

REEF FISH CONNECTIVITY IN THE HAWAIIAN ARCHIPELAGO: A BIOPHYSICAL  
MODELING APPROACH

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE  
UNIVERSITY OF HAWAII'Ī AT MĀNOA IN PARTIAL FULFILLMENT OF  
THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

OCEANOGRAPHY

AUGUST 2016

By

Johanna L. K. Wren

Dissertation Committee:

Robert J. Toonen, Chairperson

Barbara C. Bruno

Anna B. Neuheimer

Brian S. Powell

Amy L. Moran

© 2016

Johanna Linnéa Kristina Wren

This work is licensed under a Creative Commons BY-NC-SA License.

---

## Acknowledgements

---

First and foremost, I would like to thank my advisor, Rob Toonen, for his unwavering support throughout my doctoral studies. Thank you for welcoming me into the ToBo lab and supported my scientific aspirations, even though they were sorely lacking in genetics. I am humbled by your brilliance and grateful that I got the opportunity to learn from you. I could not have asked for a better mentor and teacher, and for that I am forever grateful.

From the very start of my time at UH I had the great pleasure to work with Don Kobayashi at NOAA. I am eternally grateful for the patience he showed me when I was taking my first stumbling steps into the numerical modeling world. It is because of Don's support and encouragement that I was able to succeed as a modeler, graduate student and scientist. I am humbled by the generosity and kindness he has shown me, and I am thankful I can call him a colleague and a friend.

Another important mentor for me in the past five years has been Barb Bruno. My heartfelt thanks goes out to you for being a mentor, role model and friend. Your energy and enthusiasm is unrivaled, and her door is always open. I am grateful for the opportunities you have given me to challenge myself and share my love of science. Thank you for always being my champion, you are a life saver and an inspiration.

I would also like to thank my committee – Anna Neuheimer, Brian Powell, Amy Moran and Margaret McManus – for sharing your wisdom and pushing me to become a better scientist. Thank you

for staying with me through indecisiveness and last minute inspiration. I have grown tremendously as a scientist and a person under your guidance and I will carry with me your knowledge for the rest of my life.

Graduate school challenges you on many levels and often pushes you to the extremes. I am forever grateful for having brilliant and beautiful friends to help me through the darkness and celebrate the triumphs. Dutch Michelle, for keeping me sane and well fuel on coffee, beer and conversation. Christie, for always listening and. Signe, for being closer to me than anyone despite the oceans that separate us. And to Old Boss Michelle and all the folks at the dojo, to my office mates and lab mates, and friends that have kept me sane. To Bernie and Nancy who welcomed me with open arms and made me feel like family.

I am privileged to have a family that has always encouraged my curiosity and always supported my decision, even when it took me to the other end of the world. To morfar Sven for sharing your love of nature with me and feeding my curiosity of the living world. To mormor Inga-Britt, who was a role model and who taught me the importance of family and to whom I am forever indebted. To Russ for being the brother I never had and an inspiration to try new things and for teaching me to never give up. To mom and dad for your unwavering love and support, for encouraging me to follow my dreams and for making me feel like I could achieve anything. To Jessica, for showing me what it means to be a strong, successful woman, and for making my world more beautiful.

Last but not least, I would like to thank Josiah for sharing this experience with me. You are my inspiration, my safe haven, my home, and my heart. Thank you for being my sounding board, my voice of reason, and my person. I love you.

---

Abstract

---

Despite decades of research, factors that drive population patterns and connectivity in the ocean are hotly debated and largely unknown. With a changing climate and an ever increasing anthropogenic strain, protecting our oceans for future generations is vital. Coral reefs are some of the most productive ecosystems on earth, and in order to protect them we need to gain a deeper understanding of the biological and physical dynamics that govern species distributions and survival.

This dissertation aims to explore larval dispersal and population connectivity in the Hawaiian Archipelago. To effectively manage coral reef ecosystems, it is imperative to understand where the new generation comes from. To gain insight into the drivers behind observed larval distribution patterns I ground-truthed a biophysical model with *in situ* larval distributions obtained during midwater trawling off the coast of West Hawai'i Island. I was able to show that a connectivity model explained observed larval abundances and distributions of the yellow tang, *Zebrasoma flavescens*, to a significant degree. The dispersal model also showed that successful larvae most likely inhabit the deeper waters around 100 m for optimum settlement success and that larvae can travel from one end of the Main Hawaiian Islands to the other in 45 days.

The groundtruthed model allowed me to explore modeled potential connectivity in the Hawaiian Archipelago and generate a comprehensive estimate of connectivity of passive particles for the region. Genetic population connectivity has been studied extensively in the Hawaiian Archipelago,

but to date no study has looked at large scale modeled larval connectivity patterns. By comparing genetic population connectivity patterns with modeled larval connectivity patterns driven by the physical environment we can begin to understand drivers of population connectivity. I found that modeled self-recruitment was high throughout the archipelago. This is important because being able to provide your own young makes a population less reliant on outside sources of genes and larvae. Results from the biophysical model indicate that connectivity in the NWHI is predominantly driven by physical factors e.g. ocean currents. Connectivity patterns in the Main Hawaiian Islands are not explained by the physical oceanographic environment, rather, biological and anthropogenic factors are likely important for dispersal. The biophysical model identified distinct breaks in the archipelago where larval exchange is limited, and I was able to describe the directionality and relative size of dispersal between the MHI and the NWHI. Understanding larval exchange between the MHI and NWHI is important because the MHI are heavily fished while the NWHI are protected as part of one of the largest marine protected areas in the world, Papahānaumokuākea Marine National Monument.

In the final part of this work I investigate how El Nino Southern Oscillation (ENSO) change connectivity patterns in the Hawaiian Archipelago. Having a deeper understanding of changes in connectivity during relatively extreme events such as ENSO allows us to better plan for management in a changing climate. The study showed that unique connectivity pathways open up between the Hawaiian Archipelago and Johnston Atoll during El Niño events providing a pathway for larval exchange between the Hawaiian Archipelago and other islands in the Pacific Ocean. During La Niña years Johnston Atoll acts as an outpost, with modeled connectivity pathways opening up from Hawai'i towards Johnston Atoll. El Niño years had longer mean dispersal distances, and more larvae that traveled further, compared with normal and La Niña years. These periodic long distance dispersal events may contribute to the exchange of genes between distant populations, and allowing greater genetic diversity and potentially building resilience towards changing environments.

---

## Table of Contents

---

<b>ACKNOWLEDGEMENTS</b> .....	<b>III</b>
<b>ABSTRACT</b> .....	<b>V</b>
<b>TABLE OF CONTENTS</b> .....	<b>VII</b>
<b>LIST OF TABLES</b> .....	<b>IX</b>
<b>LIST OF FIGURES</b> .....	<b>X</b>
<b>CHAPTER 1: INTRODUCTION</b> .....	<b>1</b>
1.1 ECOSYSTEM BASED MANAGEMENT .....	2
1.2 CONNECTIVITY .....	2
1.3 HAWAIIAN ARCHIPELAGO .....	3
1.4 METHODS TO STUDYING CONNECTIVITY .....	4
1.5 CONNECTIVITY STUDIES IN HAWAI'I TO DATE .....	5
1.6 DISSERTATION OUTLINE.....	6
<b>CHAPTER 2: EXPLORATION OF THE LARVAL POOL: DEVELOPMENT AND GROUND-TRUTHING OF A LARVAL TRANSPORT MODEL OFF LEEWARD HAWAI'I</b> .....	<b>8</b>
2.1 INTRODUCTION .....	9
2.2 METHODS .....	12
2.2.2 <i>Dispersal modeling</i> .....	13
2.2.3 <i>Ocean circulation data</i> .....	13
2.2.4 <i>Hindcast simulation</i> .....	15
2.2.5 <i>Forecast simulation</i> .....	15
2.2.6 <i>Statistical methods</i> .....	16
2.3 RESULTS .....	17
2.3.1 <i>Field sampling</i> .....	17
2.3.2 <i>Hindcasting simulation</i> .....	17
2.3.3 <i>Forecasting simulation</i> .....	18
2.4 DISCUSSION.....	19
<b>CHAPTER 3: MODELED POPULATION CONNECTIVITY ACROSS THE HAWAIIAN ARCHIPELAGO</b> 32	

3.1 INTRODUCTION .....	33
3.2 METHODS .....	36
3.2.1 <i>Dispersal Model</i> .....	36
3.2.1.1 MITgcm .....	36
3.2.1.2 Habitat.....	36
3.2.1.3 Model initialization .....	37
3.2.2 <i>Statistical analysis</i> .....	38
3.3 RESULTS .....	41
3.3.1 <i>Potential connectivity</i> .....	41
3.3.2 <i>Total “settlement”</i> .....	43
3.3.3 <i>Distance traveled</i> .....	43
3.3.4 <i>Self-recruitment</i> .....	44
3.3.5 <i>Source-Sink dynamics</i> .....	45
3.4 DISCUSSION.....	45
3.4.1 <i>Potential connectivity</i> .....	46
3.4.2 <i>Total “Settlement”</i> .....	49
3.4.3 <i>Distance traveled</i> .....	49
3.4.4 <i>Self-recruitment and source-sink dynamics</i> .....	51
3.4.5 <i>Connectivity breaks</i> .....	52
<b>CHAPTER 4: EXTREME DISPERSAL EVENTS? HOW ENSO EVENTS AFFECT CORAL REEF POPULATION CONNECTIVITY IN THE HAWAIIAN ISLANDS .....</b>	<b>65</b>
4.1 INTRODUCTION .....	66
4.2 METHODS .....	69
4.3 RESULTS .....	72
4.4 DISCUSSION.....	74
<b>CHAPTER 5: SYNOPSIS .....</b>	<b>87</b>
5.1 BACKGROUND AND DISSERTATION GOAL.....	87
5.2 COMPLETE CONNECTIVITY MAP.....	88
5.3 ROBUSTNESS OF CONNECTIVITY PATTERNS .....	90
5.4 EL NIÑO CHANGES PATTERNS OF EXCHANGE.....	90
5.5 MANAGEMENT IMPLICATIONS AND FUTURE DIRECTIONS .....	91
<b>APPENDIX A: HAWAI’I CONNECTIVITY CIRCULATION MODEL COMPARISONS .....</b>	<b>94</b>
A.1 METHODS.....	94
A.1.1 <i>HYCOM</i> .....	94
A.1.2 <i>Connectivity Matrices</i> .....	94
A.2 RESULTS .....	95
A.2.1 <i>Difference Matrices for the Hawaiian Archipelago</i> .....	95
A.2.2 <i>Difference Matrices for the Main Hawaiian Islands</i> .....	96
<b>APPENDIX B: ENSO CONNECTIVITY MATRICES.....</b>	<b>105</b>
<b>REFERENCES .....</b>	<b>107</b>



---

## List of Tables

---

- 2.1: Summarizing larval shore fish counts from seven familial groups, as well as latitude, longitude and moon phase for all stations visited during SE1104 cruise from July 1 to July 14th, 2011. Trawl 6 and 8 has no data on larval shore fish abundance because the cod end of the trawl was compromised by cookie cutter sharks (*Isistius brasiliensis*) and trawl catch lost..... 30
- 4.1: A list of years used for each ENSO state. We defined a year July 1 – June 30 to minimize effects of seasonality and capture the peak ENSO phase in the winter. .... 78

---

## List of Figures

---

### CHAPTER 2: EXPLORATION OF THE LARVAL POOL: DEVELOPMENT AND GROUND-TRUTHING OF A LARVAL TRANSPORT MODEL OFF LEEWARD HAWAII

- Figure 1. Main surface currents around the Main Hawaiian Islands (after Lumpkin 1998). .....24
- Figure 2. Location of Cobb trawl stations off the Kona coast of Hawaii Island used in this study and visited by the SE1104 cruise. ....25
- Figure 3. Mean HYCOM currents between July 2 and July 13, 2011, for Big Island of Hawaii. Red circles show trawl sites during field sampling. ....26
- Figure 4. Summary of larval shorefish catch from Cobb trawl samples used in this study. Bar graphs show average counts of larval shore fish for each station caught during the SE1104 cruise. The graphs are placed in the location of the trawl. ....27
- Figure 5. Generalized additive model output showing relationships between modeled settlement success and a) PLD and b) depth strata used in biophysical model. Higher values denote higher modeled settlement success. Gray area shows +/- two standard errors. ....28
- Figure 6. Generalized additive model output showing relationship between trawled larval abundance of Acanthurids and a) simulated larval Acanthurid abundance and b) a moon phase and moon angle surface. The linear predictor is the observed and modeled abundance from figure a). Higher values denote higher values of modeled larval catch and gray area in a) shows +/- two standard errors. ....29

### CHAPTER 3: MODELED POPULATION CONNECTIVITY ACROSS THE HAWAIIAN ARCHIPELAGO

- Fig 1: Top panel showing the Hawaiian Archipelago domain of the dispersal model with the major surface currents (in green) identified (after Lumpkin 1998). Bathymetry lines denote 1000 and 50 m isobaths. Bottom panels show coral reef habitat pixels for the Northwestern Hawaiian Islands and Main Hawaiian Islands respectively, with each island's habitat pixels shown as a separate color. Bathymetry lines in NWHI denote 50 m depth isobath. ....55
- Fig 2. Potential Connectivity matrix for the Hawaiian Archipelago. (A) The values in each cell are "settlement" probabilities scaled to the receiving site for year-round particle release. Arrows indicated the breaks mentioned in the text. Each row in the matrix adds up to 1. High values (red) indicate high connectivity and low numbers (blue) indicate low connectivity, and white cells denote no connectivity. (B) Difference matrix showing the difference in connectivity between year-round and May-June particle release. The May-June release matrix is subtracted from the year-round release matrix (in A above). Positive values (red) denote a higher connectivity value for year-round releases and a negative number (blue) denotes higher connectivity for May-June released particles. ....56
- Fig 3. Total percent successful settlement for all sites in the Hawaiian Archipelago for the five-year model run. The

green bars represent particles spawned during peak spawning season May-June each year. ....58

Fig 4. Total percent successful settlement at each island for the five-year model run. Green bars show settlement for particles spawned during May-June, gray bars show settlement for year-round spawning. ....59

Fig. 5. Density kernel for dispersal distance from source site for all islands May 2009-May 2014. Green kernel denotes May-June spawning and gray kernel year-round spawning.....60

Fig. 6. Island specific mean particle dispersal distances from the source island. Green color denotes particles released during May-June and gray denotes distances for year-round release. ....61

Fig 7. Island specific self-recruitment for the five-year model run. Green bars show settlement for particles spawned during May-June, gray bars show settlement for year-round spawning.....62

Fig 8: Source-Sink index for all islands in the Hawaiian Archipelago for the 5-year model run. Positive numbers indicate a net source location, and negative numbers indicate a sink location. Green color denotes particles released during May-June of each year and gray denotes distances for year-round releases.....63

Figure 9. Modeled flow fields produced by the regional Hawai'i MITgcm for May 2009-May 2014. The eastward zonal flows are visible near 25°N and 27°N and major surface currents are marked.....64

**CHAPTER 4: EXTREME DISPERSAL EVENTS? HOW ENSO EVENTS AFFECT CORAL REEF POPULATION CONNECTIVITY IN THE HAWAIIAN ISLANDS**

Figure 1. Modeled region of the Pacific Ocean showing the Hawaiian Archipelago. Bathymetry lines show 50 m and 1000 m. Papahānaumokuākea Marine National Monument is located in the Northwestern Hawaiian Islands. ....79

Figure 2. Daily total successful transport for the 17-year model run. Gray colors represent Normal years, red are El Niño years and blue are La Niña years. Smooth line is the GAM model fit line, generated using the *mgcv* package in R. ....80

Figure 3. Transport probability as a function of pelagic larval duration (PLD) for all three ENSO states. ....81

Figure 4. Total transport matrices ( $T_{ij}$ ) for Normal (a), El Niño (b) and La Niña (c) years for all sites. White areas show a zero exchange of particles. Gray lines delineate the 24 regional island groupings seen in Figure 6. Self-recruitment falls along the diagonal. ....82

Figure 5. Difference matrix for total number of particles transported ( $T_{ij}$ ) at all sites for (a) Normal - El Niño, (b) Normal - La Niña, and (c) El Niño - La Niña. Red colors indicate the first listed state having more particles transported, blue indicate the second state having more particles transported. White denotes no difference between the two matrices. Gray lines delineate the 24 regional groupings seen in Figure 6. Please note the difference in scales.....83

Figure 6. Regional potential upstream probability matrices ( $C_{ij}$ ) for a) Normal, b) El Niño, and c) La Niña years. White numbers indicate a zero connectivity. Diagonal of matrix represent self-recruitment and columns add up to one.....84

Figure 7. Dispersal distance density kernels for all sites during the three different ENSO states. Brown color shows where all three ENSO states overlap. ....85

Figure 8. Number of downstream connections for particles released from the 687 habitat sites for each of the three ENSO states. Gray lines delineate the 24 regional island groupings seen in Figure 6. ....86

**APPENDIX A: HAWAI’I CONNECTIVITY CIRCULATION MODEL COMPARISONS**

Figure A1. Difference matrices comparing (A) forward and (B) rearward “settlement” probabilities between year round particle releases and releases during May - June only. Red indicated year round probabilities were higher and blue colors indicate releases during May -June only had higher probability of transport. White indicate no probability of transport. ....97

Figure A2. Forward probability matrix for the model run using MITgcm currents. Colored tiles represent probability of transport from source sites to receiving sites. White areas indicate no probability of transport between source and receiving sites .....98

Figure A3. Potential connectivity matrices for particle tracking model run using 0.08° HYCOM currents for (A) forward probabilities and (B) rearward probabilities. Colored tiles represent probability of transport from source sites to receiving sites, scaled after receiving site with each row adding up to zero. White represents a zero probability of connectivity. ....99

100

Figure A4. Difference matrices comparing (A) forward and (B) rearward transport probabilities between year round releases in the dispersal model run using 0.08° HYCOM and regional (0.04°) MITgcm. Red indicated HYCOM driven probabilities were higher and blue colors indicate the MITgcm driven model run had higher probability of transport. White indicate no probability of transport.....100

Figure A5. Probability matrices for forward (A1, B1, C1) and rearward (A2, B2, C2) potential connectivity for the Main Hawaiian Islands for three transport model runs. (A) is a subset of Fig 2a for the MHI, (B) shows probabilities from a model run using regional 0.04° HYCOM currents, and (C) is a MHI subset of figure A4. Colored tiles represent probability of transport from source sites to receiving sites. Forward matrices are scaled after receiving site with each row adding up to zero. White represents a zero probability of connectivity.....101

Figure A6. Difference matrices for the Main Hawaiian Islands for forward (A1, B1, C1) and rearward (A2, B2, C2) transport probabilities for year round releases in the dispersal model run between the regional MITgcm and 0.04 HYCOM (A), between 0.08° HYCOM and regional (0.04°) MITgcm (B) and between the two resolutions of HYCOM (C). Red colors indicated 0.08° HYCOM driven probabilities were higher in (B) and (C) and MITgcm in (A). Blue colors indicate the MITgcm driven model run had higher probability of transport in (B) and 0.04 HYCOM in (A) and (C). White represents no probability of transport. ....102

Figure A7. Map showing averaged surface circulation from global 0.08 HYCOM generated data for the Hawaiian Archipelago. Major surface currents are marked. Zonal flows in the NWHI are not present in this dataset. .103

Figure A8. Map showing averaged surface circulation from the regional 0.04 HYCOM generated data for the Main Hawaiian Islands. Major surface currents are marked. ....104

**APPENDIX B: ENSO CONNECTIVITY MATRICES**

Fig B1. Potential upstream probability matrices ( $C_{ij}$ ) for Normal (a), El Niño (b) and La Niña (c) years. White areas show a zero probability of connections. Gray lines delineate the 24 regional groupings. Self-recruitment falls along the diagonal.....106

# CHAPTER 1

---

## Introduction

---

With a changing climate and ever growing human population, the stress on our oceans is increasing. Currently, 44% of the world's 7.4 billion people live within 150 km of the ocean, and that number is increasing as populations are trending from inland rural areas to coastal cities. The world's oceans are an essential food source, providing more than 2.9 billion people with at least 15% of their animal protein intake (FAO 2014). Coral reefs are among the world's most valuable ecosystems, providing ecosystem services (e.g. coastal protection, food, recreation, cultural benefits) worth \$797.4 billion (Cesar et al. 2003), and sustenance and survival for an estimated 500 million people (Wilkinson 2008, Hoegh-Guldberg 2011). However, in recent years, they have been experiencing severe stresses due to climate change. Warming ocean temperatures and ocean acidification affect both the coral animal and the reef structure, leaving people hungry and coastlines unprotected (Worm et al. 2006, Hoegh-Guldberg et al. 2007, Knowlton & Jackson 2008, Cooley et al. 2009, Watson et al. 2015).

## 1.1 Ecosystem based management

With growing threats to our oceans and coral reefs, the need to create a framework of protections has garnered increased attention and support. Historically, marine resource management was focused on single-species protections and often failed in protecting the ecosystem as a whole (Slocombe 1993, Sharp 1995). In recent years, ecosystem based management (EBM) has largely replaced single-species approaches (Slocombe 1993, Browman et al. 2004, McLeod & Leslie 2009). EBM devises management strategies based on multiple stakeholder needs (e.g., cultural, commercial, recreational, and industrial) toward an overall goal of preserving ecosystems and ecosystem services for the future (Foley et al. 2010). Marine Spatial Planning (MSP) is a tool used to implement EBM, and Foley and colleagues (2010) identified connectivity as one of four guiding principles for effective MSP.

## 1.2 Connectivity

In the most general sense, connectivity is the exchange of individuals (young or adults) from geographically separate sub-populations (Cowen et al. 2007, Anadón et al. 2013, White et al. 2014). To understand connectivity in marine populations we need to first take a step back and first consider the life-cycle of marine organisms. The majority of marine animals have a biphasic life history strategy in which relatively sedentary adults produce tiny pelagic larval stages (Thorson 1950, Strathmann 1993, Raff 2008, Marshall et al. 2012). The larval stage and the adult stage differ greatly in biology and ecology. The larval stage is predominantly the dispersive stage for most benthic marine organisms and many reef fish. Adult reef fish show high site fidelity, and are not likely to move between islands or reefs (Meyer et al. 2010). The growth and survival of larvae in the plankton is dependent on a host of biotic and abiotic factors, e.g. temperature, food availability, predation, and ocean chemistry (Meekan et al. 2003, O'Connor et al. 2007, Stumpp et al. 2011). Connectivity describes the scale of dispersal and helps

define the ecosystem boundaries, and in extension, the boundaries of EBM. It aids us in determining how self-sufficient a population is, or if it is dependent on outside sources of larvae to persist (Jones et al. 2007, Burgess et al. 2014). Connectivity also helps us understand which populations are connected, and over what geographic scale exchange takes place (Cowen et al. 2006). Connectivity can be divided into two sub-categories. Potential connectivity is estimated from physical oceanographic attributes with limited biological input and only tracks the arrival of larvae (Calabrese & Fagan 2004), while realized connectivity takes into account the survival of larvae to reproduction (Burgess et al. 2012).

