41-56*[12] | Sand, rock, reef[10] |
| Kole / Spotted surgeonfish | *Ctenochaetus strigosus* | Broadcast | 1,177,200 | 60-120 | - | - | 50-100[11] | 50*[12] | Rock, reef, rubble[10] |
| 'Ōmilu / Bluefin trevally | *Caranx melampygus* | Broadcast | 1,310,616 | 121-243 | - | - | 0-80*[11] | 140*[13,14] | Sand, reef[10] |
| Ulua / Giant trevally | *Caranx ignoblis* | Broadcast | 1,151,040 | 152-243 | - | Full | 0-80*[11] | 140[13,14] | Sand, rock, reef[10] |
| Ula / Spiny lobster | *Panulirus* spp. | Benthic[15] | 1,573,248 | 152-243 | - | - | 50-100[16] | 270[17] | Rock, pavement[16] |

# Figure 1

Spawning sites used in the model by species.

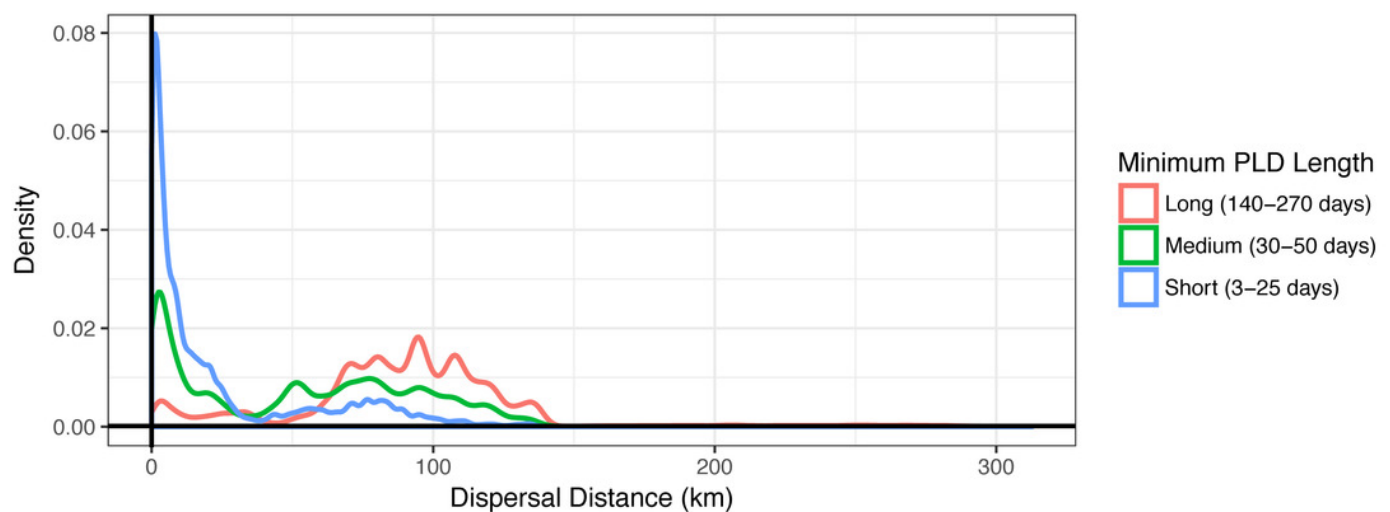
**(A)** *C. perspicillatus*, *S. rubroviolaceus*, *P. porphyreus*, *C. strigosus*, *C. ignoblis*, and *C. melampygus*, n=109, **(B)** *P. meandrina*, n=129, **(C)** *O. cyanea* and *Panulirus* spp., n=136, **(D)** *P. sexfilis*, n=115, and **(E)** *Cellana* spp., n=87. Region names are displayed over associated spawning sites for fish species in (A). Regions are made up of 2 to 11 sites, grouped based on coastal geography and surrounding benthic habitat, and are designated in (A) by adjacent colored dots. Kalaupapa National Historical Park is highlighted in light green in (A).

Summary statistics for each species network.

Summary statistics are displayed in order of increasing minimum pelagic larval duration from left to right. Heatmap colors are based on normalized values from 0-1 for each analysis. Successful settlement refers to the proportion of larvae settled out of the total number of larvae spawned. Local retention is measured as the proportion of larvae spawned from a site that settle at the same site. Shortest path is measured as the minimum number of steps needed to connect two sites. Strongly connected sites refers to the proportion of sites in a network that belong to a strongly connected component. Mean dispersal distance is measured in kilometers from spawn site to settlement site.

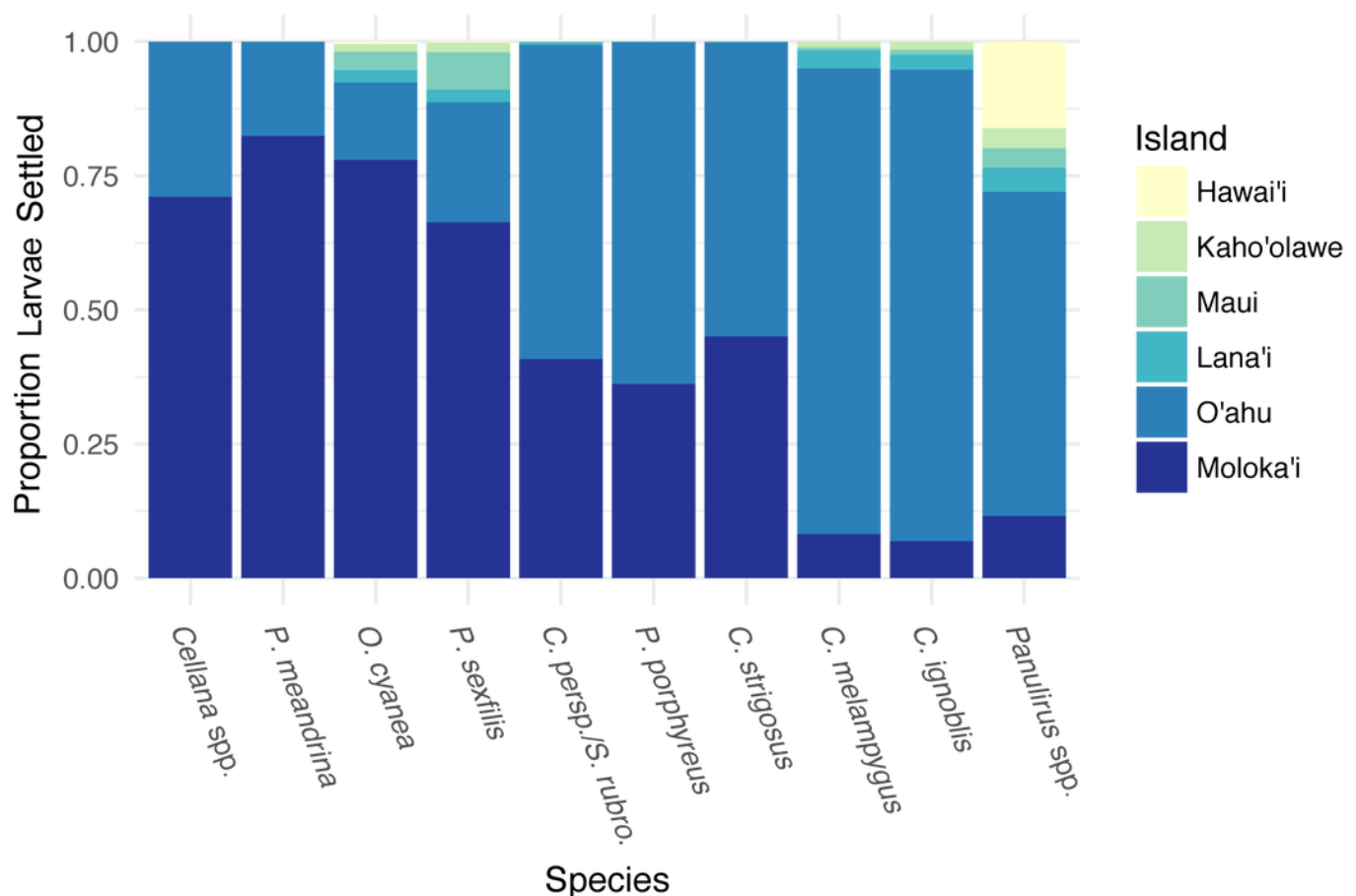
| | Cellana spp. | P. meandrina | O. cyanea | P. sexfilis | C. persp./S. rubro. | P. porphyreus | C. strigosus | C. melampygus | C. ignobilis | Panulirus spp. |
|---|---|---|---|---|---|---|---|---|---|---|
| Successful Settlement | 0.25 | 0.22 | 0.15 | 0.19 | 0.13 | 0.14 | 0.16 | 0.04 | 0.05 | 0.02 |
| Mean Local Retention | 0.02 | 0.04 | 0.08 | 0.1 | 0.06 | 0.02 | 0.03 | 0.01 | 0.01 | 0.01 |
| Mean Shortest Path | 1.71 | 2.12 | 1.62 | 1.63 | 1.81 | 1.92 | 1.84 | 2.17 | 2.56 | 1.99 |
| Maximum Shortest Path | 5 | 5 | 3 | 3 | 3 | 4 | 4 | 4 | 6 | 4 |
| Strongly Connected Sites | 0.58 | 0.56 | 1 | 1 | 0.7 | 0.4 | 0.71 | 0.55 | 0.26 | 0.4 |
| Mean Dispersal Distance (km) | 27.88 | 22.29 | 21.24 | 26.28 | 51.82 | 59.81 | 48.05 | 87.3 | 87.7 | 96.51 |