### 1.3 Hawaiian Archipelago

The Hawaiian Archipelago is a 2,600 km long chain of islands and atolls in the central north Pacific Ocean. The islands and atolls in the Hawaiian Archipelago are created from a stationary hotspot in the earth's mantle, and the chain is forged as the Earth's crust moves over the hotspot (Clague & Dalrymple 1987). The Main Hawaiian Islands (MHI) are located in the southeast end of the chain and is made up of eight emergent islands. The MHI are densely populated with heavy anthropogenic influences both above and below the water. The Northwestern Hawaiian Islands (NWHI) make up 75% of the linear distance of the Hawaiian archipelago, and consist of low lying islands, atolls, and banks. They are uninhabited and due to their remoteness have some of the most pristine coral reef ecosystems in the world (Halpern et al. 2008, Selkoe et al. 2009). The NWHI are home to Papahānaumokuākea Marine National Monument (PMNM). First protected in 2000, and formally established in 2006, with its 360,000 km<sup>2</sup>, PMNM was the largest marine reserve in the world at the time. Governing agencies in Hawai'i have adopted EBM, mainly through the creation of Marine protected areas (MPA's) with varying levels of protection (Christie et al. 2007, Tissot et al. 2009). PMNM enjoys high levels of resource protection, and only Native Hawaiian cultural practices and limited research activities are allowed. The MHI are exploited with active fisheries, and current management strategies rely on the overabundance

from the unfished stocks in PMNM to spill over and replenish the MHI. However, evaluation of the effectiveness of this strategy is lacking. Connectivity studies are ideal to evaluate the effectiveness of marine reserves, and if the spillover effect is boosting fish populations in the MHI. They can shed light on the geographic scale on which to manage resources, and evaluate the connection between the NWHI and the MHI. Additionally, because Hawai'i is isolated with high levels of endemism which makes it ideal to study population connectivity, since everything that has colonized the Hawaiian Archipelago originally came from somewhere else (Hourigan & Reese 1987).

#### 1.4 Methods to studying connectivity

There are two main ways to study connectivity: directly or indirectly. Direct methods involve actively tagging clusters of eggs or individual females that incorporate isotopes signatures into their offspring (Thorrold et al. 2007, Almany et al. 2007) or to physically follow larvae around. These methods provide *in situ* data on dispersal of organisms but is labor intensive and costly (Cowen & Sponaugle 2009). In addition, direct methods, while providing detailed data on individual's movements, is limited to the geographic area or species studied. Interpolation to other geographic locations are often limited (Kool et al. 2012). Indirect methods involve examining already present 'tags', such as microchemistry in otoliths and genetic markers (Cowen & Sponaugle 2009). The benefits of indirect methods are that all individuals are already marked, so no tagging is needed. Genetic and otolith sampling still require collection of individual specimen, but compared to direct methods is less costly and labor intensive.

In recent years, a third method to studying population connectivity has emerged: biophysical modeling. Using spatially explicit Individual based models, or other biophysical models, to study connectivity has been utilized for the past 20 years or more, but have been limited by computing speeds and lack of physical data. However, with increasing availability to high resolution physical datasets and



increasing computer processing speeds this field is quickly growing (See reviews by Werner et al. 2001, 2007). Biophysical individually based models incorporate realistic modeled ocean circulation with a varying degree of biological traits and behaviors, from highly parameterized (North et al. 2008, Liggins et al. 2015) to simplified physical transport models (Siegel et al. 2003, Wood et al. 2014) and all stages in between. One of the main benefits of biophysical models is the ability to quantitatively study population connectivity on a wide ranging temporal and geographic scales (Werner et al. 2007, Cowen & Sponaugle 2009).

## 1.5 Connectivity studies in Hawai'i to date

In Hawai'i, all three methods have been used in efforts to understand population connectivity in the archipelago. Otolith studies conducted in the MHI for reef fish showed no discernable differences in microchemistry between islands and has not been pursued further (Ruttenberg et al. 2008) as a tool to study connectivity. Genetic connectivity has been studied extensively in the Hawaiian Archipelago for a suite of 60+ mammal, fish and invertebrate species (Toonen et al. 2011, Selkoe et al. 2016a). These studies have identified areas where connectivity is limited, and important pathways and stepping stones connecting the Hawaiian Archipelago with coral reef ecosystems to the south and west (see Bowen 2016). With more efficient and cost-effective methods constantly developing, the factor limiting population genetic studies is not the laboratory/sequencing step, but rather, the ability to collect enough samples (Selkoe et al. 2016b). In Hawai'i, the remoteness of the NWHI and the permitting involved makes it difficult to access habitats and organisms for sampling. Modeling is one way to overcome that hurdle and answer questions that are otherwise difficult to investigate.

While a handful of studies have used biophysical modeling to describe connectivity in Hawai'i all studies to date are limited to small geographic areas (Kobayashi & Polovina 2006, Vaz et al. 2013,

DeMartini et al. 2013), short time periods (Kobayashi 2006, Friedlander et al. 2009), or are species specific (Polovina et al. 1999, Christie et al. 2010, Rivera et al. 2011). These modeling studies have explored the role of Johnston Atoll as a gateway to Hawaii, the effectiveness of marine reserves, and compared modeled connectivity with *in situ* recruitment data and genetic connectivity. However, due to their limited spatial and temporal scales, extrapolation of their results to the whole archipelago is limited.

The aim of my dissertation work was to create a null model of potential connectivity for the entire Hawaiian Archipelago. I opted for a simple model with habitat and pelagic larval duration as biological factors, because information on population size, mortality rates and behavior is not available for most species of reef fish in Hawai'i. If we can accurately predict larval distributions or connections using physical forcing, it excludes the need for detailed and highly parameterized IBM's. Once the null model was in place, I wanted to see how sensitive connectivity was to climate change. I accomplished this by determining if and how El Niño /Southern Oscillation (ENSO) changes connectivity patterns.

## 1.6 Dissertation outline

In this dissertation I explore potential connectivity in the Hawaiian Islands. Chapter 2 focuses on ground-truthing a Lagrangian dispersal model. Firstly, I conducted field surveys to document *in situ* larval abundances off west Hawai'i Island. These larval abundances were used to ground-truth the Lagrangian particle tracking model written by (Polovina et al. 1999). Because this model is the basis for my dissertation work, ground-truthing it was essential to understand the strengths and caveats of the model. I showed that a simple physics driven model was capable of recreating the observed larval distribution patterns off west Hawai'i. Building on the model, in Chapter 3 I expanded my study area in order to create a null model of reef fish connectivity in the Hawaiian Archipelago. By keeping the model

physics driven and including simple biological variables like reef fish habitat and larval duration, the resulting connectivity patterns would be a result of physical forcings. Comparing these connectivity patterns with published genetic connectivity for the Hawaiian Archipelago allowed me to find patterns of congruence, and determine that connectivity in the NWHI is mainly physics driven. In the MHI other factors determine connectivity patterns, such as habitat degradation, fishing pressure and anthropogenic loading (Selkoe et al. 2016a). I confirmed findings from previous genetic and modeling studies (Friedlander et al. 2009, Rivera et al. 2011) that dispersal in the Hawaiian archipelago was directional, with the prevailing currents to the northwest. Management scales should not exceed 150 km for the archipelago, since islands separated by longer distances show little exchange of individuals. Climate change has and will continue to affect coral reef ecosystems, and I wanted to gain a better understanding of how climate change may likely impact larval dispersal and reef fish connectivity. ENSO phenomena occur every 2-7 years and affect marine and terrestrial ecosystems in the Pacific and across the globe. With climate change scientist predict more frequent and stronger ENSO events in the future. To that end, in Chapter 4 I explored how sensitive connectivity in Hawai'i is to ENSO by running a model study spanning 17-years. I identified connectivity pathways with Johnston Atoll that are only present during El Niño, and determined that self-recruitment is decreased and long distance dispersal increased during El Niño.

## CHAPTER 2

---

### Exploration of the larval pool: development and ground-truthing of a larval transport model off leeward Hawai‘i

---

Most adult reef fish show site fidelity thus dispersal is limited to the mobile larval stage of the fish, and effective management of such species requires an understanding of the patterns of larval dispersal. In this study, we assess larval reef fish distributions in the waters west of the Big Island of Hawai‘i using both in situ and model data. Catches from Cobb midwater trawls off west Hawai‘i show that reef fish larvae are most numerous in offshore waters deeper than 3,000 m and consist largely of pre-settlement Pomacanthids, Acanthurids and Chaetodontids. Utilizing a Lagrangian larval dispersal model, we were able to replicate the observed shore fish distributions from the trawl data and we identified the 100 m depth strata as the most likely depth of occupancy. Additionally, our model showed that for larval shore fish with a pelagic larval duration longer than 40 days there was no significant change in settlement success in our model. By creating a general additive model (GAM) incorporating lunar phase and angle we were able to explain 67.5% of the variance between modeled and in situ Acanthurid abundances. We took steps towards creating a predictive larval distribution model that will greatly aid in understanding the spatiotemporal nature of the larval pool in west Hawai‘i, and the dispersal of larvae throughout the Hawaiian archipelago.

---

Based on: Wren, J.L.K. and D.R. Kobayashi (2016) Exploration of the “larval pool”: development and ground-truthing of a larval transport model off leeward Hawai‘i PeerJ 4:e1636; DOI 10.7717/peerj.1636

## 2.1 Introduction

Population connectivity, defined as the exchange of individuals among geographically separate sub-populations (Cowen et al. 2007, Fogarty & Botsford 2007, Pineda et al. 2007, Cowen & Sponaugle 2009) is widely recognized as important in effective marine conservation (e.g. Jones et al. 2007, Toonen et al. 2011, Trembl et al. 2012). Because traditional maximum sustainable yield fisheries management has consistently failed (Sharp 1995, Hilborn 2011), there is a general movement towards Ecosystem Based Management (EBM) to replace single-species management approaches (Slocombe 1993, Panel 1999, Browman et al. 2004, Pikitch et al. 2004, Kappel et al. 2006, McLeod & Leslie 2009). A common approach in EBM is to establish networks of marine protected areas (MPAs) to protect breeding populations which can then “spill-over” into surrounding areas to enhance stocks in areas of heavy human exploitation (Gerber et al. 2005, Halpern et al. 2009, Lester et al. 2013). Management efforts focus on regulating the adult fish, but an effective management for healthy ecosystems and sustainable fisheries requires understanding of not only adult habitats and spawning areas, but also larval dispersal and population connectivity (Gaines et al. 2010, Toonen et al. 2011).

The majority of marine organisms show a bi-phasic life style with a free-living, dispersive larval stage, that can last hours to weeks, and a more sessile or sedentary adult form (Thorson 1950, Thresher & Brothers 1985, Strathmann 1993, Raff 2008, Marshall et al. 2012). Although fish are mobile animals, most adult reef fish show strong site fidelity (Meyer et al. 2000, 2010, Wetherbee et al. 2004), thus dispersal is primarily limited to the egg and larval stages when the pelagic propagules can be transported across wide geographic areas depending upon the oceanographic regime. The importance of the larval life stage of marine fish and invertebrates in understanding population dynamics has long been recognized (Thorson 1950, Knight-Jones 1953, Scheltema 1971) yet little is still known about dispersal of marine larvae, and factors affecting dispersal and near shore retention (Levin 2006, Hellberg 2009, Cowen & Sponaugle 2009). However, an important driver of horizontal dispersal is the vertical

strata occupied by these early life-history stages (Olivar & Sabate 1997, Muhling & Beckley 2007) since abiotic and biotic gradient vary greater on the vertical scale than the horizontal scale.

The Hawaiian Archipelago is located in the central north Pacific gyre and ocean circulation patterns are primarily driven by prevailing easterly trade winds (Lumpkin 1998). The main surface flow along the island chain is from east to west: from the Main Hawaiian Islands (MHI) to the North Western Hawaiian Islands (NWHI) and westward into the Central and Western Pacific (Fig 1). The Hawaiian Lee Counter Current that flows along the southern perimeter of the islands is the main mode of surface flow towards the Hawaiian Island chain from the west to the east (Chavanne et al. 2002, Qiu & Durland 2002). Cyclonic (cold core) and anti-cyclonic (warm core) wind-generated mesoscale eddies are consistently formed in the lee of the Hawaiian Islands (Patzert 1969, Lumpkin 1998, Jia et al. 2011). Cold core eddies travel northeast along the southern perimeter of the island chain, transporting water from the Island of Hawai'i, henceforth referred to as Big Island, along the MHI chain (Seki et al. 2001). Warm core eddies are spun up off the Big Island and travel southwest, transporting water away from the island chain (Bidigare et al. 2003). These eddies have the potential to boost primary production as well as aid with water dispersal or retention within the islands themselves (Seki et al. 2002).

The hydrodynamic environment around the Hawaiian Islands is complex making it difficult to generalize physical dispersal pathways for pelagic propagules (Friedlander et al. 2009). It has long been hypothesized that the mesoscale eddies that form in the lee of the Hawaiian Islands are responsible for retaining larval fish near the islands, preventing the larvae from being swept away from appropriate settlement habitat (Lobel & Robinson 1983, Lobel 1989, 2011). The majority of spawning in Hawaiian reef fishes takes place during spring and summer (February through June), although most reef fish are believed to have low levels of spawning year round (Watson & Leis 1974, Lobel 1989, Bushnell et al. 2010). Reef fish spawning season in Hawai'i coincides with "eddy season" (Lobel & Robinson 1983, Lobel 1989, 2011), that is, the time of year when eddies are more prevalent (Flament et al. 1996). Donahue et

al. (2015) showed that timing of spawning and the subsequent timing with the presence of near shore eddies is more important than the location of spawning for larval settlement success in the lane snapper (*Lutjanus synagris*) off Cuba. In Hawai'i, the temporal and spatial dynamics of eddy entrainment of propagules is not well understood, and while mesoscale eddies are shown to have an effect on larval dispersal elsewhere (Baums et al. 2006, Harrison et al. 2013), the effects of mesoscale eddies in larval transport and settlement in Hawai'i has proven contradictory (Vaz et al. 2013), ranging from shown correlations between time of spawning and eddy activity (Lobel 1989) to no observed effect on recruitment (Fox et al. 2012). Spawning has also been linked with lunar cycles, and many reef fishes in Hawai'i are shown to spawn on or near full moon (Walsh 1987, Bushnell et al. 2010).

Studies on larval reef fish distributions suggest that larval abundances of insular marine fish that spawn pelagic eggs are more numerous off shore than near shore (see Leis & Miller 1976, Wren & Kobayashi pers. obs.). Many of the most common reef fish species in Hawai'i fall into this category, and larvae of Pomacentrids, Chaetodontids and Acanthurids are very rare in inshore plankton tows, but numerous in deeper, offshore tows (Leis & Miller 1976) although this does depend on the stages of the larvae sampled by the gear. Studying later stage larvae in situ is generally intractable, because most shorefish larvae are not easily captured/identified/enumerated, are found in low densities, and are spread over large geographical areas (Clarke 1991). One approach that could yield insights into the vertical and horizontal distributions of these elusive early life-history stages is using computer simulation coupled with field sampling (Botsford et al. 2009, Leis et al. 2011, 2013, Sponaugle et al. 2012, Kough et al. 2013, Wood et al. 2014).

Given the common spawning season and the presence of mesoscale eddies in the lee of the Hawaiian Islands, we wanted to test the hypothesis that there is a common "larval pool" in the lee of Big Island (Sale 1978). This was accomplished with field sampling and through numerical modeling. We use two different biophysical modeling approaches to investigate larval distributions. The first approach

uses a computer simulation to hindcast likely sites of propagule origin from midwater trawl samples and employs statistical tools to indicate the most likely vertical strata of propagule occupancy. This information will improve understanding of horizontal and vertical movements as well as be useful for targeted sampling of these elusive early life history stages. The second approach uses computer simulation to forecast field samples, in essence generating a virtual “larval pool”, and uses a similar comparative approach to identify the most likely vertical strata of propagule occupancy using observed and predicted patterns of relative larval abundance.

## 2.2 Methods

### 2.2.1 *Field sampling*

Midwater trawl samples collected during the SE1104 research cruise aboard the NOAA ship *Oscar Elton Sette* July 1-July 14, 2011 were used in this analysis. Two replicate 2-hour dual-warp Cobb midwater trawls (see Baltz et al. 2002 for gear specifications) were conducted nightly, at ca. 2100 and 0100 hrs, at a speed of 3 knots at 11 stations off the west coast of the Big Island (Fig 2). Maximum trawl depth targeted the shallow scattering layer, and was determined nightly from EK60 active acoustics identification of the lower boundary of the shallow scattering layer, which ranged between 150-250m. Each trawl sampled three depth strata evenly (stepped oblique) divided between 50m and the deepest bounds of the scattering layer. Tow time for each depth interval was 20 minutes following net equilibration at the deepest depth, for a minimum duration of 1h at depth and a total trawl time of approximately 2h. The trawl is constructed of graded nylon mesh (6",3", and a 1.5" liner terminated with a 1mm Nitex plankton net) and has a mouth area of approximately 690 m<sup>2</sup> at the most forward position of the coarsest mesh.

Trawl catch was quantified based on weight and volume, and the catch was sorted into six



categories: Myctophid fish, non-Myctophid fish, cephalopods, crustaceans, gelatinous zooplankton and miscellaneous zooplankton. From the non-Myctophid fish category, shore fish larvae were removed and preserved in 95% EtOH. Fish larvae from seven familial or similar groups, Chaetodontidae; Acanthuridae; Pomacanthidae; Labridae and Cirrhitidae; Muraenidae; Aulostomidae and Fistulariidae; and Mullidae, were measured and counted. These groupings were chosen because they are relatively easy to distinguish visually and their members are almost exclusively shore fish (Mundy 2005, Randall 2007). Identification to species level was not possible in the scope of this study due to time constraints and difficulty/impossibility of identification without genetic analysis (Mundy, pers. comm.) for many larval fish (e.g., Acanthurids, Pomacanthids). It is important to note that we used trawl catch data for the family of Acanthurids, not specifically for *Zebrasoma flavescens*.

### 2.2.2 Dispersal modeling

Larval dispersal simulations were performed using a two dimensional, Lagrangian advection diffusion model (Polovina et al. 1999, DeMartini et al. 2013). In the model, larvae are moved at each timestep by advective displacement caused by water flow combined with a random displacement caused by diffusion. Current velocities used by the model consist of daily snapshots of  $u$  (east) and  $v$  (north) velocities obtained from a regional implementation of the HYbrid Coordinate Ocean Model (HYCOM) for the Main Hawaiian Islands (MHI) [HYCOM described in the following section]. We used an eddy diffusivity of  $250 \text{ m}^2/\text{s}$ , which is derived from drifters in the MHI (Jia pers comm, Rivera et al. 2011). Spawning habitat was defined in the model as a suite of 302 sites uniformly located every 5 km around the perimeter of each of the emergent MHI. The dispersal model is conventionally run forward in time, but is capable of running in reverse (backwards in time) for hindcasting purposes, facilitated by using off-line storage arrays of the daily currents.

### 2.2.3 Ocean circulation data

The HYbrid Coordinate Ocean Model (HYCOM), a data-assimilative ocean circulation model developed by the multi-institution HYCOM Consortium, was the source of the modeled ocean circulation flow fields used in this study. Forcing and assimilation for HYCOM are accomplished using the Navy Operational Global Atmospheric Prediction System (NOGAPS) winds to drive the dynamics, and the Navy Coupled Ocean Data Assimilation (NCODA) system to incorporate external measurements of satellite altimetry, sea surface temperature, and *in-situ* vertical profiles of temperature and salinity. The NOGAPS and NCODA data can vary in temporal resolution from hours to weeks as well as be snapshot inputs from vessels, moorings, or profiling buoys; however, the standard temporal resolution of the HYCOM output data is daily, which is what was used in this study (Jia et al. 2011). The daily HYCOM data is a regional implementation of the University of Miami global model using K-Profile Parameterization for characterizing the mixed layer, and is made available at the Asia-Pacific Data-Research Center (APDRC) at the International Pacific Research Center (IPRC), School of Ocean and Earth Science and Technology (SOEST), University of Hawai'i (point of contact Dr. Yanli Jia). Daily HYCOM data covering the temporal domain of the calendar year 2011 and the spatial domain of 166°W to 150°W longitude and 16°N to 26°N latitude were downloaded as NetCDF files using the APDRC/IPRC website as a data conduit.

HYCOM is vertically structured with 32 layers ranging in thickness from 5-500m, with thinner layers in the upper portions of the water column and an average layer width of 10m in the upper 40m of the water column. For this exercise, several different vertical strata and averages of vertical strata of the HYCOM data were used: surface waters representing the upper 5m only, 50m depth only, 100m depth only, 0-50m average, and 0-100m average. Extraction and averaging was undertaken using R language subroutines (R Core Team 2012). The horizontal structure of the HYCOM is a variable width resolution averaging ~0.04 degree over both longitude and latitude. For ease of use, the daily variable resolution output was regridded to a daily uniform 0.04 degree coordinate system in latitude and longitude for the study domain using the mapping software Generic Mapping tools (GMT) subroutines named *blockmean*

and *surface* (Wessel & Smith 1991).

#### 2.2.4 Hindcast simulation

Hindcasting simulations used the dispersal model (described above) run backwards in time with reversed currents (i.e., starting at the trawl site and extending up to 75 days prior to the trawl date). This approach was used to predict the likely origination site and depth strata of occupancy for larval shore fish caught at the 11 trawl sites by comparing the five different depth scenarios (depths=the upper 5m, 50m depth, 100m depth, 0-50m average, and 0-100m average) and by using a plausible range of pelagic larval durations (PLDs=15, 30, 45, 60, and 75 days). The averaged depth strata were used in an effort to emulate diel vertical migration (DVM) over 50m and 100m vertical horizons, realizing that this is only an approximation of what DVM would cause. For each trawl sample and PLD/depth combination, 1000 simulated hindcast trajectories were generated for analysis. When a particle was within 5km of the 302 pre-defined spawning sites on day 1 it was defined as originating from that spawning area.

#### 2.2.5 Forecast simulation

In the forecast simulation the dispersal model was run in conventional forward mode. This approach was intended to simulate a generic “larval pool” for shorefish (*sensu* Sale 1978), and specifically for the yellow tang, *Zebrasoma flavescens*. We used the HYCOM current vectors from the 100m depth layer, based on results from our hindcast simulation (see results section) and the PLD was parameterized after the yellow tang and set to 54 days (Claisse et al. 2009b, Christie et al. 2010). Size at settlement for *Z. flavescens* is estimated at 30-55mm total length (Claisse et al. 2009b). Virtual larvae were released daily from the spawning habitat during 2011. For each of the 302 release sites and for each day, 1000 simulated forecast trajectories were generated for analysis. Pelagic abundance of older larvae (defined as ages  $\geq 50\%$  of PLD) was tabulated into daily  $0.1^\circ \times 0.1^\circ$  bins for the trawl survey dates, and actual larval catch of Acanthurids was compared to simulated larval abundance at that point in time

and space. There are to our knowledge no published growth rates for larval yellow tang, thus the age of the Acanthurids used to parameterize our model are estimates. Based on the size at settlement (~30 mm) and a 55 day PLD, we felt comfortable comparing trawl catch with data modeled using a 54 day PLD and estimating the larval pool using 50% of the PLD.

#### 2.2.6 Statistical methods

A generalized additive model (GAM) was constructed in R using the *mgcv* package (Wood 2011), and used to characterize effects from vertical layering and PLD on the predicted origin. Operationally this was accomplished by using the GAM to predict hindcast settlement success. Smoother functions for the significant terms were plotted and examined. Degrees of freedom for the smoothing splines were scrutinized and intentionally kept as low as possible (1-2 inflection points) to minimize issues of overfitting the data.

GAM was also used to characterize the relationships between actual larval catch and simulated larval abundance. We used *in situ* Acanthurid abundances from trawl catches and compared them to modeled abundances from the forecast simulation parameterized after *Zebbrasoma flavescens*. A key linkage between larval abundance and larval catch involves efficiency of the sampling gear (e.g., Clarke 1983), thus the GAM was parameterized with variables that have been known to impact visual avoidance such as moon phase and moon angle. Additionally, moon phase is known to affect biomass and abundance of mesophotic boundary layer communities in the study region (Drazen et al. 2011). Moon data was obtained from the open source astronomical package named *PyEphem* written in the programming language Python. Moon phase and moon angle were calculated for the individual trawls based on their position, date, and time of day/night. Because both the moon phase (amount of illumination) and moon angle (important scalar of the amount of illumination) could be independently or jointly important we entered them as a bivariate smoothing term in the GAM function. The *k* term for

the smoothers were set to  $k = 5$  for simulated larval abundance and  $k=6$  for the moon phase and moon angle smoothing term (to keep inflection points at a reasonable level), and a Poisson distribution was assumed for the GAM. While there are likely many other variables that could relate to the efficiency of the sampling gear, these were thought to be the most important because tow speed and weather conditions were relatively constant over the course of these surveys.

## 2.3 Results

### 2.3.1 *Field sampling*

A strong cyclonic eddie was present off the west shore of Big Island during field sampling. Additionally, there was a weaker, anti-cyclonic eddie near shore, moving water southward along the coast south of Kailua-Kona. Mean circulation on the Kohala shelf was north-eastward until the 'Alenuihāhā channel (between Maui and Big Island) pushed surface waters westward (Fig 3). Most of our stations were located in the smaller anti-cyclonic eddy near the Kona coast. Trawling took place between a new moon on June 30, 2011 and a full moon on July 14, 2011.

Larval shore fish counts were highest in stations further offshore (Fig 4), consistent with the observations of Leis & Miller (1976) and Leis (1982).. Offshore stations had the greatest diversity of shore fish, with individuals from all seven familial groups present (Table 1). Acanthurids were present at 8 of the 11 stations and mirrored total shorefish abundance patterns in the trawl catch (Fig 4). Variability between replicates was low relative to variability between stations. The average length of the collected Acanthurids was 26.1 mm pre-caudal length (PCL); near their size at recruitment (Claisse et al. 2009a).

### 2.3.2 *Hindcasting simulation*

A GAM was constructed to identify effects from vertical layering and PLD on the predicted origin by using these variables in a model predicting hindcast settlement success. PLD is highly significant ( $p < 0.001$ ) for dispersal in the model. The PLD function shows that shorter PLD's coincide with higher hindcast settlement success, and that after 40 days there is little change in the probability of originating from a suitable adult habitat (Fig 5a). After 40 days of dispersal the effect PLD has on dispersal ability remains stable, indicating that fish with PLD's longer than 40 days have the same potential for dispersal based on PLD alone. Thus, a 45 day PLD can be representative for longer PLD's, which has implications for future dispersal modeling as well as predicting dispersal ability based on PLD alone.

The vertical function from the GAM suggests that the depth layer that is most optimal for larval shore fish in order to have originated from a suitable adult habitat is 100m ( $p < 0.001$ ) followed by the 50m depth layer ( $p < 0.05$ ) (Fig 5b). There is no statistically significant difference between the effect of the surface strata or the two averaged (0-50m and 0-100m) strata on origin sites according to the GAM, indicating that the surface layer is disproportionately influencing the averaged depth scenarios.

### *2.3.3 Forecasting simulation*

The forecast simulations showed that actual larval catch was significantly related to simulated larval abundance ( $p < 0.05$ ) with the moon phase and moon angle surface ( $p < 0.001$ ) explaining 67.5% of the deviance (Fig 6). The relationship between the larval catch and simulated larval abundance was positive and the moon variables were incorporated with lower larval catch associated with higher moon angle (moon higher in the sky) and higher moon phase (brighter moon). There was indication of an intermediate moon phase corresponding to higher larval catch visualized by the hump on the surface in Figure 6.

## 2.4 Discussion

We corroborated the larval dispersal model for July 2011 by field sampling, showing that the predicted larval densities are found to significantly feed into a plausible model of abundance. While treating larvae as passive particles in the dispersal simulation, and accounting for larval behavior and gear catchability through the lunar phase and angle variable in the GAM, we were able to account for nearly 68 percent of the variance when modeling Acanthurids. Furthermore, all seven familial categories of larval fish showed the same distribution pattern in trawl data with higher abundances off shore compared to near shore, lending further evidence of the presence of a common larval pool in the water off Kona (Sale 1978).

There is ample evidence that larval fish undergo both ontogenic and diel vertical migration and that incorporating these behaviors into a biophysical model can increase the predictive power of the model (Drake et al. 2011, 2013, Sponaugle et al. 2012, Sundelöf & Jonsson 2012, Robins et al. 2013, Bidegain et al. 2013). However, little is known about the behavior of larval Acanthurids in general and *Z. flavescens* in particular. There are published swimming speeds for Acanthurids in the field and they illustrate a highly variable behavior and swimming speeds of late stage larvae (Sancho et al. 1997, Leis & Carson-Ewart 2000). Our model is parameterized for larvae approximately half way through their larval period (compared with *in situ* larvae that range between 10 and 30 mm in standard length). With such variable size and range of developmental stages, we could not venture a guess as to the swimming speed of the larvae, thus we opted for a conservative approach. Keeping the modeled larvae passive seemed appropriate in this initial evaluation of the performance of the model. Keeping larvae passive can also yield information about possible drivers of the observed distribution; achieving a high congruence between *in situ* and modeled distributions when modeled larvae were not attributed any behavior and were treated as passive drifters, indicates that the observed larval distribution is forced by physical oceanographic drivers. For example, Kough and colleagues (2013) identified an area in the

Caribbean where lobster larvae aggregated, referred to as 'nursery areas' in the study, and hypothesized that this might be a physical oceanography-driven aggregation area for lobster larvae that could play an important role in the management of the lobster stock.

The presence of a mesoscale eddie during field sampling may have helped retain larvae near the trawl sites, driving the pattern of observed as well as modeled larval distributions. It has long been hypothesized that the eddies that form along the Kona coast are responsible for retaining larvae nearshore (Sale 1970, Leis & Miller 1976, Lobel 1989, 2011, Vaz et al. 2013), thus increasing the chance of settlement success and self-recruitment. Eddies form off Kona mainly during summer when the trade winds are stronger, which coincides with the major spawning season of most Hawaiian reef fish (Walsh 1987, Bushnell et al. 2010). The eddies develop 10-15 days after a strong wind event and last for 55-70 days (Patzert 1969, Lobel & Robinson 1986). The majority of eddies move northwest at approximately 6 cm/s which may aid in transporting larvae away from the Big Island and along the south perimeter of the Main Hawaiian Island chain (Patzert 1969, Vaz et al. 2013). However, some eddies remain stationary in the lee of Big Island, and have been observed to remain in that location for 70 days (Lobel & Robinson 1986), making it possible for larvae spawned on reefs along the leeward coast of the Big Island to be entrained in eddies and remain near the coast for the duration of their pelagic larval stage.

The larger 'off shore' eddie present during our field sampling (Fig 3) spun up on or near June 1, 2011 and was present throughout sampling, whereas the smaller eddie located close to shore during field sampling spun up on or near July 3, 2011 and lasted the duration of field sampling. Considering that *Z. flavescens* spawns at full moon (Bushnell et al. 2010) and the PLD is estimated at 55 days (Claisse et al. 2009b, Christie et al. 2010), it is likely that larvae we caught during trawling were spawned near the full moon on either May 17 or June 16, 2011 and possibly entrained in the eddie shortly thereafter. Genetic analysis of the Acanthurid larvae can be done to verify the origin location of the larvae against published genetic connectivity data (Eble et al. 2009, Christie et al. 2010).



The hindcast simulation showed that larvae can reach the full extent of the Main Hawaiian Islands (MHI) in 40-45 days, which is important for future dispersal modeling studies. Connectivity patterns in the MHI will not change significantly if PLD is increased past 45 days, thus connectivity studies using a 45 day PLD can be representative of fish species with a longer PLD in Hawai'i. The results from the hindcasting simulation suggest that the larvae should primarily occupy the 100m depth layer if settlement success is the primary driver. Little is known about larval shore fish depth distributions around the Hawaiian Islands, however Acanthurid larvae have been found as deep as 575m in the Caribbean, with the highest concentrations at or slightly above the chlorophyll a maximum (Oxenford et al. 2006) which in the study was at 100 m. Boehlert & Mundy (1996) reported that Acanthurids are found in the upper 80 m in waters off O'ahu (mean mixed layer depth at Station ALOHA north of O'ahu (22° 45'N, 158° 00'W) is 60.1m [<http://hahana.soest.hawaii.edu/hot/hot-dogs/mldepth.html>]). The chlorophyll maximum at Station ALOHA is located near 110 m depth and the salinity maximum near 100 m (<http://hahana.soest.hawaii.edu/hot/methods/chl.html>; <http://hahana.soest.hawaii.edu/hot/methods/salinity.html>), making our hypothesis derived from model results that larvae should occupy the 100m depth layer plausible.

By identifying both physical and biological features, such as preferred depth strata and the effect of PLD on dispersal ability, we can better understand and evaluate population dynamics in fish or invertebrate populations. Essential Fish Habitat (EFH) mapping is used in determining areas of high importance for a variety of commercially important fish species, but little to no consideration is taken to the larval stage of the fishes (Kobayashi pers. comm., Warner et al. 2000). Additionally, creating an archipelago-wide larval hotspot map will aid in identifying important larval fish habitat and this study lays the groundwork for that effort. The approach of generating a baseline population of organisms and applying a simulated capture process to allow comparison with actual catch data is similar to approaches used in stock assessment methodologies. The methodological approach called stock

synthesis (Methot 1990) is an example of such an inverse type approach (Murray-Smith 2000). This approach is of value for identifying complex yet important drivers of the system under study when an observed value is the synergistic result of layered and interacting processes. In such instances the parameters cannot be simply incorporated in conventional linear approaches modeling observed values against a suite of predictor variables. The insights into the capture process presented here might be useful for future inverse modeling of insular fish stocks and their recruitment dynamics.

As more detailed abundance, behavior and growth data become available for *Zebrasoma flavescens*, the modeling approach can be better tuned to model both patterns of connectivity and the spatiotemporal nature of the “larval pool”. Future trawl surveys can test the hypothesis of the 100 m depth occupancy, as well as target areas that are predicted to have high larval abundance if specimen acquisition is prioritized. Similarly, such areas of high larval abundance can potentially be protected from deleterious effects in an effort to preserve essential fish habitat and areas of particular concern, ideas that have received national attention in both the public and scientific communities (Warner et al. 2000, Kough et al. 2013). If species are recruitment-limited and/or the propagules are localized and vulnerable in time and space, pelagic areas might be warranted for management scrutiny.

Computer simulation modeling proved to be a powerful tool for furthering our understanding of larval transport in the Hawaiian Islands region. Even though the parameterization of the model was kept conservative with respect to larval behavior and life history traits (e.g. we did not include mortality, ontogenic or diel vertical migrations, or swimming behavior) we were able to reproduce *in situ* larval distributions and account for two thirds of the variance in the model. By ground-truthing the dispersal model with field sampling, we took steps towards making predictions about the spatiotemporal dynamics of the larval pool in west Hawai'i. Future projects will incorporate additional years of *in situ* trawl catches so that we can make the biophysical model predictive, thus rendering it a valuable tool in management efforts of important commercial fish, not only the reef associated yellow tang (*Zebrasoma*

*flavescens*) but for commercially important bottomfish in Hawai'i such as eteline snappers.

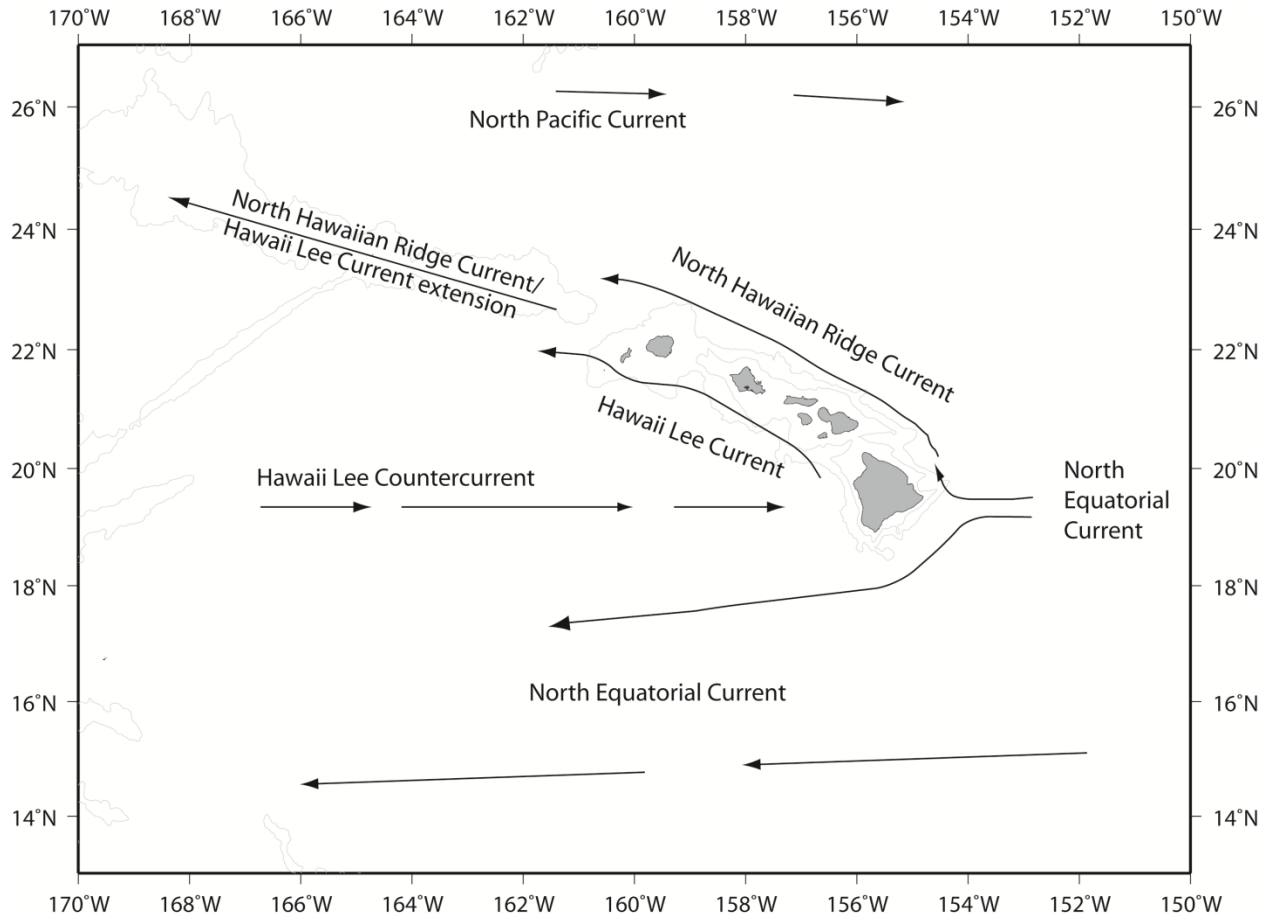


Figure 1. Main surface currents around the Main Hawaiian Islands (after Lumpkin 1998).

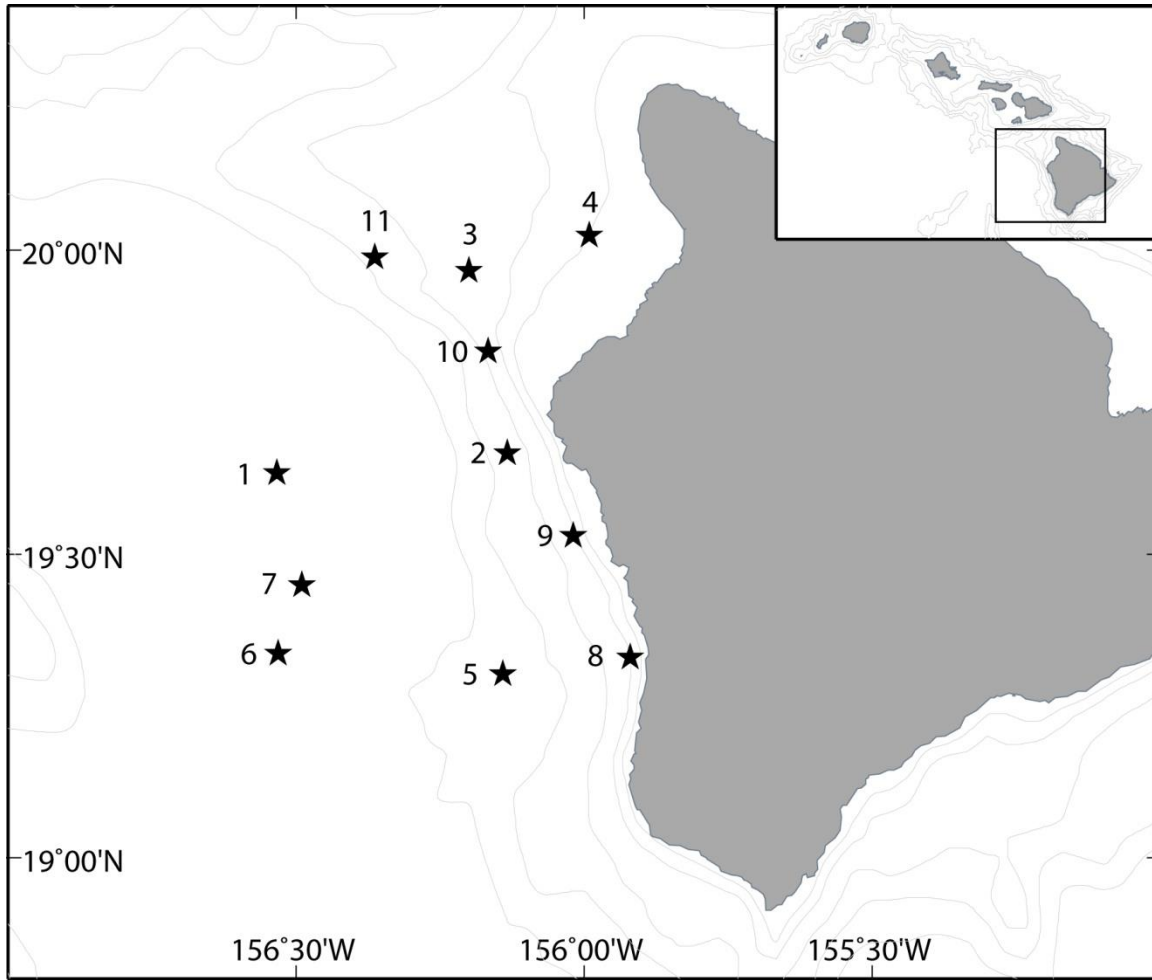


Figure 2. Location of Cobb trawl stations off the Kona coast of Hawai'i Island used in this study and visited by the SE1104 cruise.

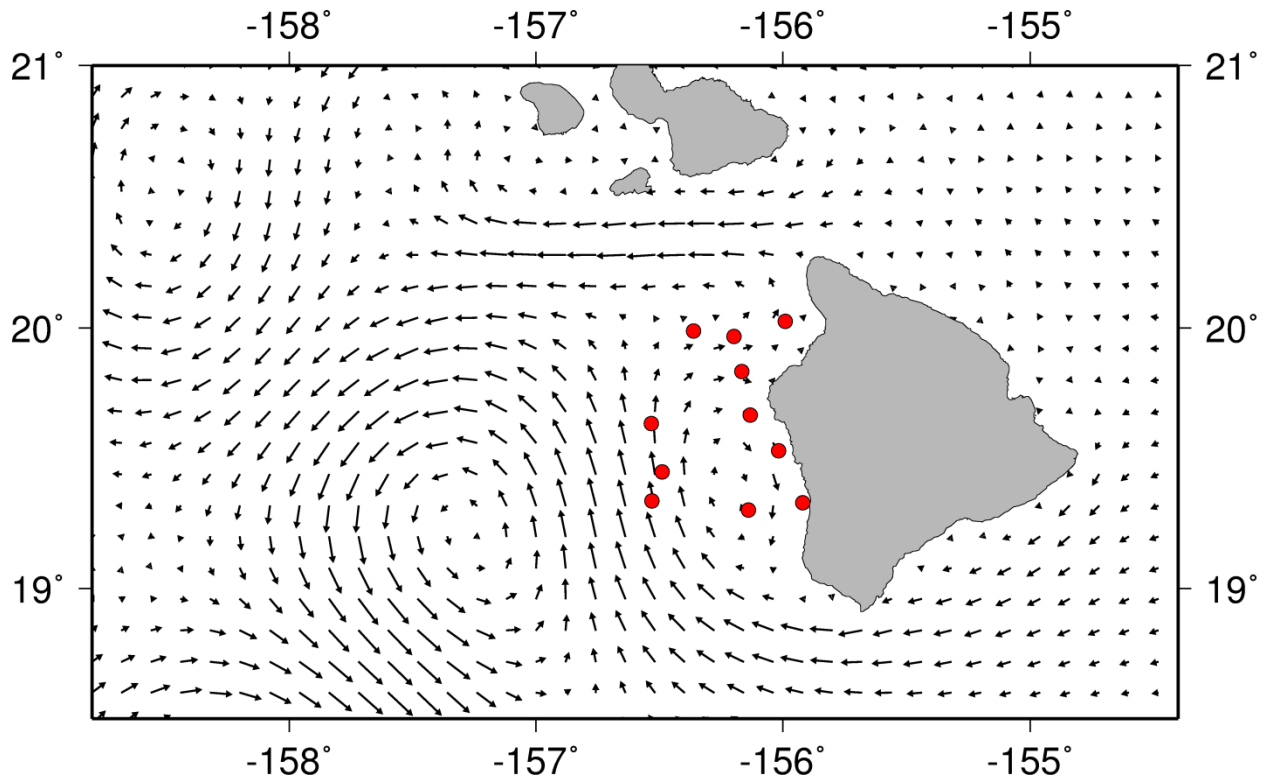


Figure 3. Mean HYCOM currents between July 2 and July 13, 2011, for Big Island of Hawai‘i. Red circles show trawl sites during field sampling.