# Figure 3

Dispersal distance density kernels.

Dispersal distance is combined across species by minimum pelagic larval duration (PLD) length in days (short, medium, or long). Most short dispersers settle close to home, while few long dispersers are retained at or near their spawning sites.

# Figure 4

Forward settlement from Moloka'i to other islands.

Proportion of simulated larvae settled to each island from Moloka'i by species, organized in order of increasing minimum pelagic larval duration from left to right.

# Figure 5

Species-specific temporal recruitment patterns.

Proportion densities of settlement to specific islands from Molokaʻi based on day of year settled, by species. Rare dispersal events (e.g. Maui or Lanaʻi for *Cellana* spp.) appear as narrow spikes, while broad distributions generally indicate more common settlement pathways.

Island

Hawai'i    Maui    O'ahu
Kaho'olawe    Lana'i    Moloka'i

*Cellana spp.*

*P. meandrina*

*O. cyanea*

*P. sexfilis*

*C. persp./S. rubro.*

*P. porphyreus*

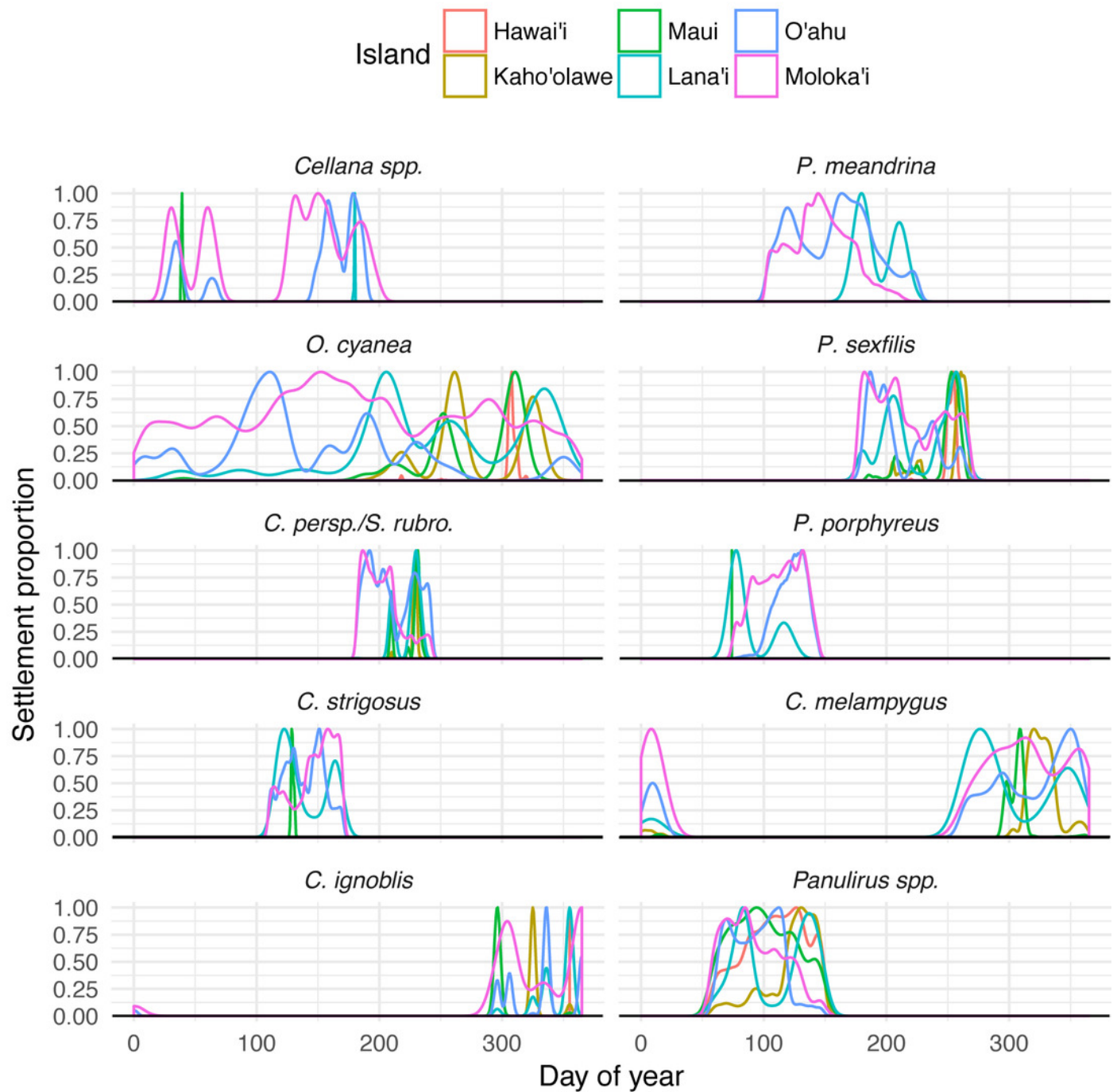
*C. strigosus*

*C. melampygus*

*C. ignoblis*

*Panulirus spp.*

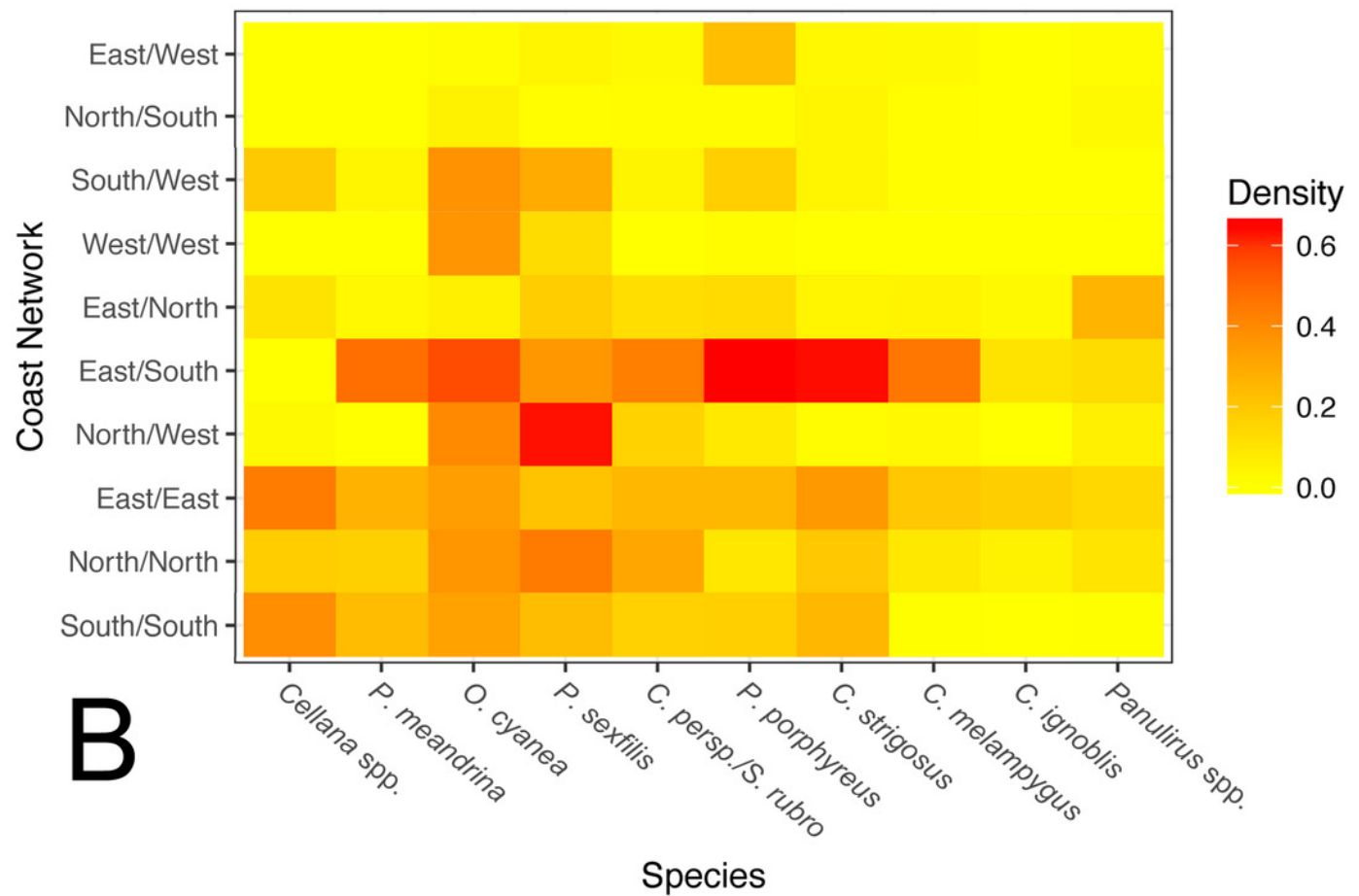
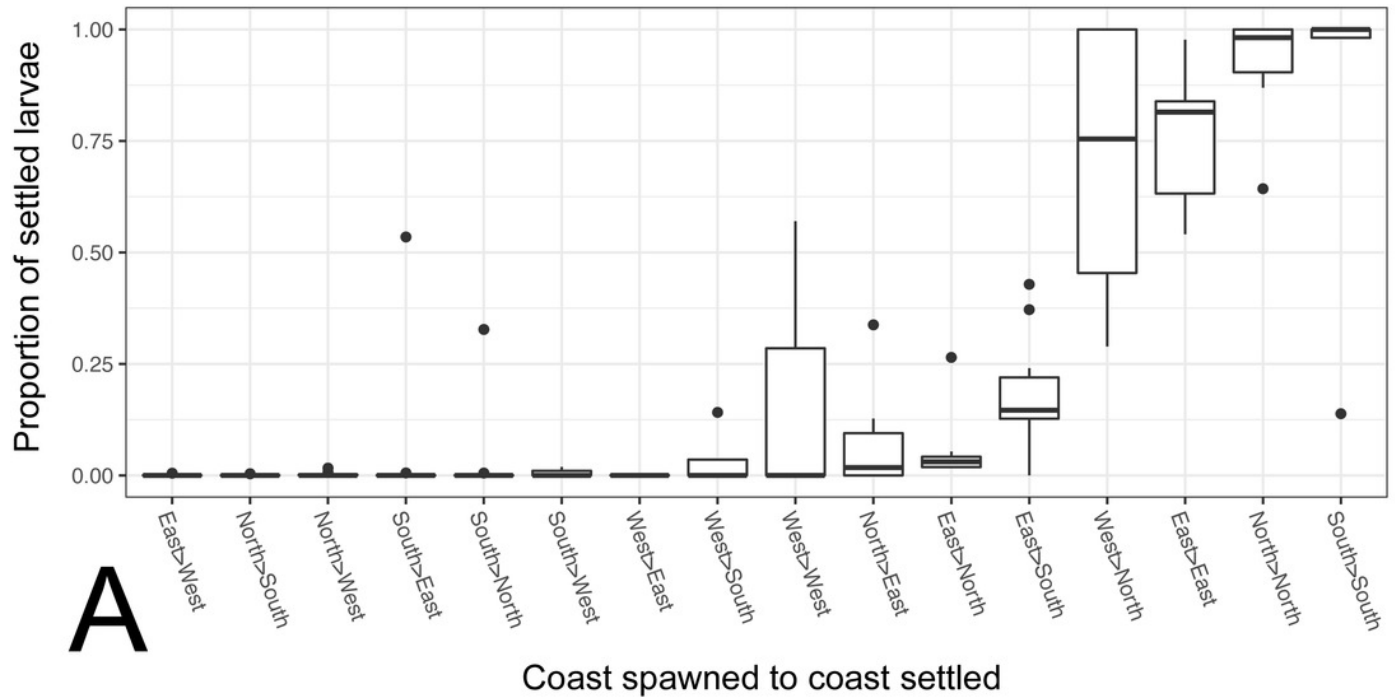
Settlement proportion

Day of year

# Figure 6

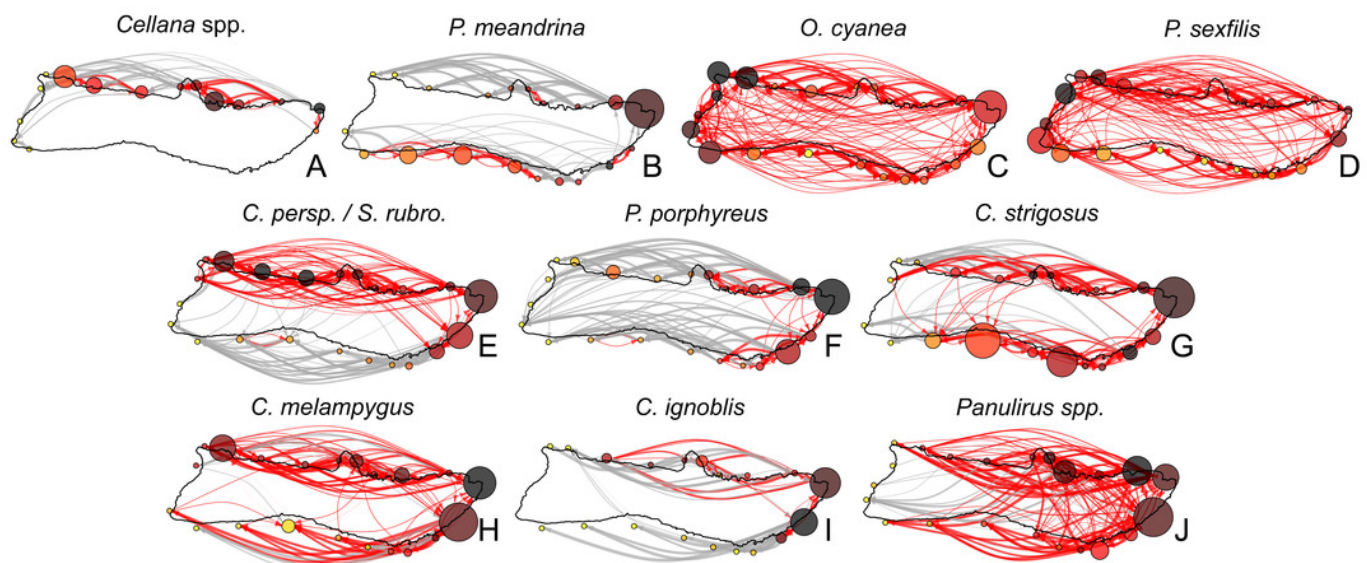
Coast-by-coast patterns of connectivity on Molokaʻi.

**(A)** Average rearward settlement proportion by species per pair of coastlines, calculated by the number of larvae settling at site *s* from site *o* divided by all settled larvae at site *s*. Directional coastline pairs (Spawn>Settlement) are ordered from left to right by increasing median settlement proportion. **(B)** Heatmap of edge density for coast-specific networks by species. Density is calculated by the number of all realized paths out of total possible paths, disregarding directionality.