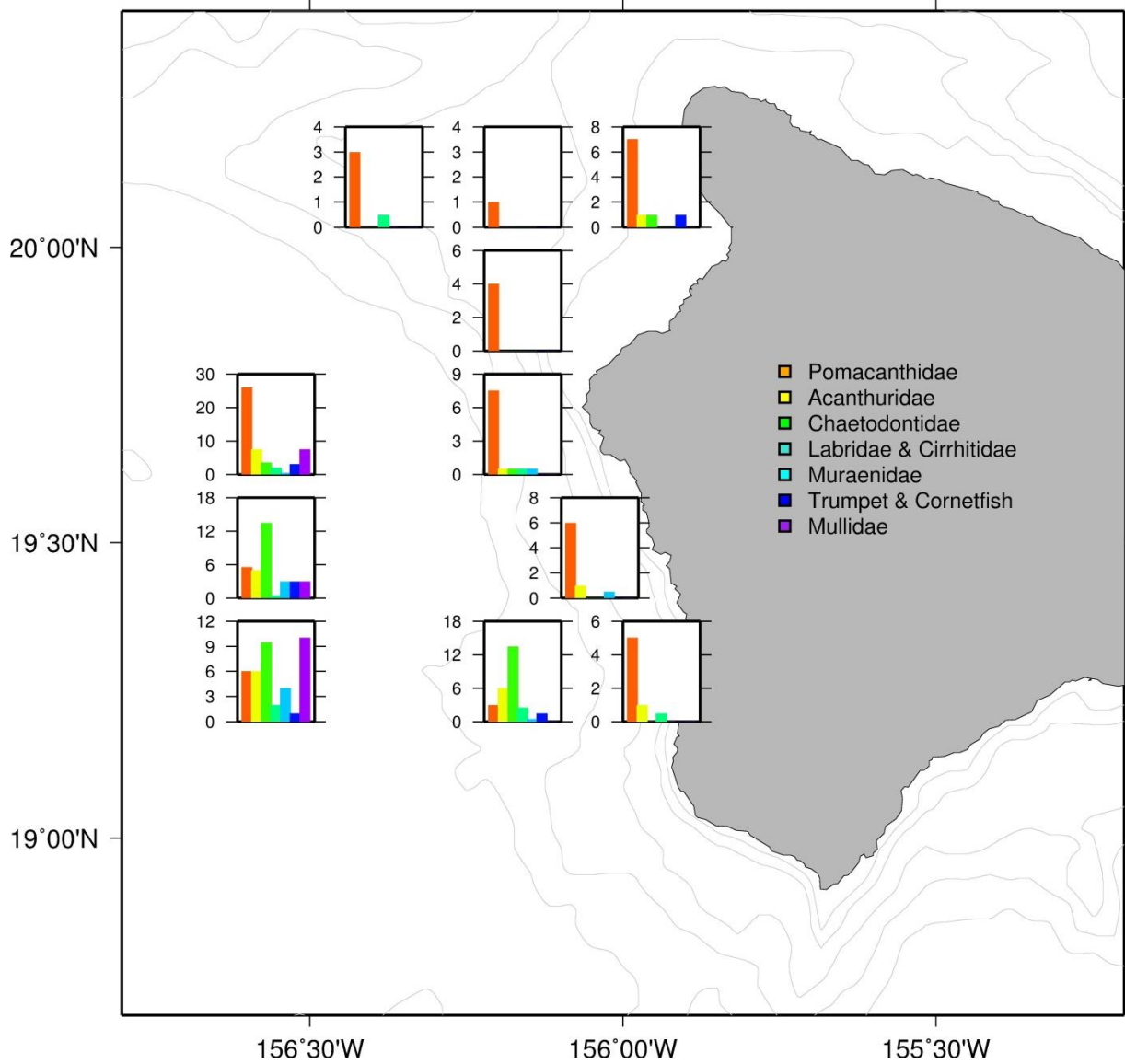
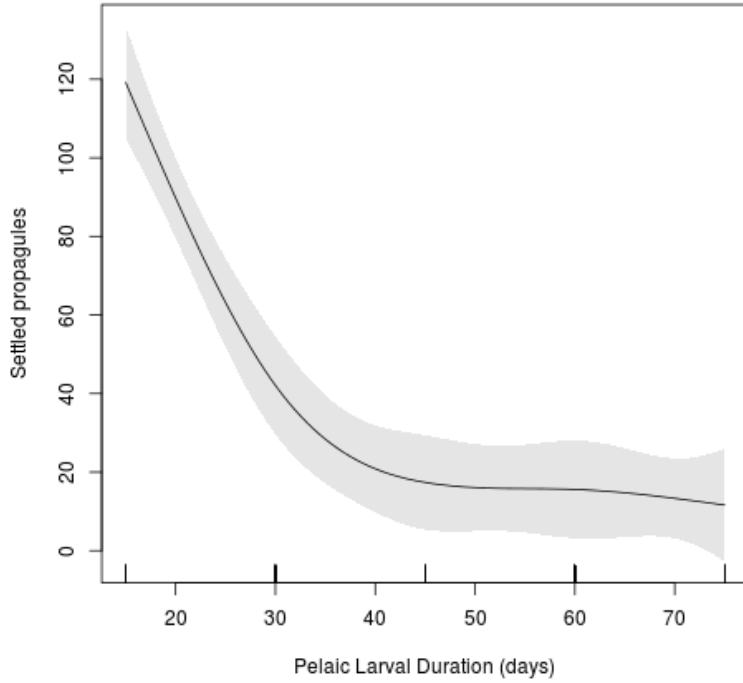
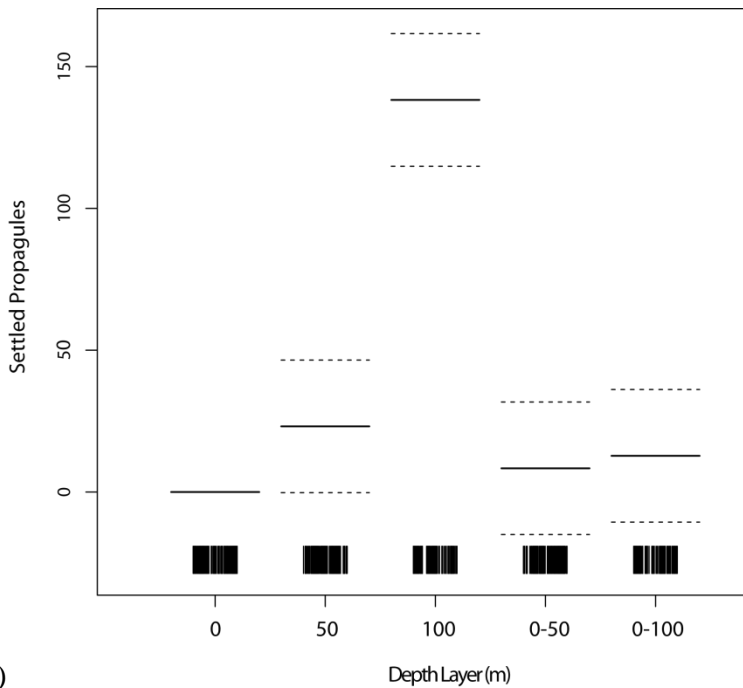


Figure 4. Summary of larval shorefish catch from Cobb trawl samples used in this study. Bar graphs show average counts of larval shore fish for each station caught during the SE1104 cruise. The graphs are placed in the location of the trawl.



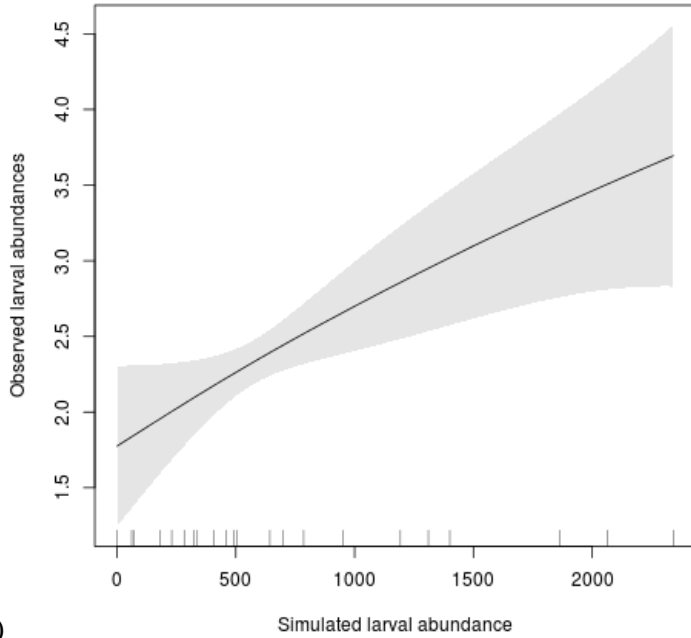
a)



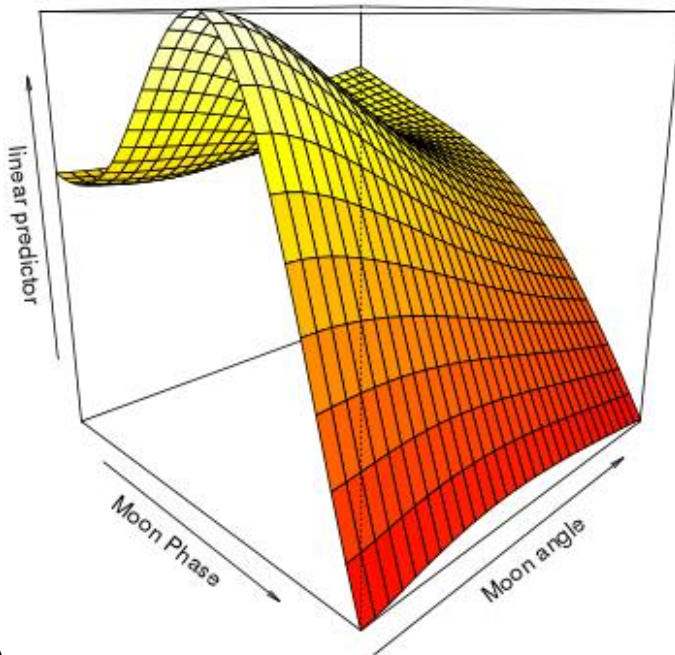
b)

Figure 5. Generalized additive model output showing relationships between modeled settlement success and a) PLD and b) depth strata used in biophysical model. Higher values denote higher modeled settlement success. Gray area shows +/- two standard errors.





a)



b)

Figure 6. Generalized additive model output showing relationship between trawled larval abundance of Acanthurids and a) simulated larval Acanthurid abundance and b) a moon phase and moon angle surface. The linear predictor is the observed and modeled abundance from figure a). Higher values denote higher values of modeled larval catch and gray area in a) shows  $\pm$  two standard errors.

Table 1. Summarizing larval shore fish counts from seven familial groups, as well as latitude, longitude and moon phase for all stations visited during SE1104 cruise from July 1 to July 14th, 2011. Trawl 6 and 8 has no data on larval shore fish abundance because the cod end of the trawl was compromised by cookie cutter sharks (*Isistius brasiliensis*) and trawl catch lost.

Trawl number	Station number	Longitude	Latitude	Moon Phase	Moon Angle	Pomacanthidae	Acanthuridae	Chaetodontidae	Labridae & Cirrhitidae	Muraenidae	Fistulariidae	Mullidae
1	1	203.50	19.65	4.5	36.8	24	5	2	3	1	2	15
2	1	203.47	19.63	5.4	58.2	28	10	5	1	0	4	0
3	2	203.87	19.67	10.4	25.0	14	1	1	1	1	0	0
4	2	203.87	19.67	11.9	52.9	1	0	0	0	0	0	0
5	3	203.80	19.98	18.4	12.7	2	0	0	0	0	0	0
7	4	204.03	20.01	28.0	0.7	7	1	1	0	0	1	0
9	5	203.85	19.30	38.9	0.0	1	7	5	0	0	1	0
10	5	203.86	19.30	40.8	24.8	5	5	22	5	1	2	0
11	6	203.49	19.35	50.4	0.0	5	4	4	4	2	2	17
12	6	203.47	19.34	52.3	13.6	7	8	15	0	6	0	3
13	7	203.54	19.50	61.8	0.0	3	6	12	1	4	4	6
14	7	203.51	19.45	63.6	2.5	8	4	15	0	2	2	0
15	8	204.17	19.33	72.9	0.0	4	2	0	1	0	0	0
16	8	204.08	19.33	74.2	0.0	6	0	0	0	0	0	0
17	9	203.98	19.53	82.0	0.0	4	0	0	0	1	0	0
18	9	203.98	19.53	83.4	0.0	8	2	0	0	0	0	0
19	10	203.81	19.86	89.8	0.0	1	0	0	0	0	0	0
20	10	203.83	19.83	90.9	0.0	7	0	0	0	0	0	0
21	11	203.64	19.99	95.5	0.0	1	0	0	1	0	0	0
22	11	203.64	19.99	96.2	0.0	5	0	0	0	0	0	0



# CHAPTER 3

---

## Modeled population connectivity across the Hawaiian Archipelago

---

We present the first comprehensive estimate of connectivity of passive pelagic particles released from coral reef habitat throughout the Hawaiian Archipelago. Potential connectivity is calculated using a Lagrangian particle transport model coupled offline with currents generated by an oceanographic circulation model, MITgcm. The connectivity matrices show a surprising degree of self-recruitment and directional dispersal towards the northwest, from the Main Hawaiian Islands (MHI) to the northwestern Hawaiian Islands (NWHI). We identify three predicted connectivity breaks in the archipelago, that is, areas in the mid and northern part of the archipelago that have limited connections with surrounding islands and reefs. Predicted regions of limited connectivity match observed patterns of genetic structure reported for coral reef species in the uninhabited NWHI, but multiple genetic breaks observed in the inhabited MHI are not explained by passive dispersal. The congruence between our modeling results based on physical transport of passive particles in the low-lying atolls of the uninhabited NWHI, but not in the anthropogenically impacted high islands of the MHI begs the question of what ultimately controls connectivity in this system?

---

Based on: Wren, J.L.K. , D.R Kobayashi, Y Jia and R.J. Toonen (in revision) Modeled population connectivity across the Hawaiian Archipelago. PLoS ONE.

### 3.1 Introduction

Determining levels and patterns of connectivity is vital for understanding metapopulation dynamics and persistence, and is essential for effective resource management (see Mora and Sale 2002; Swearer et al. 2002; Kritzer and Sale 2004; Lipcius et al. 2008; Botsford et al. 2009). Over ecological time scales population persistence depends on either the ability to retain locally produced larvae, i.e. self-recruitment, or the ability to import larvae from nearby areas, i.e. connectivity (Cowen et al. 2000; Jones et al. 2009; Burgess et al. 2014). Self-recruitment is a metric describing how open or closed a population is, which in turn describes its resilience (Hastings and Botsford 2006; Jones et al. 2009). Open populations receive an influx of larvae from outside sources, making them more resilient to local disturbances but limited in potential for local adaptation (Roughgarden et al. 1988; Hughes 1990). Closed populations are more sensitive to local disturbances and possess a greater potential for local adaptation since they are dependent on locally produced offspring and have a more direct link between local production and recruitment. Marine population studies have historically worked under the assumption that marine fish populations are open - that is, they receive larvae from other populations some distance away (Roughgarden et al. 1985) due to the dispersal ability and relatively long larval duration of marine fish larvae. However, studies in recent years have challenged this notion, showing that despite a strong larval dispersal ability many marine reef populations are closed, with larvae staying “close to home” (Swearer et al. 1999; Cowen et al. 2000; Jones et al. 2005; Concepcion et al. 2014). We no longer assume all marine populations to be open, and the focus is now on determining the extent to which marine populations exchange larvae (see Mora and Sale 2002; Swearer et al. 2002). Knowing the connectedness of a population is vital in effectively managing the population and designing functioning marine reserves.

Most coastal marine species have a biphasic life cycle, in which dispersal takes place

predominantly during the pelagic larval stage of the life cycle (Thorson 1950). Some species lay benthic eggs that develop into pelagic larvae, whereas others spawn gametes directly into the water column, where they drift as passive particles until they develop swimming abilities similar to benthic hatchlings. Larvae can be feeding or non-feeding in the water column, and the pelagic larval phase may last for minutes to months in the pelagos before they return to the benthos to settle. Each of these life-history differences has predictable impacts on observed population genetic structure (Bradbury et al. 2008; Riginos et al. 2011), but the biological and physical factors driving dispersal in the sea are not well understood and difficult to generalize. Factors controlling successful dispersal can be species specific (Toonen et al. 2011; Concepcion et al. 2014; Holstein et al. 2014; Selkoe et al. 2014), depend on timing of spawning events (Carson et al. 2010; Donahue et al. 2015) and vary among locations (Baums et al. 2006; White et al. 2010; Selkoe et al. 2010; Liggins et al. 2015; Treml et al. 2015).

The Hawaiian Archipelago, located in the subtropical North Pacific Ocean, is a 2,500 km long chain of volcanic islands and atolls, stretching from 19°N in the MHI to 30°N in the NWHI. The Hawaiian Archipelago is one of the most isolated on the planet, and home to one of the largest marine reserves in the world, Papahānaumokuākea Marine National Monument (PMNM). There is a high level of endemism in the Hawaiian Archipelago (Hourigan and Reese 1987; Kay and Palumbi 1987), and due to its remote location, has unique management needs (Kittinger et al. 2011; Toonen et al. 2013). While the MHI are populated with active fisheries and heavy anthropogenic loading, the NWHI are uninhabited and fully protected with little anthropogenic influence (Selkoe et al. 2009). One of the hopes for establishing PMNM, which was the largest MPA on the planet at that time, was a spillover effect where the protected fish populations in PMNM would replenish fish stock in the MHI. Unfortunately, this hope has been little supported among studies to date of both invertebrates and fishes (Bird et al. 2007; Friedlander et al. 2009; Rivera et al. 2011; Skillings et al. 2011). The lack of spillover from PMNM to the MHI has been attributed to the prevailing surface currents moving larvae up the island chain from the

MHI towards the NWHI (Kobayashi and Polovina 2006; Rivera et al. 2011).

Because management needs vary greatly between the heavily populated MHI and the uninhabited PMNM, it is vital that we understand the population dynamics between these areas as well as within them. Well-connected populations with numerous dispersal pathways among sites are more resilient, that is, more likely to recover from disturbance. Conversely, isolated populations that are highly dependent on self-recruitment for population maintenance, are less likely to recover after a disturbance and face a greater risk of extinction (Kritzer and Sale 2004; Lipcius et al. 2008; Botsford et al. 2009; Jones et al. 2009).

Extensive population genetic work has been done to characterize population structure for fish and invertebrates to infer exchange among sites throughout the Hawaiian Archipelago (reviewed by Toonen et al. 2011; Selkoe et al. 2014) but only a handful of studies have focused on estimating dispersal during the larval stage (Polovina et al. 1999; Kobayashi and Polovina 2006; Kobayashi 2006; Friedlander et al. 2009; Christie et al. 2010; Rivera et al. 2011; Vaz et al. 2013; DeMartini et al. 2013; Wren and Kobayashi 2016). To date, all such studies focus on either a single species of interest, a small region of the archipelago or a very limited time period. Here, we present the first comprehensive dataset describing modeled potential connectivity among sites throughout the entire Hawaiian Archipelago using a biophysical model coupled with eddy resolving ocean currents. We use a purely physical model with passive particles to determine likely patterns of potential connections within the archipelago and Johnston Atoll because detailed information on larval behavior, mortality rates, and population sizes are not currently available for the vast majority of species in Hawai‘i. The results from this study will set the groundwork for future studies to use more realistic biophysical models that incorporate such factors as larval behavior as they become available.

## 3.2 Methods

### 3.2.1 *Dispersal Model*

#### 3.2.1.1 MITgcm

The Massachusetts Institute of Technology general circulation model (MITgcm) solves the incompressible Navier-Stokes equations on a sphere in discretized forms employing a finite-volume technique (Marshall et al. 1997). The regional MITgcm implementation for the Hawaiian Archipelago extends from 175°E to 150°W and from 15°N to 35°N at a 0.04° (~4km in the region) resolution. In the vertical direction, the water depth is divided into 50 layers with a thickness ranging from 5 m near the surface to 510 m near the bottom. It is forced at the surface by winds derived from the Advanced Scatterometer (ASCAT) observations with a 0.25° resolution, and heat and freshwater fluxes were obtained from European Center for Medium-Range Weather Forecast (ECMWF) Interim Reanalysis at a 1.5° resolution. The ocean state as estimated by the global HYCOM prediction system at a 0.08° resolution (Chassignet et al. 2009) is used to define the initial and open boundary conditions. The simulation period runs from May 2009 to May 2014. We use the flow fields in the 100 m model layer to disperse particles in our Lagrangian tracking experiments (see below), as this layer has shown to be the best predictor of settlement in the region (Vaz et al. 2013; Wren and Kobayashi 2016).

#### 3.2.1.2 Habitat

For this study we included all available coral reef habitat in the Hawaiian archipelago and Johnston Atoll. Johnston Atoll is the nearest reef to the Hawaiian Archipelago, located 1390 km southwest of the Island of Hawai‘i. We chose to include Johnston Atoll in the habitat definition because there are shown biogeographic ties between Johnston Atoll and the Hawaiian Archipelago (Grigg 1981;



Maragos and Jorkiel 1986; Kosaki et al. 1991; Kobayashi 2006; Timmers et al. 2011). To generate our habitat map, we used habitat defined as ‘coral reef’ in IKONOS-derived data for the Northwest Hawaiian Islands (Battista et al. 2007; Weiss et al. 2009) and the data set presented in (Franklin et al. 2013) for the MHI, and created a 4-km<sup>2</sup> grid of that habitat, totaling 687 habitat pixels. The habitat pixels were additionally grouped into 31 different islands/banks/atolls (hereafter referred to as islands) to allow for island scale comparisons (Fig 1).

### 3.2.1.3 Model initialization

To investigate the exchange of particles among locations in the Hawaiian Archipelago we used a Lagrangian bio-physical particle tracking model (Polovina et al. 1999; Wren and Kobayashi 2016) coupled with the flow fields from the MITgcm simulation described above. Eddy diffusivity was set to 250 m<sup>2</sup>/sec consistent with drifters in Hawaiian waters (following Rivera et al. 2011). We released 50 particles (virtual larvae) daily from May 2, 2009, until April 10, 2014, from 687 coral reef habitat pixels totaling just over 62 million released particles for each model run. We used a pelagic larval duration (PLD) of 45 days, representative for most reef fish (Shanks 2009) and previous studies show that PLD’s longer than 45 days do not significantly alter settlement probabilities in the MHI (Wren and Kobayashi 2016). For a particle to be considered “settled” it had to be within a 5 km radius of the center of a habitat pixel on the last day of its PLD (on day 45). The dispersal model was run three times and the output averaged for consistency.

To test the robustness of the model with respect to ocean circulation model resolution (Putman and He 2013) we ran identical biophysical model runs, forcing the model with current velocities from the global HYCOM at a 0.08° resolution and a regional implementation of HYCOM at 0.04° (available for the MHI only) resolution in addition to the MITgcm (see supplemental).

### 3.2.2 Statistical analysis

We are focusing on potential connectivity in this study, which estimates the connectivity of a site using physical oceanographic attributes and limited biological factors influencing dispersal ability (in our case PLD and habitat) (Calabrese and Fagan 2004; Burgess et al. 2012). To evaluate patterns of potential connectivity in the Hawaiian Archipelago, we created a connectivity matrix that measures the likelihood of particle exchange by currents among sites. The model generates a 687 x 687 settlement matrix  $S_{ij}$  containing the number of particles released from habitat  $i$  (source site) that successfully reached habitat  $j$  (receiving site) for the full run of the model (five years). To create the rearward probability matrix, we scaled  $S_{ij}$  to island specific total released particles. Rearward probability matrices report origin sites of particles arriving at the receiving site and can be written:

$$P_{ij}(\text{rearward}) = S_{ij} / \sum S_j$$

We then binned the 687 habitat sites used in the dispersal model by island, resulting in a 31 x 31 island matrix, to allow for a more meaningful comparison of potential connectivity. The resulting probability matrix ( $P_{ij}$ ) shows the origin island of successfully transported particles at each island. The number in each cell of the  $P_{ij}$  matrix is the probability of a particle transported to island  $j$  having originated from island  $i$  for the five years the model was run, and each row in the matrix adds up to one. The diagonal of the probability matrix shows the self-recruitment for each island. Forward probability matrices were also generated and are described in the supplemental material. Since the majority of coral reef fish spawn during May-June (Lobel 1989; Bushnell et al. 2010), we calculated all metrics on both year-round releases and releases restricted to May-June of each year. All matrices were plotted using the software program Generic Mapping Tools (GMT) 4.5.11 (Wessel and Smith 1991).

*Subtraction matrices* were generated by subtracting the probability matrix for year round releases from the matrix for May-June releases using the subroutine *grdmath* in GMT 4.5.11. The

resulting subtraction matrix shows where the two connectivity matrices differ. Only “forward” matrices were compared with each other, and “rearward” matrices with each other. We used mantel tests for each pair of connectivity matrices using function *mantel* in the *Vegan* package version 2.2-1 in the statistical software R (Oksanen et al. 2015) to calculate the correlation between the probability matrices.

*Successful transport*, defined as any particle within 5km of the center of a habitat pixel on day 45 after release, was calculated by tallying the daily number of successfully transported particles for all islands and dividing it by the total number of daily particles released for the five-year model run, allowing us to determine annual and seasonal variability. Additionally, we calculated island specific “settlement” success over five years.

*Dispersal distance*, the geographic distance between the release site and receiving site for a successfully transported particle at the receiving site, was determined by first calculating distances between all 687 settle habitat pixels using the distance matrix function *dism* with the *Haversine* formula in the R-package *geosphere* (Hijmans 2015). The *dism* function calculates the great circle distance (Haversine formula) between two points using their latitudes and longitudes in degrees and creates a 687 x 687 distance matrix ( $D_{ij}$ ) with the release sites ( $i$ ) on the x-axis (rows) and receiving sites ( $j$ ) on the y-axis (columns). We multiplied the settlement matrix ( $S_{ij}$ ) generated by the biophysical model (see above) with the distance matrix ( $D_{ij}$ ) to generate a product matrix ( $P_{ij}$ ). Because there is more than one spawning and settlement site (henceforth habitat site) per island (for example, Big Island has 129 habitat sites, O‘ahu has 62 and Kure Atoll has 13) we added all the distances for all the habitat sites in the product matrix belonging to each island, generating a 31x31 matrix containing the sum of all the distances of all the particles for each island called the island product matrix ( $PI_{ij}$ ). The same procedure was followed to generate an island settlement matrix ( $SI_{ij}$ ); a square 31x31 matrix containing the total number of successful settlers for each island. We then divided the column sums from the island product

matrix with the column sums of the island settlement matrix to obtain the mean dispersal distance for successfully settled particle at each island. These calculations were performed for year-round releases, as well as for particle releases confined to May and June of each year to allow us to explore seasonal patterns.

*Self-recruitment*, defined as the proportion of successfully transported particles at each island that originated from that same island, is an important metric when evaluating the persistence of a population (Wood et al. 2014; Burgess et al. 2014). We calculated self-recruitment for the duration of the model run for each island by dividing the number of released particles from an island that was transported back to the same island by the total number of “settlers” at that island. This allows us to determine how dependent an island is on recruitment from outside locations to maintain the population.

*Source-sink dynamics* were assessed by calculating a source-sink index following Holstein et al. (2014). We define a source as an island that exports (outgoing) more particles than it imports (incoming), and a sink island imports more particles than it exports (Wood et al. 2014; Holstein et al. 2014). The source-sink index is a ratio of the difference between successful transport out of the island (export) and successful transport into the island (import), divided by the total of all successfully transported particles in and out of the island (Wood et al. 2014; Holstein et al. 2014). Because the index looks at the difference in the total flux of particles into and out of each island, it allows us to compare islands with varying amount of habitat and islands that have total numbers of transported particles that differ by orders of magnitude. The index spans from -1 to 1, and a positive index implies a source site and a negative index imply a sink site. The stronger the index the more likely the site is to be a persistent source or sink site. A zero index indicates that the flux of particles that are successfully transported onto the island and out of the islands are the same. This index allows us to compare islands in the archipelago, and evaluates source-sink dynamics on a regional scale, whereas self-recruitment allows

us to characterize islands as sources or sinks on a local scale.

### 3.3 Results

#### 3.3.1 *Potential connectivity*

The probability matrix shows an isolation by distance pattern with sites far away from each other having little or no potential connectivity (Fig. 2). Restricting particle release to the typical May-June spawning season minimally alters the overall potential connectivity patterns [ $r=0.932$ ](Fig. 2b and A1, A2). During spawning season O‘ahu and Maro Reef shows stronger connections with neighboring islands while Ni‘ihau and Kaua‘i become less connected. Self-recruitment is more important for Kure and Midway Atolls (Fig. 2) during spawning season whereas Raita is more dependent on self-recruitment year round (Fig. 2).

There is limited potential connectivity between the NWHI and the MHI, and the direction of dispersal is predominantly from the MHI to the NWHI. Particles originating in the MHI form 37 unique connections with sites in the NWHI, while particles originating from the NWHI only form 24 unique connections with sites in the MHI (marked areas in the upper right and bottom left in Fig 2a). Four times as many particles are successfully transported from the MHI to the NWHI than vice versa (3.1% from MHI to NWHI and 0.77% from NWHI to the MHI of the total successfully settled larvae). The MHI do not export any particles northwest of Necker and islands located between Kaula and Nihoa in the center of the archipelago are the only islands in the NWHI to contribute particles to the MHI. Most particles released from Nihoa are lost to the system, indicated by the low self-recruitment (< 1%) and low contribution ( $6.067E-4\%$  - 0.72%) to the “settlement” at nearby islands (Fig 2).

While transport between the MHI and the NWHI is predominantly northwestward, total transport between all islands in the archipelago is reversed, with 37% of the successfully transported

particles arrive at islands to the south (islands below the diagonal in Fig 2a), while 32% of particles are transported to islands to the north (islands above the diagonal in Fig 2a). However, 96.3% of the successfully transported particles originating in the MHI end up settling within the MHI and 3.73% are successfully transported to the NWHI, while 95.1% of successfully transported particles originating in the NWHI are successfully transported to sites within the NWHI and 4.87% of particles are successfully transported to the MHI.

There are three breaks in the connectivity matrix present both for year-round and seasonal particle release. Very few particles successfully cross these breaks. These breaks are more pronounced during spawning season releases (Fig 2b) and are more distinct in the forward matrices (Fig A1, A3). The southernmost break located between Nihoa and Necker is the most pronounced. No particles cross this break into or out of the MHI, effectively cutting the MHI off from the NWHI. The central break at Gardner Pinnacles and Maro Reef is traversed only by particles to and from Raita Bank. The northern break between Lisianski and Pearl & Hermes Atoll effectively isolates Kure Atoll and Midway Islands, resulting in high self-recruitment for the northernmost islands in the archipelago.

Using flow fields from different oceanographic circulation models at different spatial resolutions allows us to elucidate how robust the potential connectivity patterns are. There is a strong correlation between the potential connectivity described above and the connectivity matrix generated from a dispersal model run that used current velocities from the coarser global HYCOM [ $r=0.9291$ ](Fig A4). For the MHI we compared connectivity matrices generated from three dispersal model runs that used current velocities from the 0.04° MITgcm (Fig A5a), 0.04° regional HYCOM (Fig A5b), and 0.08° global HYCOM (Fig A5c). Potential connectivity for the MHI generated from the model run using different resolutions of the HYCOM currents showed the strongest correlation ( $r=0.974$ )(Fig A6a) followed by connectivity matrices generated from the model runs with the same spatial resolution of the flow field, MITgcm and 0.04 regional HYCOM ( $r=0.9533$ )(Fig A6b). We observed the largest difference between

potential connectivity generated from model runs using MITgcm and the 0.08 km HYCOM flow fields ( $r=0.9305$ (Fig A6c).

### 3.3.2 Total “settlement”

Successful transport across all islands is highly variable with a mean of 1.416 % (SE 7.708e-5) of all released particles successfully arriving at a receiving site over the five-year model run. The lowest total successful transport was seen on July 6, 2011 (0.682 %) and the highest total successful transport on November 2, 2012 (2.405 %). There is no discernible seasonal pattern in total arrivals observed for the archipelago as a whole (Fig. 3). The highest rates of successful transport in 2009 (2.27%) and 2010 (2.22%) coincided with particles released during peak spawning season (marked by green bars in Fig. 3), however the following three years had some of the lowest rates of successful transport for particles released in May-June (0.68%, 0.95%, and 0.96%).

The MHI have overall larger relative successful arrivals while islands near connectivity breaks have the lowest relative successful arrivals. Johnston Atoll has the lowest relative successful arrival value of all at 0.0637% for year-round release and 0.0337% for peak spawning season releases (Fig. 4). At Kaula, the relative arrival success is almost two orders of magnitude larger compared with Johnston Atoll, with 3.574% for year-round spawning. We see the largest relative arrivals for seasonal release at Lāna‘i with 2.713%. Hawai‘i Island is the only MHI to show higher arrival success for particles released during spawning season (2.523%) compared to year-round releases (2.298%).

### 3.3.3 Distance traveled

The spatially averaged mean distance traveled is 112.32 km (SE=1.705) for year-round particle release. Particles released during peak spawning season travel further, having a mean distance of 124.37 km (SE=2.372). Median distances are shorter, 101.39 km and 110.80 km for year-round and May-June

release respectively, indicating that a few particles disperse significantly longer distances driving up the mean. This is also evident from the long right tail on the density kernel (Fig. 5).

Particles arriving at islands in the center of the archipelago have the longest mean distances traveled while Johnston atoll has the shortest (100% self-recruitment) (Fig. 6). Particles successfully transported to the bank just south of Nihoa dispersed on average 341.4 km during May-June release, and 277.2 km during year-round release, more than two times the mean distance for the archipelago. Consistent with total dispersal distances for all islands, island specific dispersal distances are greater for particles released during spawning season, for 23 out of 31 islands (Fig. 6). In the MHI, dispersal distances are consistent throughout the year except for Kaua‘i which has a much longer dispersal distance during May-June particle release. Kaua‘i had dispersal distances more similar to islands located in the center of the archipelago, likely due to the predominantly northwest direction of dispersal (Fig. 2) and the longer distances between habitats in the Northwestern Hawaiian Islands. The island located northwest of the connectivity breaks (Pearl and Hermes Atoll, Maro Reef and Necker Island) have shorter dispersal distances compared to the island just southeast of the break (Lisianski Island, Gardner Pinnacles, and Nihoa Island) with 45.6%, 63.4%, and 73.9% respectively.

#### *3.3.4 Self-recruitment*

The mean self-recruitment for the archipelago is 25.2% (SE=0.0414) but varies greatly from island to island. Johnston Atoll relies solely on self-recruitment (100%) for population persistence while at Nihoa Island self-recruitment accounts for less than 1% of total settlement (Fig. 7). During peak spawning season Nihoa, along with Gardner Pinnacles, import all their particles. Island specific self-recruitment (Fig. 7, and diagonal in the connectivity matrix [Fig. 2]) is strongest at Kure (year-round 50.5%), Pearl & Hermes Atoll (year-round 80.67%, May-June 87.10%), Raita Bank (year-round 49.52%), Maro Reef (May-June 56.22%), French Frigate Shoals (year-round 49.46%, May-June 47.04%), Hawai‘i



Island (year-round 46.93%, May-June 42.44%) and Johnston Atoll (year-round and May-June 100%). These highest self-recruitment islands are located either to the north of connectivity breaks or at the edges of the archipelago.

### 3.3.5 Source-Sink dynamics

The Source-Sink Index weighs the successful “settlers” from an island against the successful “settlers” to that same island and gives a good indication on what role an island plays within the archipelago. A positive index indicates that a site exports more particles than it imports, and is thus considered an important source site. Conversely, a negative index means a site imports more particles than it exports, and should be classified as a sink. For year-round releases, 16 islands had a negative index and 13 islands had positive indexes; Kure and Johnston Atolls each had an index of zero (Fig. 8). Gardner Pinnacles had the strongest positive index, followed by Maro Reef and Necker Island, indicating that they are persistent source sites. The middle of the archipelago, from Ni‘ihau to St. Rogatien are predominantly sink islands, with Kaula having the strongest negative index. Because the source-sink index is a ratio between particle flux into and out of an island, an island with low self-recruitment can have a positive index (net source) if it exports more successful particles than it imports. All islands but three kept their source or sink assignment when comparing year-round releases to May-June releases. Pioneer Bank and Laysan Island act as weak source sites for year-round releases, but for summer releases they act as sink sites. The bank west of St. Rogatien Bank is a sink during year-round releases but a source of particles during summer.

## 3.4 Discussion

Our passive particle dispersal model identified three predicted connectivity breaks in the

Hawaiian Archipelago, and these regions of limited connectivity match observed patterns of genetic structure reported for coral reef species in the Northwestern Hawaiian Islands (NWHI). But, multiple genetic breaks observed in the inhabited MHI are not explained by passive dispersal, rather our model show the MHI as well mixed. It is always desirable to parameterize a model with as much accurate biological data as possible (Leis 2007), but in the absence of reliable data, a simple physics driven model can still provide important information on the interaction of particles with the physical environment (Siegel et al. 2003, 2008; Mitarai et al. 2008, 2016). We have not incorporated any ontogeny, behavior or mortality into the model because such data is scarce for local fish and invertebrate species. Wren & Kobayashi (2016) groundtruthed the dispersal model using trawl surveys off Big Island, which showed that a simple physics driven dispersal model is able to predict observed larval fish distributions for the region. The predominant effect of incorporating realistic larval behaviors into oceanographic models to date is reduced passive dispersal and enhanced self-seeding (Staaterman et al. 2012; Drake et al. 2013; Paris et al. 2013; Rasmuson and Shanks 2014; reviewed by Morgan 2014; Wolanski and Kingsford 2014). Even without larval behavior, our results show a surprising predominance of self-recruitment for the Hawaiian Islands, with more limited exchange than by conventional wisdom, so we predict that explicit incorporation of larval behaviors in future iterations of the model will only enhance that trend for islands throughout the Hawaiian Archipelago.

#### *3.4.1 Potential connectivity*

Isolation by distance (IBD), where genetic differentiation increases with increasing geographic distance (Wright 1943), is often considered the norm in marine population genetics, especially for linear coastlines or chains of islands (Rousset 1997; Pogson et al. 2001; Bradbury and Bentzen 2007). The Hawaiian Archipelago, a linear string of islands far removed from outside genetic influences, is the ideal place to study IBD due to its stepping stone configuration (Polato et al. 2010). Indeed, we observed an

IBD pattern of particle exchange in this study, indicated by the decrease in potential connectivity with increasing distance (Fig. 2). It is also striking the degree of self-recruitment driven entirely by physics of passive particles in this system, with the vast majority of potential connectivity in the matrix falling along the diagonal. However, researchers focusing on genetic studies have failed to recover an IBD pattern from  $F_{st}$  in a majority of species, rather a regional pattern of differentiation between the MHI and NWHI is more evident (Selkoe et al. 2014). The primary breaks in the potential connectivity model correspond well to breaks in genetic structure, particularly the split between the MHI and NWHI and the far northwestern islands of the Archipelago (Toonen et al. 2011). However, we find no indication of major obstacles to the exchange of particles between islands within the MHI where genetic approaches reveal consistent barriers to exchange among neighboring islands (Toonen et al. 2011). This may indicate that physical oceanographic drivers of dispersal are trumped by other, most likely biological, drivers (Selkoe et al. 2016a), or that more sensitive techniques are required to recover a significant IBD signal from data with regional structure (e.g., Crandall et al. 2012). The congruence between our modeling results and genetic analysis in the NWHI, but not MHI begs the question of what ultimately controls connectivity in this system? Does the lack of congruence in the MHI have to do with the imprecision of the oceanographic model, the lack of biological realism and larval behavior in the model, the differences between the high main Hawaiian Islands and the low-lying atolls of the NWHI, or the strong ecological differences and anthropogenic impacts that differentiate the MHI and NWHI?

The current management strategy for the MHI is based in part on the unfished stock in Papahānaumokuākea Marine National Monument that is expected to spill over and replenish fished stocks in the MHI. Our results, coupled with previous genetic work, do not support this expectation, warranting revision of stock boundaries and resource management plans. A growing number of studies support directional dispersal in the Hawaiian Islands for corals (Trembl et al. 2008; Friedlander et al. 2009; Concepcion et al. 2014), limpets (Bird et al. 2007), cucumbers (Skillings et al. 2011), and fish (Rivera et al.

2011). These studies use Eulerian and Lagrangian dispersal modeling, population genetic techniques, or both. Congruence between different study methods and approaches lends credence to the emerging idea that dispersal in the Hawaiian Archipelago is primarily directional, from the MHI to the NWHI. While the number of unique connections from the MHI to the NWHI were 65% higher than from the NWHI to the MHI, and 60% of the habitat is located in the MHI, the shallow reef fish biomass in the NWHI is 260% greater than in the MHI (Friedlander & DeMartini 2002). Although the probability of larval transport is greater from the MHI to the NWHI and not the other way around, the total amount of larvae transported may be greater to the MHI from the NWHI when accounting for the larger standing stock biomass in the NWHI.

The predominant surface currents (Fig 1) in the Hawaiian Archipelago, the Hawai‘i Lee Current (HLC) and the North Hawaiian Ridge Current (NHRC), flow along the flanks of the MHI then continue westward. A possible barrier preventing transport between the MHI and the NWHI is the NHRC/HLC Extension that parts from the Hawaiian Islands just north of Kaua‘i, near 22°N, diverting waters west across the Pacific (Qiu et al. 1997). The location of this current extension coincides with the location of the potential connectivity breaks suggested here between the MHI and the NWHI between Necker and Nihoa.

The presence of zonal flows in the Pacific (Maximenko et al. 2005) might influence transport and potential connectivity patterns. The regional implementation of the MITgcm shows two locations with zonal flows near 25°N and 27°N (Fig. 9). Water is moving eastward in these areas and may pose a barrier to particle transport. The connectivity breaks in the NWHI are located between Raita and Gardner near 25°N and between Lisianski and Pearl and Hermes near 27°N. The zonal flows seen in the MITgcm flow field are not present in the global HYCOM flow fields (Fig A8) but the breaks are still present in the probability matrix from the model run using global HYCOM currents (Fig A4).

### 3.4.2 Total “Settlement”

Mesoscale eddies that form in the lee of the Big Island during summer have long been hypothesized to retain larval near the island, thus increasing the regional settlement probability for those larvae (Lobel and Robinson 1983; Lobel 1989, 2011; Seki et al. 2002). If this hypothesis is correct, we would expect to see increased settlement success and higher self-recruitment for the Big Island during summer month particle releases when mesoscale eddies are common. Our results do not support this hypothesis however, as self-recruitment for BI was lower for particles released during May-June, indicating that the eddies are not retaining particles released from the Big Island and transporting them back to the Big Island. Our findings are congruent with recent studies conducted by Fox et al. (2012) and Vaz et al. (2013) who found no relationship between eddy activity and recruitment on the Big Island and calling into question the longstanding hypothesis that eddies increase regional settlement on the Big Island. Both Fox et al. (2012) and Vaz et al. (2013) focused solely on the Big Island and did not investigate recruitment or connectivity between BI and other islands. While self-recruitment at BI wasn’t enhanced during summer, our model shows that successful transport was higher for particles released from the Big Island during May-June. This stands in contrast to other islands throughout the archipelago where total successful transport is higher for particles released year-round. While the eddies don’t appear to increase retention and self-recruitment of larvae on the Big Island, they may facilitate transport and increase settlement of BI larvae on other islands in the archipelago by capturing particles released on Big Island and moving them up the island chain.