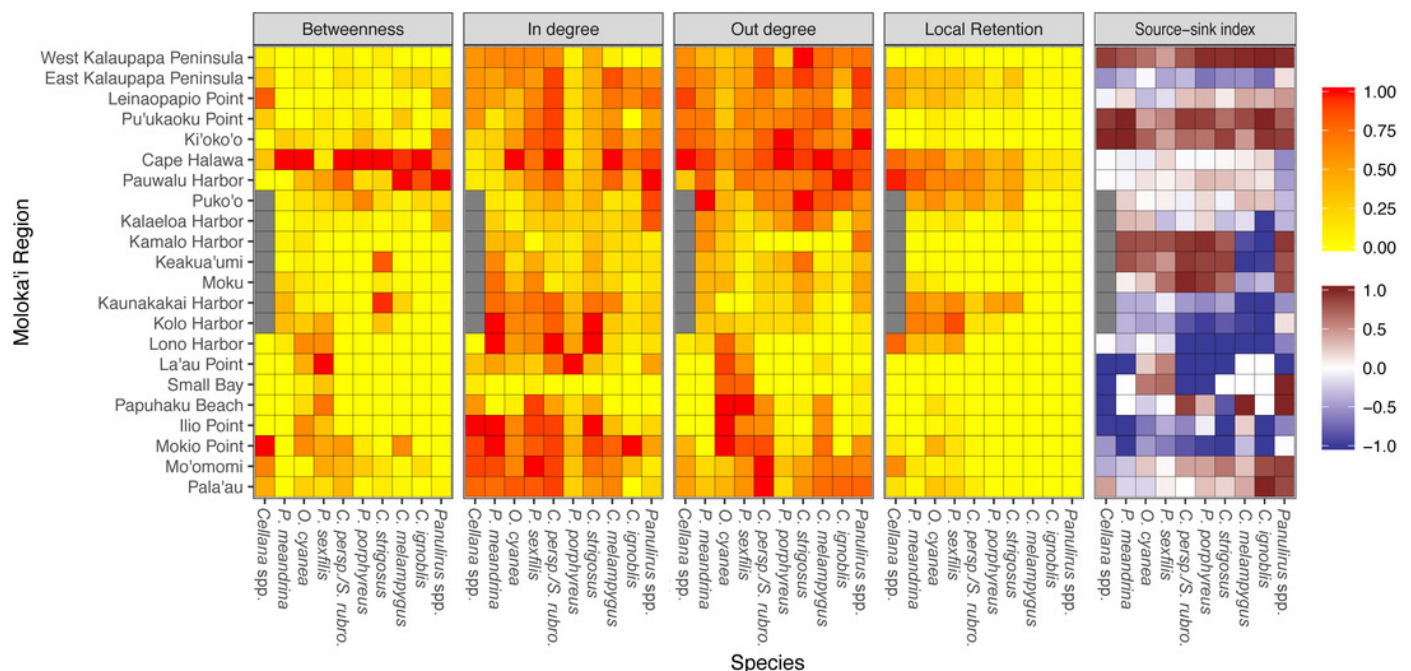
A

B

# Figure 7

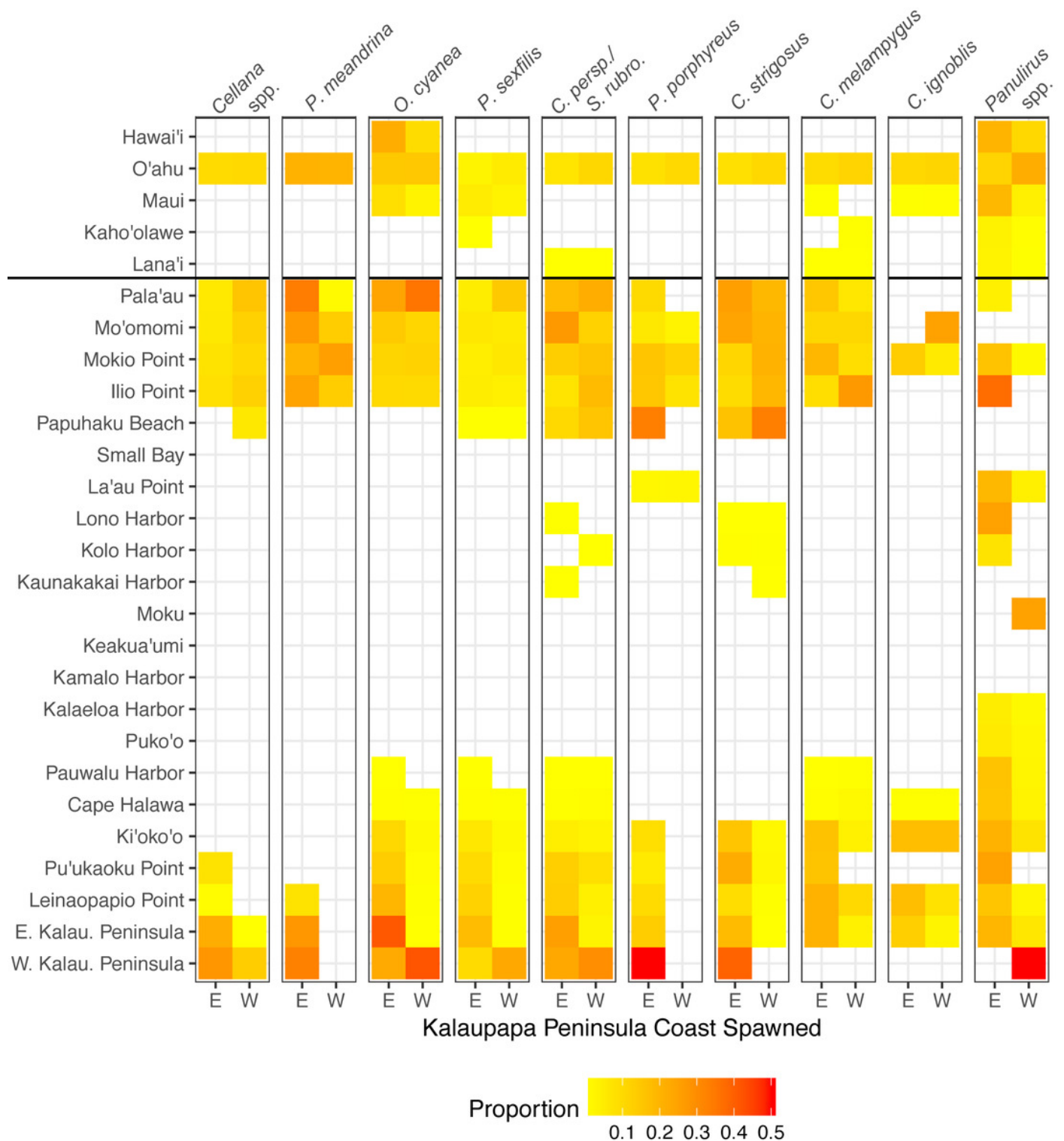
Moloka'i connectivity networks by species.

Graph-theoretic networks between regions around Moloka'i by species arranged in order of minimum pelagic larval duration. **A-D:** Short dispersers (3-25 days), **E-G:** medium dispersers (30-50 days), and **H-J:** long dispersers (140-270 days). Node size reflects betweenness centrality of each region, scaled per species for visibility. Node color reflects out-degree of each region; yellow nodes have a low out-degree, red nodes have a medium out-degree, and black nodes have a high out-degree. Red edges are connections in a strongly connected component, while gray edges are not part of a strongly connected component (although may still represent substantial connections). Edge thickness represents log-transformed proportion of dispersal along that edge.

# Figure 8

Region-level summary statistics across all species.

Betweenness centrality is a measure of the number of paths that pass through a certain region; a high score suggests potentially important multi-generation connectivity pathways. In-degree and out-degree refer to the amount of a node's incoming and outgoing connections. Betweenness centrality, in-degree, and out-degree have all been normalized to values between 0 to 1 per species. Local retention is measured as the proportion of larvae that settled back to their spawn site out of all larvae spawned at that site. Source-sink index is a measure of net export or import; negative values (blue) indicates a net larval sink, while positive values (red) indicates a net larval source. White indicates that a site is neither a strong source nor sink. Gray values for *Cellana* spp. denote a lack of suitable habitat sites in that particular region.

# Figure 9

Connectivity matrix for larvae spawned on Kalaupapa Peninsula.

Includes larvae settled on Molokaʻi (regions below horizontal black line) and those settled on other islands (regions above horizontal black line), spawned from either the east (E) or west (W) coast of Kalaupapa. Heatmap colors represent rearward proportion, calculated by the number of larvae settling at site *s* from site *o* divided by all settled larvae at site *s.* White squares indicate no dispersal along this path.

# Figure 10

Larval spillover from Kalaupapa National Historical Park.

Site-level dispersal to sites around Molokaʻi from sites in the Kalaupapa National Historical Park protected area, by species. **A-D:** short dispersers (3-25 days), **E-G:** medium dispersers (30-50 days), and **H-J:** long dispersers (140-270 days). Edge color reflects proportion of dispersal along that edge; red indicates higher proportion while yellow indicates lower proportion. Kalaupapa National Historical Park is highlighted in light green.