### 3.4.3 Distance traveled

Average dispersal distances for a 45 day PLD are just over 110 km, equal to the width of the Ka‘ie‘ie Waho channel separating the islands of O‘ahu and Kaua‘i. Dispersal distances increase for

summer released particles, in part, because self-recruitment is lower so the mean distance traveled by successful settlers tends to be longer. For an archipelago that spans roughly 2,500 km, such relatively short dispersal distances indicate that most exchange will be among neighbor islands and it would take many generations for genes to make it from one end of the archipelago to the other. However, the seasonal analysis indicates that summer months may play a disproportionately important role in long-range dispersal, and the majority of spawning in coral reef fish populations take place during these months. There is less information about spawning seasons of invertebrates, but coral spawning is clearly more variable, with some species spawning year-round and other species having peak release between the months of April through September (Stimson 1978; Krupp 1983; Richmond and Hunter 1990; Baird et al. 2009; Padilla-Gamiño and Gates 2012). Our distances are likely over-estimates of realized dispersal distances achieved by larvae in the Hawaiian Archipelago. The inclusion of realistic larval behavior in the model is expected to shorten mean dispersal distances given the wealth of studies showing that larvae tend to minimize passive dispersal and orient and swim towards settlement habitat (reviewed by Leis 2007; Paris et al. 2013; Robins et al. 2013; Kough et al. 2013; Leis et al. 2014; Staaterman and Paris 2014; Cowen et al. 2015; Kool et al. 2015). The greatest management unit scale for the archipelago should be limited to less than 150 km because connectivity at greater distances is not only highly limited but typically driven by few individuals transported disproportionately long distances. Individuals in the long tail of a dispersal kernel may influence gene flow but are not expected to contribute anything to the persistence or demography of populations for management (Botsford et al. 2009; Burgess et al. 2014). One such example is the connection between Johnston Atoll and the central Hawaiian Archipelago. Although exchange including Johnston is exceedingly rare, it is none-the-less present, and a few particles traveling the 1300 km between the Hawaiian Archipelago and Johnston Atoll drastically increases the average dispersal distance calculated from these simulations. The connection with Johnston Atoll is important as it provides a stepping stone ‘gateway’ into and out of Hawai‘i for marine organisms

(Kobayashi 2006; Skillings et al. 2011; Eble et al. 2011; Wood et al. 2014), but does not represent a relevant source of propagules and should be excluded when evaluating the scale of management units for the Hawaiian Archipelago.

#### *3.4.4 Self-recruitment and source-sink dynamics*

Pearl and Hermes, Kure Atoll, French Frigate Shoals, Big Island, and Johnston Atoll all have high self-recruitment (i.e., more than 40% of particles that “settle” at each of those islands were released from that same island). High self-recruitment suggests that they can persist without propagule input from other islands and implies that these islands are less sensitive to regional disturbances. Conversely, they are at greater risk from local disturbances, and if local extinction occurs, they are not able to recover without external sources of larvae. At the other end of the spectrum, Gardner Pinnacles, Necker, and Nihoa Islands all have very low self-recruitment and low recruitment overall, making them much more sensitive to fluctuations in population size and larval supply. The low self-recruitment makes these sites less sensitive to local disturbances because population persistence appears primarily reliant on outside sources of recruits.

Self-recruitment describes population dynamics on each island, but to get a better idea of population dynamics on a regional scale, and make informed management decisions, the source-sink index can be informative (Holstein et al. 2014). In the simplest terms, source sites are net exporters of larvae whereas sinks sites are net importers. A sink site needs nearby areas to provide propagules in order to persist, and thus management strategies for source and sink islands will be very different. An island with a lot of available habitat, such as Big Island which accounts for roughly 1/6<sup>th</sup> of all available coral reef habitat in the archipelago, will contribute many particles, but also has many receiving habitat; thus, Big Island can import a large number of particles, and actually exceed its output. The source-sink index is useful when comparing islands with varying amount of habitat since the ratio looks at both

import into and export out of an island. It is also important to note that self-recruitment and the source-sink index are not mutually exclusive: an island with high self-recruitment can still serve as a source site for nearby islands, as is the case with Kure Atoll, Maro Reef, and French Frigate Shoals. In contrast, the Big Island, Laysan Pinnacles, and Midway Atoll have high self-recruitment but are also sink sites. These latter three islands warrant special consideration to maintain the high level of self-recruitment while also relying on the protection of nearby islands because recruitment subsidy is still important for population persistence.

#### 3.4.5 *Connectivity breaks*

We should take caution against broadly applying connectivity findings to all species as larval biology and ecology varies greatly for marine animals and those differences likely influence ocean transport. For example, our model results show that Nihoa Island strongly depends on importation of larvae to persist, however, among intertidal limpets (*Cellana* sp.), an invertebrate with a negatively buoyant and shorter lived veliger larva, estimates of self-recruitment are far higher [ $>90\%$ ] (Bird, pers. comm. 2016). In our efforts to examine the potential connectivity patterns in the Hawaiian Archipelago, we parameterized our model after a generic broadcast spawning reef fish with an “average” PLD of 45 days. It is important to recall that this generic fish is not representative of everything on the reef, and population genetic studies show some dramatic differences among species studied to date (Toonen et al. 2011). We are reporting potential population connectivity, and there are many biotic and abiotic factors influencing realized population connectivity (mortality, time to competency, metamorphosis, settlement, recruitment etc.) that may cause a mismatch between realized and potential connectivity (Neuheimer and Taggart 2007; Toonen and Tyre 2007; Burgess et al. 2012).

In the Hawaiian Archipelago we can identify three breaks in potential connectivity throughout the archipelago: a southern break between the MHI and NWHI by Nihoa and Necker, a central break



between Raita and Gardner Pinnacles, and a northern break between Lisianski and Pearl and Hermes Atoll. The NWHI breaks generated by our passive particle transport model are congruent with population genetic breaks observed for fish species (Toonen et al. 2011). Interestingly, the major differences between the modeled potential connectivity and genetics are seen in the inhabited MHI, where modeled potential connectivity is not able to resolve observed genetic breaks.

One main difference between the MHI and NWHI is the amount and quality of available habitat. The banks, pinnacles, and atolls in the NWHI are small, the largest being Midway Atoll at 6.2 km<sup>2</sup>, and north of Gardner Pinnacles are sandy and low lying. Close to 60% of the coral reef habitat used in this study is located in the MHI (402 out of 687 pixels). In addition, the MHI have a more complex geology, large channels with strong currents, like the ‘Alenuihāhā channel that passes between Big Island and Maui, and mountain-wind interactions that change surface circulation, features mostly lacking in the NWHI. The regional implementation of MITgcm at 0.04° resolution does not resolve nearshore flow. It produces the typical subtropical gyre circulation in the NWHI, with zonal jets associated with propagating mesoscale eddies (Maximenko et al. 2005); whereas in the MHI, interactions between the high mountains and the northeasterly trade winds generate strong eddies (Jia et al. 2011) and a highly variable flow field overall (Fig to create). Recent studies have shown that mesoscale circulation features like eddies can create physical barriers to dispersal (Baums et al. 2006), and although MITgcm is eddy-resolving, there may be oceanographic features, especially in the MHI, causing genetic breaks in the MHI that are not well resolved in the circulation model. In addition to physical and oceanographic differences, behavior, selection, ecological and anthropogenic differences, (e.g. Puritz and Toonen 2011) among the MHI may explain the mismatch between the realized (genetic) and potential (modeled) connectivity, but are not necessary to account for the NWHI breaks. It is likely that there is a physical barrier to dispersal in the areas where population genetics and our dispersal modeling show congruence, whether it be channels, lack of suitable habitat or oceanographic features (Baums et al.

2006; reviewed by Riginos and Liggins 2013). Expanding the biophysical model parameterization to include life history parameters and larval behavior will enhance self-recruitment and may resolve some of the genetic breaks observed in the MHI not caused by seascape features.

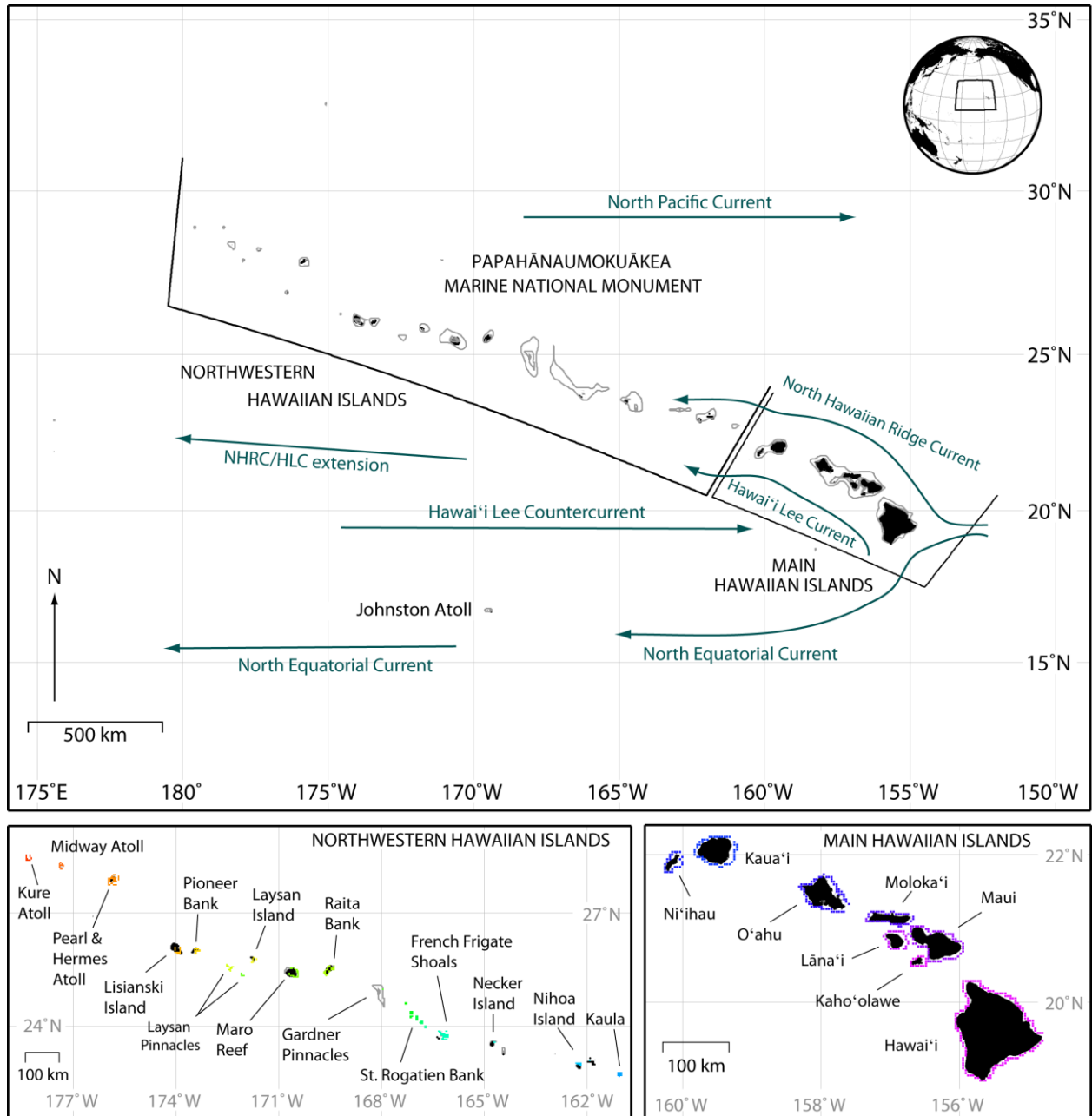


Fig 1: Top panel showing the Hawaiian Archipelago domain of the dispersal model with the major surface currents (in green) identified (after Lumpkin 1998). Bathymetry lines denote 1000 and 50 m isobaths. Bottom panels show coral reef habitat pixels for the Northwestern Hawaiian Islands and Main Hawaiian Islands respectively, with each island's habitat pixels shown as a separate color. Bathymetry lines in NWHI denote 50 m depth isobath.

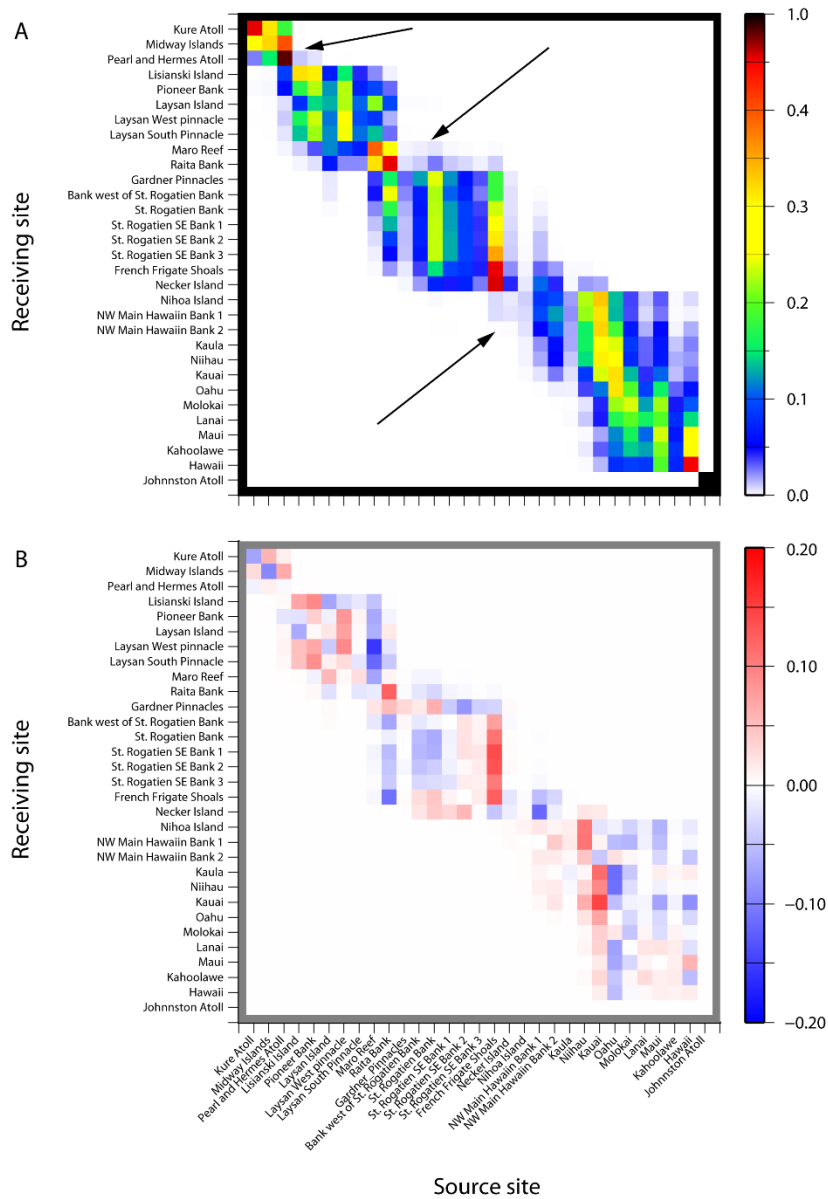


Fig 2. Potential Connectivity matrix for the Hawaiian Archipelago. (A) The values in each cell are “settlement” probabilities scaled to the receiving site for year-round particle release. Arrows indicated the breaks mentioned in the text. Each row in the matrix adds up to 1. High values (red) indicate high connectivity and low numbers (blue) indicate low connectivity, and white cells denote no connectivity. (B) Difference matrix showing the difference in connectivity between year-round and May-June particle release. The May-June release matrix is subtracted from the year-round release matrix (in A above). Positive values (red) denote a higher

connectivity value for year-round releases and a negative number (blue) denotes higher connectivity for May-June released particles.

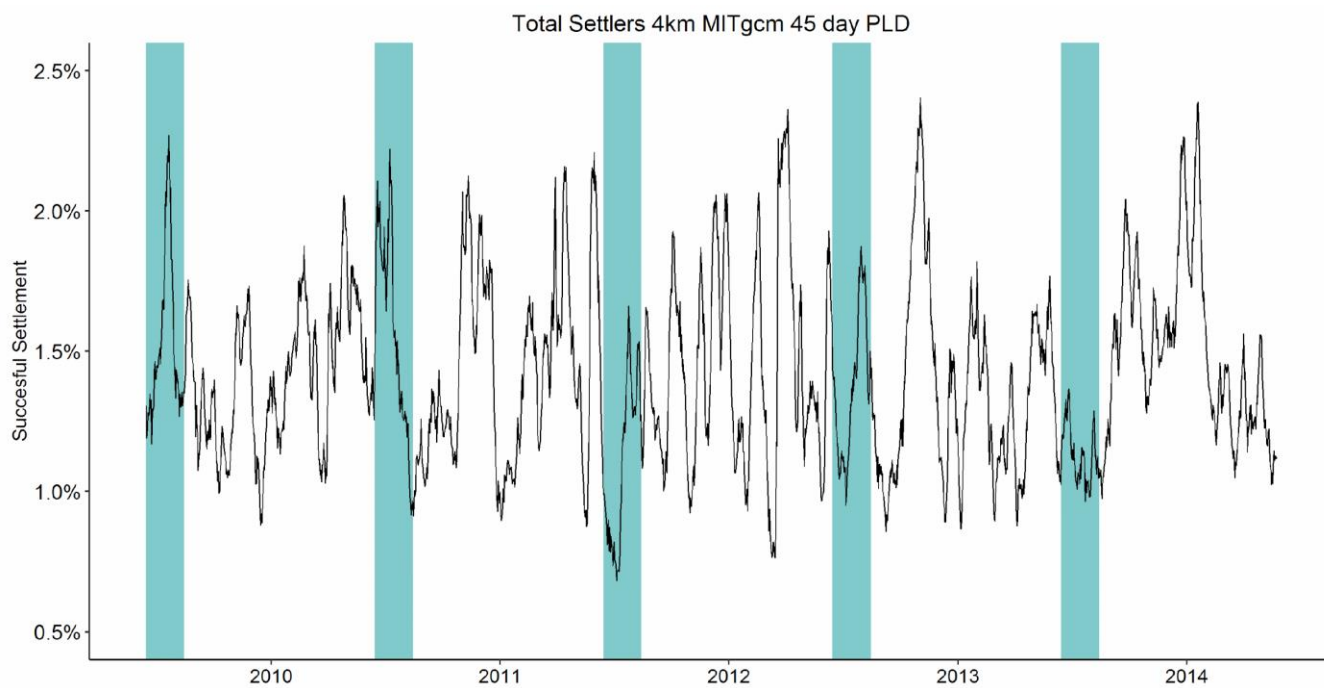


Fig 3. Total percent successful settlement for all sites in the Hawaiian Archipelago for the five-year model run. The green bars represent particles spawned during peak spawning season May-June each year.

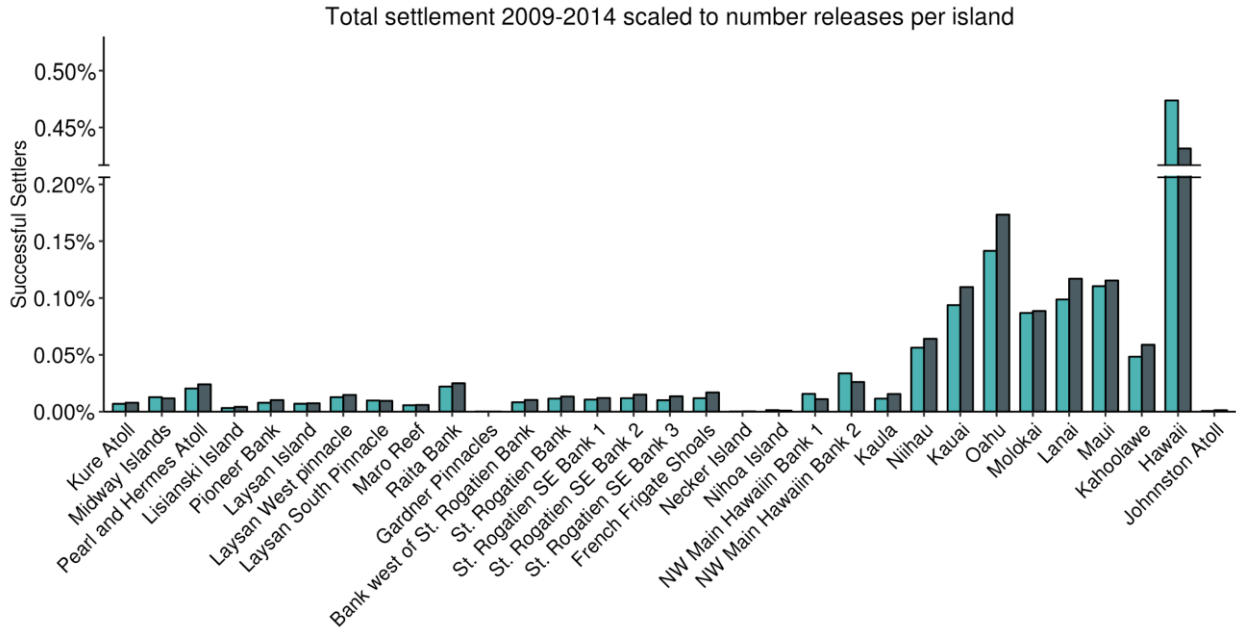


Fig 4. Total percent successful settlement at each island for the five-year model run. Green bars show settlement for particles spawned during May-June, gray bars show settlement for year-round spawning.

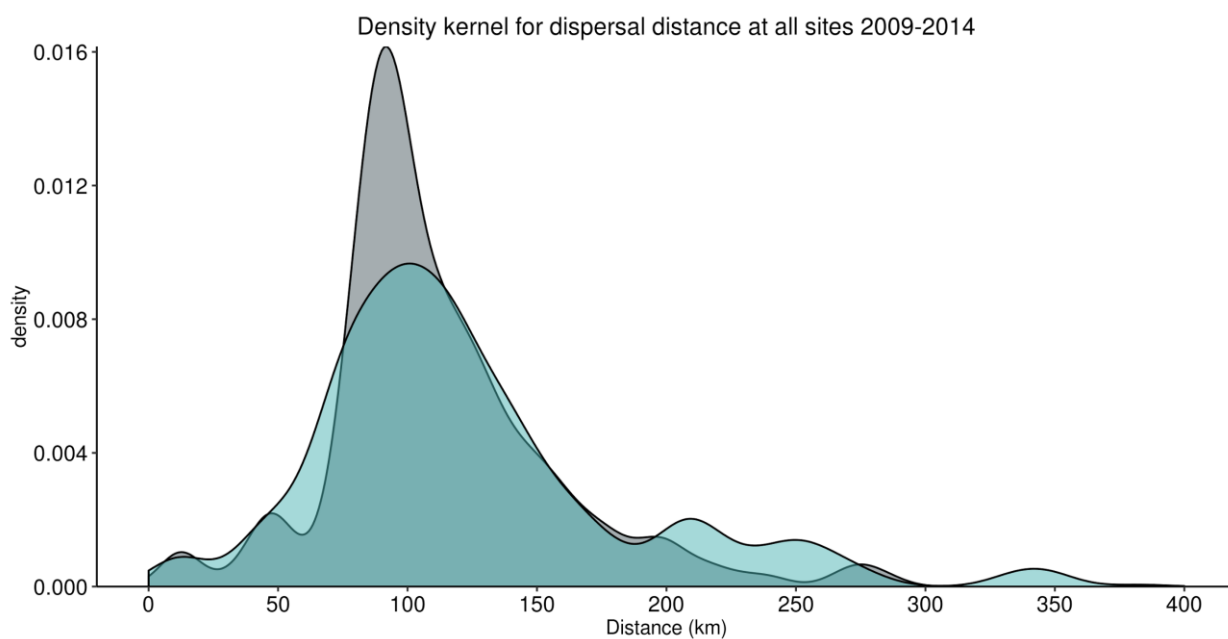


Fig. 5. Density kernel for dispersal distance from source site for all islands May 2009-May 2014. Green kernel denotes May-June spawning and gray kernel year-round spawning.



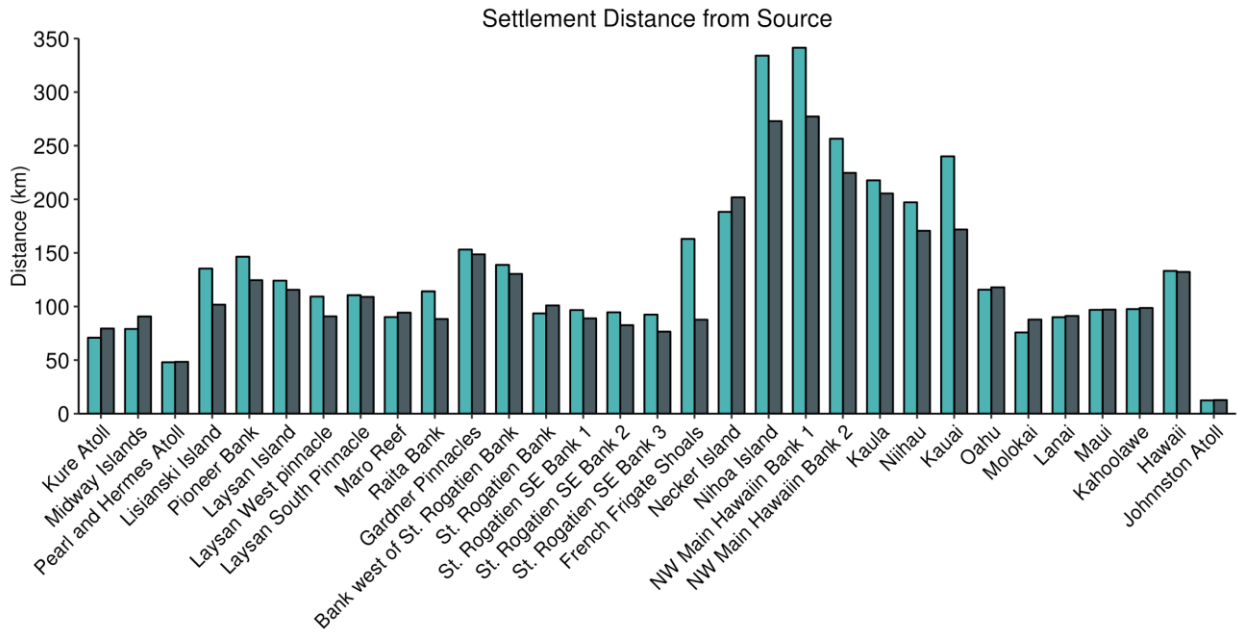


Fig. 6. Island specific mean particle dispersal distances from the source island. Green color denotes particles released during May-June and gray denotes distances for year-round release.

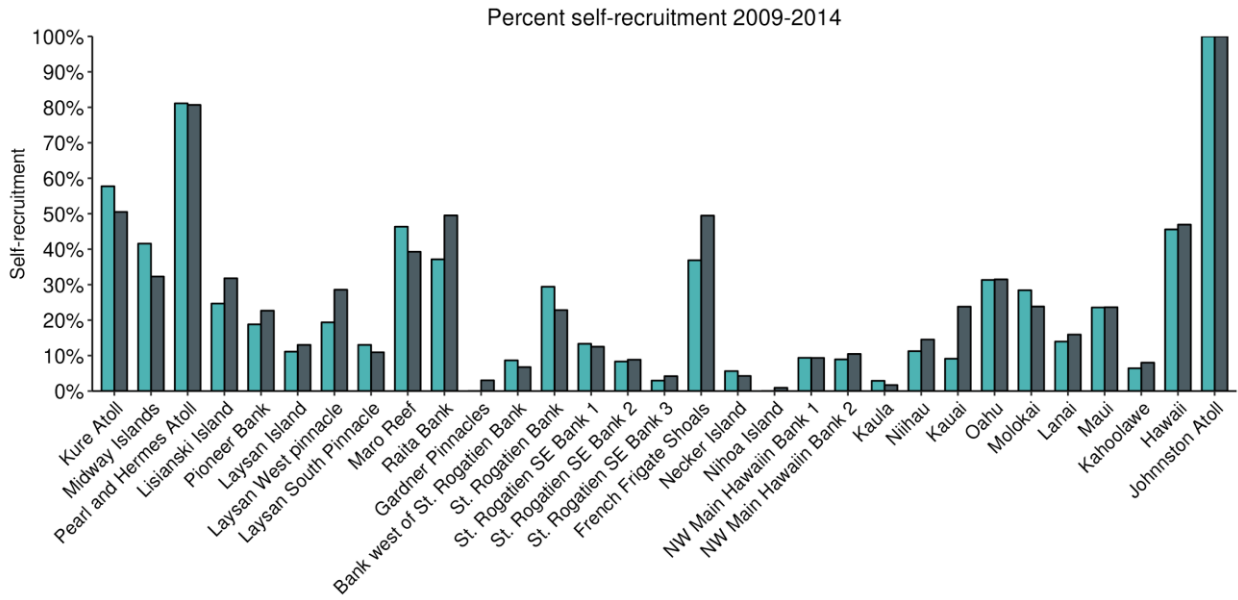


Fig 7. Island specific self-recruitment for the five-year model run. Green bars show settlement for particles spawned during May-June, gray bars show settlement for year-round spawning

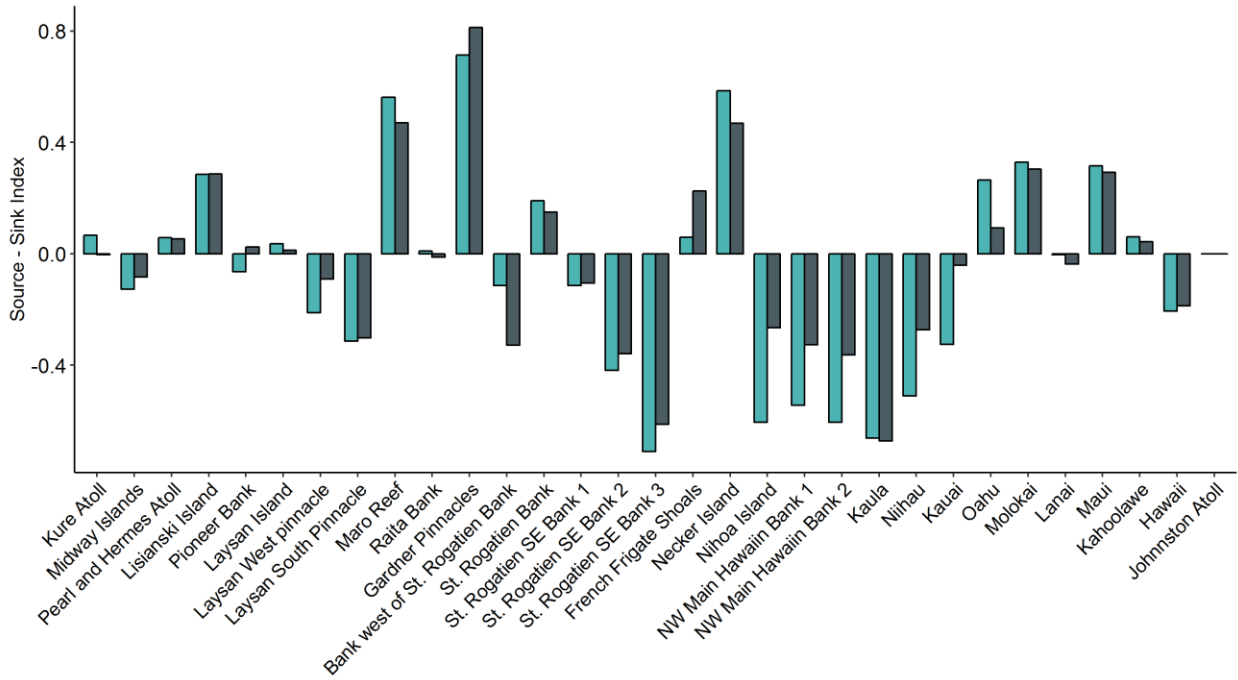


Fig 8: Source-Sink index for all islands in the Hawaiian Archipelago for the 5-year model run. Positive numbers indicate a net source location, and negative numbers indicate a sink location. Green color denotes particles released during May-June of each year and gray denotes distances for year-round releases.

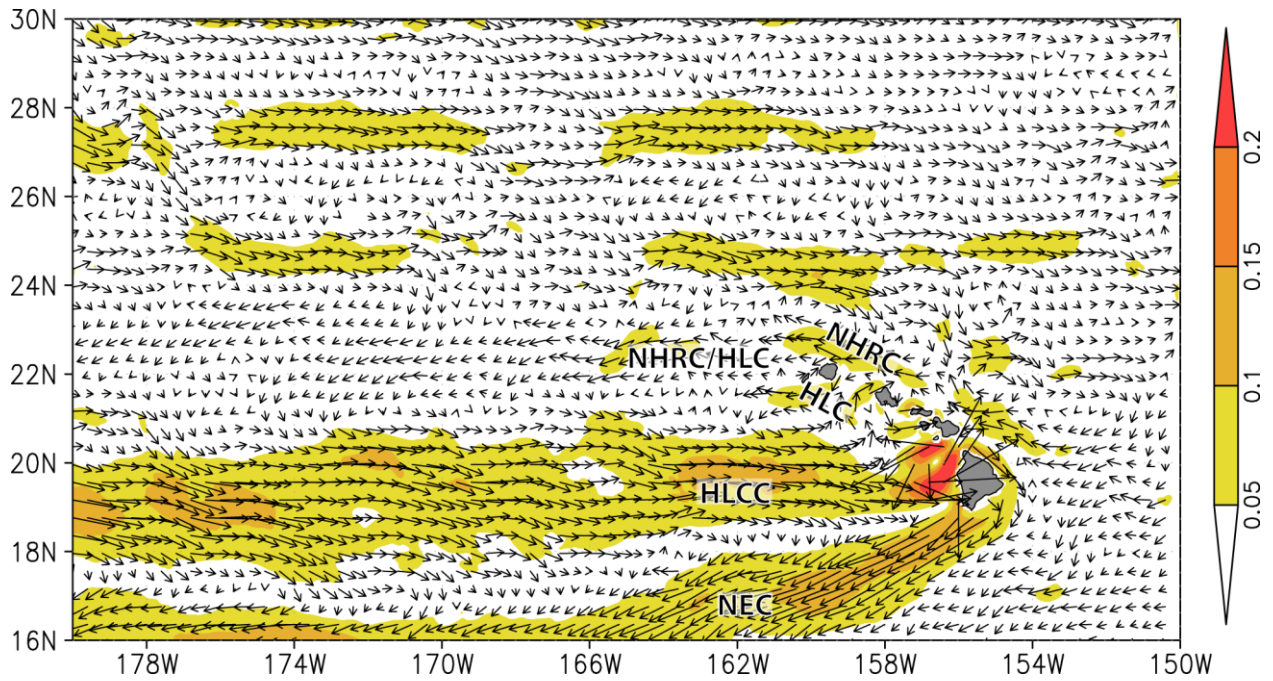


Figure 9. Modeled flow fields produced by the regional Hawai‘i MITgcm for May 2009-May 2014. The eastward zonal flows are visible near 25°N and 27°N and major surface currents are marked.

# CHAPTER 4

---

## Extreme dispersal events? How ENSO events affect coral reef population connectivity in the Hawaiian Islands

---

Climate change is predicted to cause changes in the strength and frequency of El Niño/Southern Oscillation events. These events in the Central Equatorial Pacific cause increased sea surface temperatures (SST), a depressed thermocline, and decreased primary production. The oceanographic effects in the Hawaiian Archipelago are not well understood, and have shown both increased and decreased SST and primary production. Understanding oceanographic changes caused by El Niño is the first step towards examining how larval dispersal patterns and regional connectivity throughout the Hawaiian Archipelago will be affected. Larval developmental rates are influenced by food availability and temperature, and coral reef fish have shown increased recruitment in Hawai‘i during El Niño years, but the underlying drivers of that increase remain unknown. Here, we examine annual settlement probabilities and the degree of self-recruitment using a two dimensional Lagrangian particle dispersal model coupled with Hybrid Coordinate Ocean Model (HYCOM) currents for the Hawaiian Archipelago. Comparing potential dispersal among sites in each year from 1997-2014, we see a decrease in total settlement during El Niño years. Additionally, self-recruitment was lower during El Niño and the average distance the successful settlers traveled was greater, indicating that El Niño years may be playing an important role in long distance dispersal and genetic exchange among islands that are not otherwise connected. We see much greater potential for connectivity between the Hawaiian Archipelago and Johnston Atoll during the El Niño years, with a significant increase of larval exchange from Johnston to the Hawaiian Archipelago. Because these highly variable and at times extreme events can have a disproportionate influence, it is important to understand how connectivity is affected by ENSO events, the implications of this variability under global climate change, and the role of rare events in determining species distributions and gene flow among sites in order to manage for diverse coral reefs in the future.

---

Based on: Wren, J.L.K. A.B. Neuheimer and R.J. Toonen (in preparation) Extreme dispersal events? How ENSO events affect coral reef population connectivity in the Hawaiian Islands. *Limnology and Oceanography*

## 4.1 Introduction

El Niño/Southern Oscillation (ENSO) events, centered around the Equatorial Pacific, occur when there is a shift in the pressure gradient across the equatorial Pacific, due to a westerly wind bursts and a buildup of equatorial heat content (Wyrtki 1975; Cane 1983). ENSO consists of two phases, a warm phase termed El Niño and an opposite cold phase termed La Niña. ENSO events vary in strength and duration, but there are two main El Niño types: a canonical or eastern Pacific (EP) El Niño, and a warm pool, Modoki or central Pacific (CP) El Niño (Capotondi et al. 2015). During EP El Niño the warm pool normally located in the equatorial west Pacific moves eastward, bringing with it warm moist air. The thermocline in the eastern Pacific deepens and the equatorial and coastal upwelling weakens, causing warm equatorial water to move poleward along the coast of the Americas. With the relaxation of the upwelling of cold nutrient rich waters along the west coast of the US, central, and south America follows a decrease in primary production that cascades through these very productive ecosystems (Stenseth et al. 2002). While the EP El Niño shows the largest SST anomaly along the western coast of South America, the CP El Niño, as the name implies, is centered further west with the highest SST anomalies found near the dateline and little warming of the east Pacific cold tongue region (Capotondi et al. 2015). During La Niña, which is the opposite cold phase of El Niño, the thermocline shoals in the eastern Pacific, caused by an increased upwelling along the American coast and along the equator and warm water moving eastward across the equator, pooling up in the western Pacific (and Cane 1986; see Collins et al. 2010).

Each ENSO event is different in both strength and duration, so temperature anomalies will vary year by year (Wyrtki 1975). The 2015/16 ENSO event is among the strongest on record with temperature anomalies rivaling those of the 1997/98 El Niño event (National Weather Service Climate Prediction Center). ENSO events seriously impact coral reef ecosystems throughout the Pacific Ocean, with mass coral bleaching and mortality events along with changes in fish distributions. For example, in

Hawai‘i there has been extensive coral bleaching events during August-September of the year prior (1996, 2014) to large El Niño events (Jokiel and Brown 2004; Bahr et al. 2015). Effects of ENSO events on corals throughout the Pacific Ocean are well documented (Glynn et al. 2001; Wellington et al. 2001), but implications of ENSO events on reef fish are not as apparent (Victor et al. 2001). Further, there is little understanding of how oceanographic changes caused by ENSO impact larval dispersal patterns and regional connectivity. Larval developmental rates are influenced by food availability and temperature, and these are predicted to have major implications for magnitude and patterns of larval dispersal under future climate change scenarios (O’Connor et al. 2007; Munday et al. 2009). Whether ENOS events will increase or decrease in strength and frequency due to climate change is still uncertain (Collins et al. 2010). Some climate models predict both stronger, more frequent ENSO events (e.g., Cai et al. 2014), as well as a five-fold increase in the frequency of CP El Niño events to EP El Niño (Yeh et al. 2009), while others show no change or a dampening in occurrence of ENSO (Collins et al. 2010; Xie et al. 2015). Despite the difficulty to predict ENSO, understanding the effects of ENSO events on coral reef ecosystems and implications for larval dispersal that underlies the potential for resilience and recovery of coral reefs under ENSO conditions is becoming increasingly important.

The Hawaiian Archipelago is located in the central North Pacific and stretches over 2,500 km from 180°-155°W and 19°-30°N. Due to the location of the island chain north of the El Niño 3.4 region, the Hawaiian archipelago does not show such a drastic oceanographic response as does the equatorial Pacific, and the responses are not always uniform across the archipelago. For example, during the 1998 El Niño, Jokiel et al. (2004) recorded decreased sea surface temperatures (SST) for O‘ahu, but increased SST at Midway. The 2015/16 El Niño shows the opposite pattern with a +1°C SST anomaly in the Main Hawaiian Islands, and a -0.5°C SST anomaly at the northern extent of the NWHI. In addition to temperature anomalies, Chu and Wang (1997) also showed that cyclones are more frequent near Hawai‘i during El Niño years, and their paths are different from non-El Niño year cyclones. Likewise,

because of the shift in the warm pool to the central equatorial Pacific during El Niño, there is increased rainfall preceding and decreased rainfall following El Niño (Chu 1995). These atmospheric and oceanographic changes in the central Pacific have biological consequences. In addition to the coral bleaching events mentioned previously, researchers have documented a change in phytoplankton composition and an increase in primary production attributed to El Niño with a more stable mixed layer (Karl et al. 1996; Campbell et al. 1997). The highly variable nature of ENSO events, both in strength and location of SST anomalies, makes biological responses highly variable as well and are often only documented during one ENSO event and cannot be considered the norm.

Despite what is known about the causes and consequences of ENSO events on the central Pacific, there is little known about changes, if any, in circulation patterns around Hawai‘i during ENSO. Oceanographic changes caused by ENSO can potentially alter larval dispersal patterns throughout the Hawaiian archipelago, affecting regional population connectivity. For example, Treml et al. (2008) show an increased modeled connectivity during El Niño years in the Western Pacific, with unique dispersal pathways occurring during both El Niño and La Niña conditions. However, studies suggest that the effect ENSO events have on larval fish recruitment is site and species specific. For example, Cheal et al. (2007) showed a positive correlation between reef fish recruitment and environmental factors (increased SST and decreased wind) associated with ENSO, with an increased recruitment in years following El Niño on the Great Barrier Reef, while in French Polynesia, Lo-Yat et al. (2011) showed a decrease in recruitment. In Hawai‘i persistent mesoscale circulation features have long been implicated as a major driver of coral reef fish recruitment (Lobel and Robinson 1988; Lobel 1989, 2011). However, recent studies suggest that longer term climate oscillations such as El Niño, rather than mesoscale eddies, influence reef fish recruitment. Fox et al. (2012) reported increased recruitment of the yellow tang, *Zebrasoma flavescens*, along the Kona coast during El Niño years, but the authors could not identify the underlying drivers of this recruitment success.



ENSO events can have a disproportionate influence on patterns of larval exchange (Trembl et al. 2008). It is therefore important to understand the underlying drivers of connectivity, and how those patterns can change through time, especially in the face of predicted climate change, to manage for diverse coral reefs in the future. This study seeks to document the effects of ENSO on potential connectivity throughout the Hawaiian Archipelago using a two dimensional Lagrangian particle dispersal model coupled with high resolution Hybrid Coordinate Ocean Model (HYCOM) currents. Using simple biological input such as habitat range and PLD in simulations, we calculate annual settlement probabilities and self-recruitment values, important metrics for understanding population dynamics and more effectively managing natural resources (Calabrese and Fagan 2004; Burgess et al. 2012, 2014).

## 4.2 Methods

Potential connectivity was simulated using a 2-dimensional Lagrangian particle tracking model (Polovina et al. 1999; Wren and Kobayashi 2016) coupled off-line with global  $1/12^\circ$  (~8 km for the region) resolution HYbrid Coordinate Ocean Model (HYCOM) u and v velocities (Chassignet et al. 2009). HYCOM has 32 vertical layers, varying in thickness from 5 m to 500 m. We used u and v velocities from the 100 m depth layer in this study because larval reef fish are found in the upper 100 m of the water column (Boehlert and Mundy 1996) and model studies showed that 100 m layer favored local retention and was the most likely dispersal depth (Vaz et al. 2013; Wren and Kobayashi 2016). We ran the model for 17 years, from July 1, 1997, to June 30, 2014, and the geographic domain encompassed the Hawaiian Archipelago region and Johnston Atoll ( $15^\circ\text{N}$ - $35^\circ\text{N}$ ,  $175^\circ\text{E}$ - $210^\circ\text{E}$ ) (Figure 1).

Available coral reef habitat for particle release and receiving sites was obtained from IKONOS-derived data for the NWHI (Battista et al. 2007; Friedlander et al. 2009) and from Franklin et al. (2013)

for the MHI, and included all shallow (<30m) coral reef in the archipelago. The habitat was binned into 4 km x 4 km pixels, resulting in 687 habitat pixels. From each habitat pixel, 25 particles were released every six hours for the duration of the model run (17 years). We set a pre-competency period of 45 days, before which particles were not allowed to “settle”, and a settlement window of 10 days during which time particles would recruit if they came within 5km of the center of a suitable habitat pixel. After day 55 any particles remaining in the water column were considered “dead” and removed from the transport model.

Because El Niño usually peaks in December, we defined a year as spanning from July 1 to June 31. We used the same definition as Yu et al. (2012) to identify El Niño and La Niña years, based on the Oceanic Niño Index (ONI) (National Weather Service Climate Prediction Center), which is a three month running mean of sea surface temperature (SST) anomaly in the Niño 3.4 region. If the ONI was 0.5 or higher for more than five consecutive months, we classified it as an El Niño year, and if the ONI was -0.5 or lower for five or more consecutive months we classified it a La Niña year. All other years were considered “Normal State” years. This grouping resulted in six Normal State years, six La Niña years, and five El Niño years (Table 1).

Total settlement was calculated by tallying all successfully transported particles from all sites each day and dividing that by the total released particles that same day. We built a generalized additive model (GAM) to allow us to identify seasonal and interannual changes in settlement, as well as identify differences in settlement between El Niño, La Niña and normal state years. We used total settled particles as our response variable, and ENSO state and date (as cumulative month) as predictor variables with a Poisson regression and log link function using the gam function in the mgcv package in the statistical software R (Wood 2011). K was increased to 40 to catch seasonality in the data.

We averaged the annual number of particles exchanged between sites in a transport matrix,  $T_{ij}$ , where each cell shows the number of particles released from site  $i$  and received at site  $j$ . The diagonal in

the  $T_{ij}$  shows the self-recruitment (source and receiving site is the same). We generated transport matrices for each of the three categories hereafter referred to as the following ENSO states: Normal, El Niño and La Niña. We used the  $T_{ij}$  matrix for analysis of dispersal distances by multiplying it with a distance matrix,  $D_{ij}$  where we recorded the great circle distance on a sphere between each release site  $i$  and each receiving site  $j$ . We then calculated the sum at each receiving site  $j$  and divided that with total number of particles transported to site  $j$ . The resulting site-specific dispersal distances show the mean distance a particle traveled that “settled” at each site, and we refer to this as the upstream dispersal distance. To understand the potential connectivity between islands we constructed a matrix,  $C_{ij}$ , by scaling number particles transported from site  $i$  to site  $j$  to total received particles at site  $j$ . Each column in  $C_{ij}$  adds up to one, and we call this upstream connectivity.

To compare transport between the three different ENSO states we calculated difference matrices by subtracting one  $T_{ij}$  from another in a factorial design, resulting in three difference matrices. To quantify the differences between matrices we built a generalized linear model (GLM), allowing us to determine potential drivers behind the changes in transport patterns. We set total transported particles between each site as our response variable and ENSO state as the predictor with a log link function using a Poisson regression in the function `glm` in the stats package in R (R Core Team 2012).

For regional analyses, we grouped the 687 sites from the  $T_{ij}$  and  $D_{ij}$  matrices into 24 regions, representing emergent islands, atolls, and banks throughout the Hawaiian Archipelago and including Johnston Atoll. We tabulated potential connectivity matrices, difference matrices, and dispersal distances on a regional scale using the same methods as described above.

### 4.3 Results

Total settlement was highly variable for the 17-year model run (Fig. 2) and the effect of ENSO state and seasonality are highly significant ( $R^2=0.55$ ,  $p < 0.001$ ). Among ENSO states, normal years had the highest transport success with 8.2%, followed by 7.5% for La Niña years and 7.1% during El Niño years. The probability of a particle to successfully “settle” in 45 days was 50% higher during Normal years compared with El Niño years (Fig 3.). However, the probability of successful transport was consistently higher for shorter PLDs under all three ENSO scenarios, shown by the more than a fivefold decrease in transport probability from 45-day to 55-day larval durations. This results in Normal years having an average time to “settlement” of 48.71 days, (SE=0.0009), shorter than either El Niño or La Niña years which have a mean transport time of 49.0 days (SE=0.001).

Transport matrices ( $T_{ij}$ ) for Normal, El Niño and La Niña years are shown in Figure 4. The Main Hawaiian Islands (MHI) are well connected but show limited exchange of particles with the Northwest Hawaiian Islands (NWHI) for all ENSO states, consistent with findings in Wren et al. (in revision). The largest difference between the ENSO states were seen at Johnston Atoll and Moloka‘i. Particle transport decreases to Moloka‘i during El Niño and La Niña years (Fig 4), however downstream connectivity (particles traveling from Moloka‘i) remains largely the same for all three ENSO states. During El Niño and La Niña years Moloka‘i only received particles at four of its 42 habitat sites, compared with 32 sites during Normal years (Fig 4). Downstream potential connectivity was reduced by 68.6% during El Niño and 72.9% during La Niña years. Only habitat sites located on the northeast and northwest corners of the island received particles during El Niño and La Niña years.

The relationship between successful transport and ENSO was significantly for all ENSO states ( $p < 0.0001$ ). El Niño years had fewer successfully transported particles in the MHI (except for most of Moloka‘i) compared with Normal years, but had more particles traveling further in the NWHI, indicated

by the blue fields further from the diagonal in Figure 5a. Comparing Normal and La Niña years we saw a similar pattern, with La Niña years showing fewer number of particles in the MHI and more particles traveling further in the NWHI. Curiously, during La Niña years the MHI sites had more particles dispersing towards the NWHI (blue colors below the diagonal in the MHI in Figure 5b). During Normal years for the MHI more particles were successfully transported against the prevailing currents, from northwest towards southeast (red colors above diagonal in MHI in fig 5b). El Niño years had a higher numbers of self-recruits compared with La Niña years, especially in the NWHI, but La Niña years had more transported particles overall (Fig. 5c).

The regional potential upstream connectivity ( $C_{ij}$ ) showed that during the 17-year model run Johnston Atoll received particles from 19 of the 24 islands, while only contributing particles to 11 islands (including self-recruitment) (Fig 6). Johnston Atoll always relied heavily on self-recruitment with self-recruitment rates of 96.2%, 90.6% and 87.7% for Normal, La Niña and El Niño years respectively. During Normal years Johnston Atoll only contributed particles to two islands: French Frigate Shoals and Necker Island (bottom row in Fig 6a). During La Niña years St. Rogatien and its banks were added (Fig 6c). However, during El Niño years Johnston Atoll contributed particles to 10 islands, spanning from Ni‘ihau to Laysan except for the bank NW of the MHI (Fig 6b). During Normal and La Niña years Johnston Atoll received particles from an area stretching from the Big Island (BI) to Laysan (excluding Nihoa Island and Gardner Pinnacles), however during El Niño years Johnston was cut off from the majority of the MHI (BI and Maui Nui) and received particles only from the middle of the archipelago. Local scale connectivity matrices showing all sites can be found in the supplemental material (Fig A1).

The mean upstream travel distance for particles varied between ENSO states. Normal years showed a bimodal distribution of upstream distance with a mean distance of 159.9 km (SE=1.7) (Fig 7). Particles traveled the furthest on average during El Niño years, 174.8 km (SE=2.1), followed by La Niña years with mean distances of 174.0 km (SE=2.4). The longer right-hand tail on the density kernel in

Figure 7 show that few particles dispersing long distances skews the mean upward. This is especially evident during La Niña years when median dispersal distance was 167.1 km, almost 7 km shorter than the mean distance. For Normal and El Niño years, the difference between median and mean distance fall within the standard error (157.2 km for Normal and 173.7 km for El Niño years).

The number of downstream connections were greater during Normal years compared with El Niño and La Niña years (Fig 8). During Normal years the average number of connections in the MHI increased with ~ 55%. Release sites located on Johnston Atoll were the only ones that had a higher number of upstream connections during El Niño years. Self-recruitment, defined here as a particle returning to the island it was released from, was highest during Normal years for 11 out of the 24 islands. The majority of these islands are located in the center of the archipelago. Mean self-recruitment for all islands was 23.5% during Normal years, and 22.5% for El Niño and La Niña years.

#### 4.4 Discussion

El Niño/Southern Oscillation events repeat every 2-7 years, are highly variable in strength and duration. Strong ENSO events and have profound impacts on marine ecosystem in the Pacific Ocean (Stenseth et al. 2002; Capotondi et al. 2015). In coral reef ecosystems, the effect of ENSO on corals themselves are well documented, but the effects ENSO has on reef fish has garnered little attention and remains mostly unknown (Stone et al. 1999; Glynn et al. 2001; Hughes et al. 2003). This study seeks to describe differences in modeled potential connectivity between Normal, El Niño, and La Niña years across the Hawaiian Archipelago to better inform the role of such events in the connectivity and conservation of coral reef species. Our model identifies unique connectivity pathways that are present only during El Niño, and highlight areas of reduced connectivity during ENSO events.

We recognize that larval dispersal is complex, and influenced by many biological and physical

factors that are difficult to enumerate or are unknown (Leis 2007). Our aim is to estimate connectivity across large geographic and temporal scales, and in order to do that we simplified our study system. By focusing on the physical drivers behind dispersal patterns and keeping the biological parameters minimal, we aim to identify islands in the archipelago that experience significant changes in potential connectivity. Recent studies indicate that potential connectivity is driven primarily by physical oceanographic features in some parts of the Hawaiian Archipelago: Wren et al. (in revision) showed that a Lagrangian dispersal model with minimal biological input matched important connectivity breaks observed in population genetic studies in the Northwestern Hawaiian Islands (NWHI), and the same model could explain much of the distribution of larval *Acanthurid* fishes off the west coast of Hawai‘i Island (Wren and Kobayashi 2016). Strong El Niño events, which are ecologically rare, can have a disproportionate influence on larval dispersal.

We found that total successful transport is lower during El Niño compared with Normal and La Niña years, but the differences in successful transport are small. It is important to make a distinction between potential and realized connectivity; the former indicates the possibility of dispersal given a set of physical factors and few biological influences, while the latter incorporates complex biological interactions during dispersal and post-settlement processes (Burgess et al. 2014). Potential connectivity likely overestimates connectivity and long distance dispersal while underestimating self-recruitment (Paris et al. 2013; Staaterman and Paris 2014; Wolanski and Kingsford 2014). Thus, the reduced connectivity seen during ENSO events in this study are probably overestimates of the realized transport, and should be considered the upper bounds of exchange among sites.

We chose to classify ENSO periods by calendar years running from July 1-June 30. In doing so we recognize that we are blending ENSO states within one year potentially weakening the effects of ENSO. However, if we classify ENSO periods by month June has six times as many Normal states years (13) as it does El Niño states (2) years, compounding the ENSO pattern with seasonal differences in circulation.

Blending of several ENSO states within one year will weaken the signal and decrease power to detect differences in connectivity due to ENSO states, however the GAM showed significant differences in connectivity between ENSO states when they were defined by year.

Potential coral reef organism connectivity in Hawai‘i shows a strong isolation by distance (IBD) pattern (Wren et al. in revision), which is seen in this study as well. While these large scale connectivity patterns remain consistent throughout the ENSO cycle, local differences in connectivity are observed. Moloka‘i and Johnston Atoll experience the largest differences in larval transport between the three different ENSO states. For particles released from Johnston Atoll, new connections with the center of the Hawaiian Island chain open up during El Niño years that are not present any other time (Fig. 6). Modeling and genetic studies (Bird 2006; Kobayashi 2006; Rivera et al. 2011; Skillings et al. 2011; Timmers et al. 2011; Wood et al. 2014) show Johnston Atoll acting as either an outpost of Hawaiian biodiversity, or a stepping stone into Hawai‘i, providing the main pathway for larvae to enter the Hawaiian Archipelago. The results presented here are consistent with both conclusions but the likelihood of exchange and directionality varies with ENSO state. If the connection with Johnston Atoll increases with more frequent El Niño events, new species (gene) introductions into the Hawaiian Archipelago may result, and changes in this dispersal pathway may have profound implications for Hawaiian reef ecosystems in the future. Conversely, Johnston Atoll imports particles from fewer sites in the MHI during El Niño years. During Normal and La Niña years Johnston receives particles from sites located on 18 different islands in the archipelago. During El Niño, it is reduced to 10 islands. These changes among years by ENSO state have increased importance under future climate change scenarios, and especially under the proposed expansion of PMNM to include Johnston Atoll.

Within the MHI, Moloka‘i shows a reduction in connectivity during both El Niño and La Niña years, with merely four of its 29 sites receiving particles. Only sites in the northeast and northwest corners of the island receive particles. Moloka‘i is nestled close to its southern and eastern neighbor



islands as part of the Maui Nui complex, made up by the islands of Maui, Kaho‘olawe, Lāna‘i, and Moloka‘i. Because of the 8 km resolution of the HYCOM model and the relative narrowness of the channels in Maui Nui, circulation in the HYCOM model is not well resolved there and the observed patterns are potentially artifacts of the coarse model resolution. However, this model caveat remains consistent throughout the 17 year run and should not influence the comparisons between the ENSO states. To determine if the changes in connectivity patterns are model artifacts, further study of the Maui Nui region at a much finer resolution using models that can better resolve the nearshore circulation around Moloka‘i are needed.

Here we show that for a region that does not show dramatic oceanographic changes from ENSO events and where large scale connectivity patterns remain consistent between Normal and ENSO years, connectivity is still affected on a regional scale. Overall, during El Niño, particles travel further, spend more time in the plankton, and have fewer downstream connections. For individual regions El Niño causes drastic changes in connectivity, opening up new transport pathways or reducing total potential connectivity by more than 65%. If the affected regions are important stepping stones or harbor vulnerable species, changes in connectivity due to El Niño have a real potential of cascading through larger geographic areas, affecting ecosystems far outside the region of direct influence. Understanding how connectivity is affected on different geographic scales by ENSO events becomes particularly important in the light of climate change when major changes in connectivity are compounded by changes in temperature, food availability and other biological factors.

Table 1: A list of years uses for each ENSO state. We defined a year July 1 – June 30 to minimize effects of seasonality and capture the peak ENSO phase in the winter.

	<b>Normal State</b>	<b>El Nino</b>	<b>La Nina</b>
<b>Years</b>	2001-2002	1997-1998	1998-1999
	2003-2004	2002-2003	1999-2000
	2005-2006	2004-2005	2000-2001
	2008-2009	2006-2007	2007-2008
	2012-2013	2009-2010	2010-2011
	2013-2014		2011-2012
<b>Total days</b>	2191	1825	2193

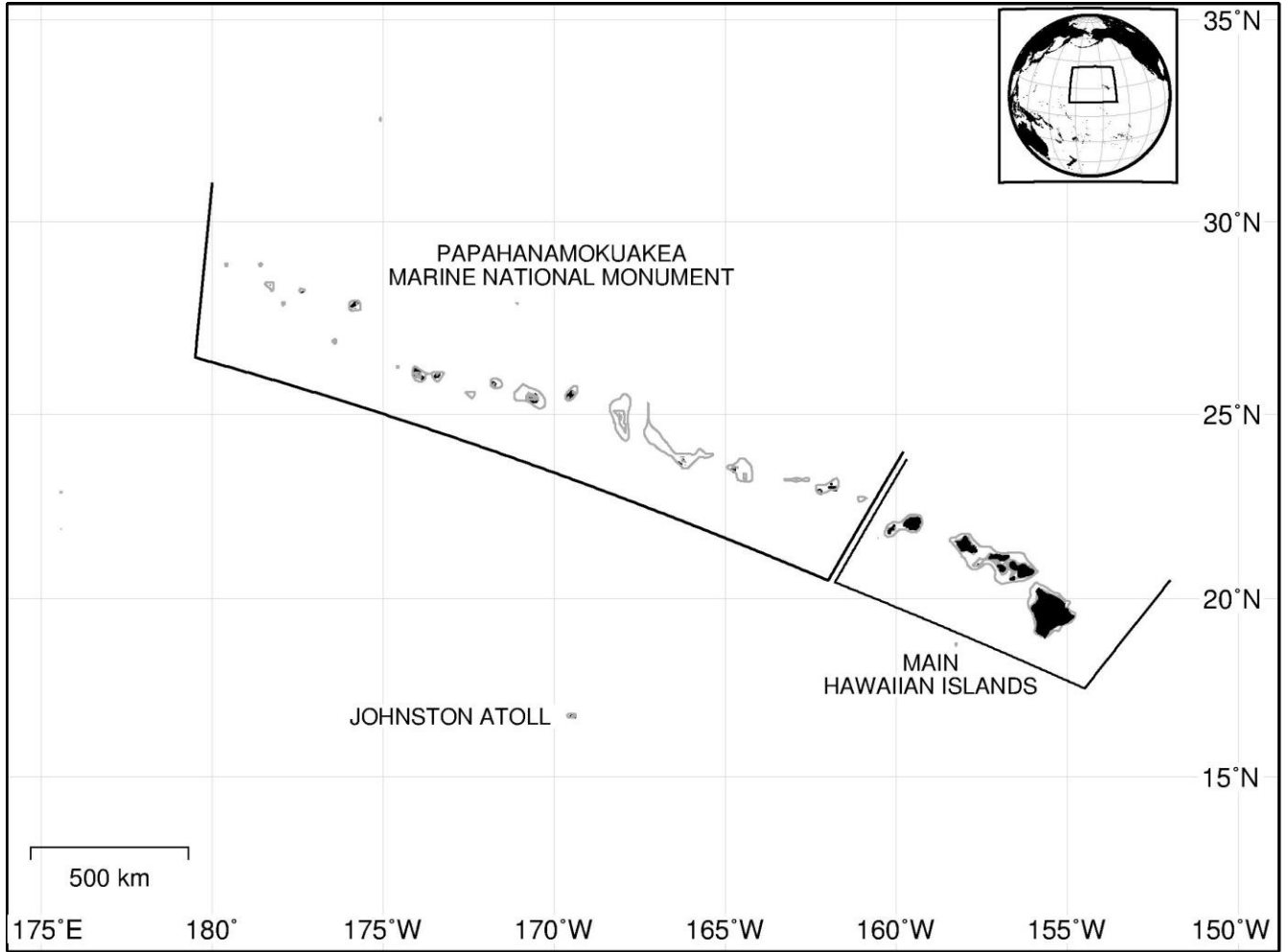


Figure 1. Modeled region of the Pacific Ocean showing the Hawaiian Archipelago. Bathymetry lines show 50 m and 1000 m. Papahānaumokuākea Marine National Monument is located in the Northwestern Hawaiian Islands.

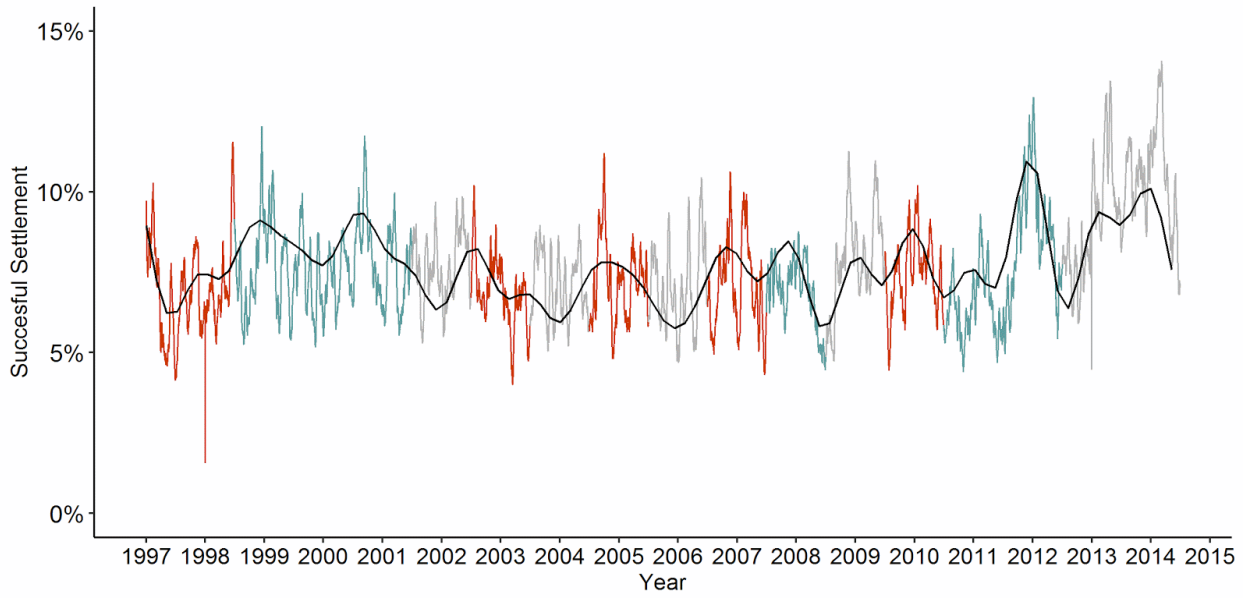


Figure 2. Daily total successful transport for the 17-year model run. Gray colors represent Normal years, red are El Niño years and blue are La Niña years. Smooth line is the GAM model fit line, generated using the *mgcv* package in R.

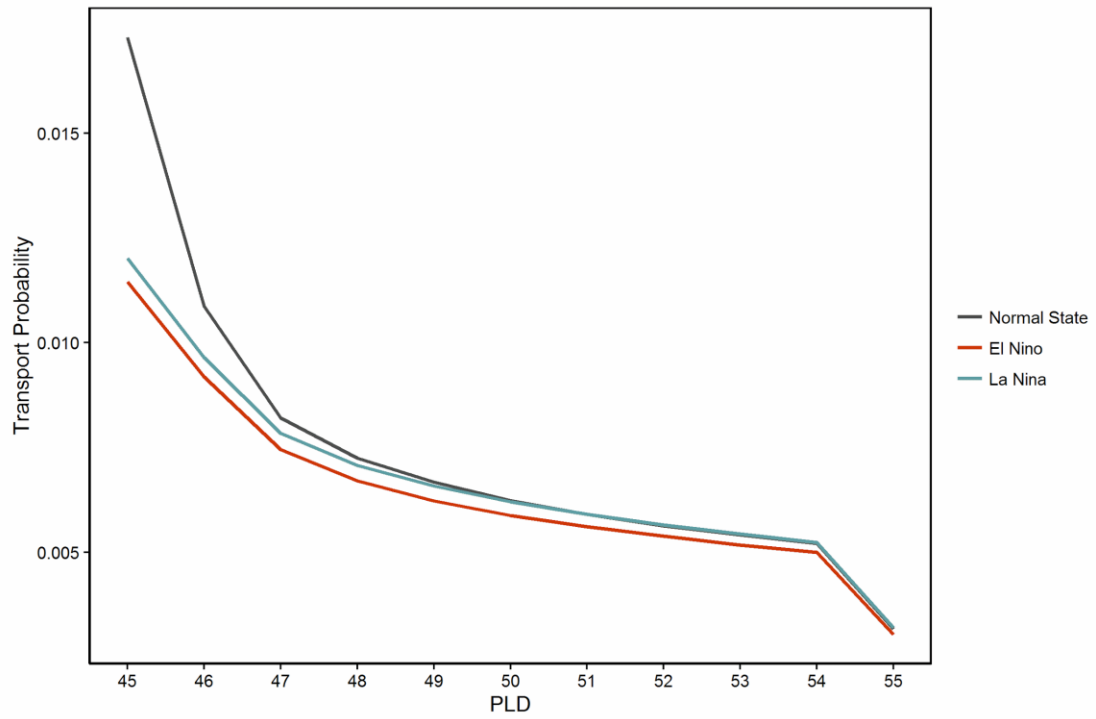


Figure 3. Transport probability as a function of pelagic larval duration (PLD) for all three ENSO states.

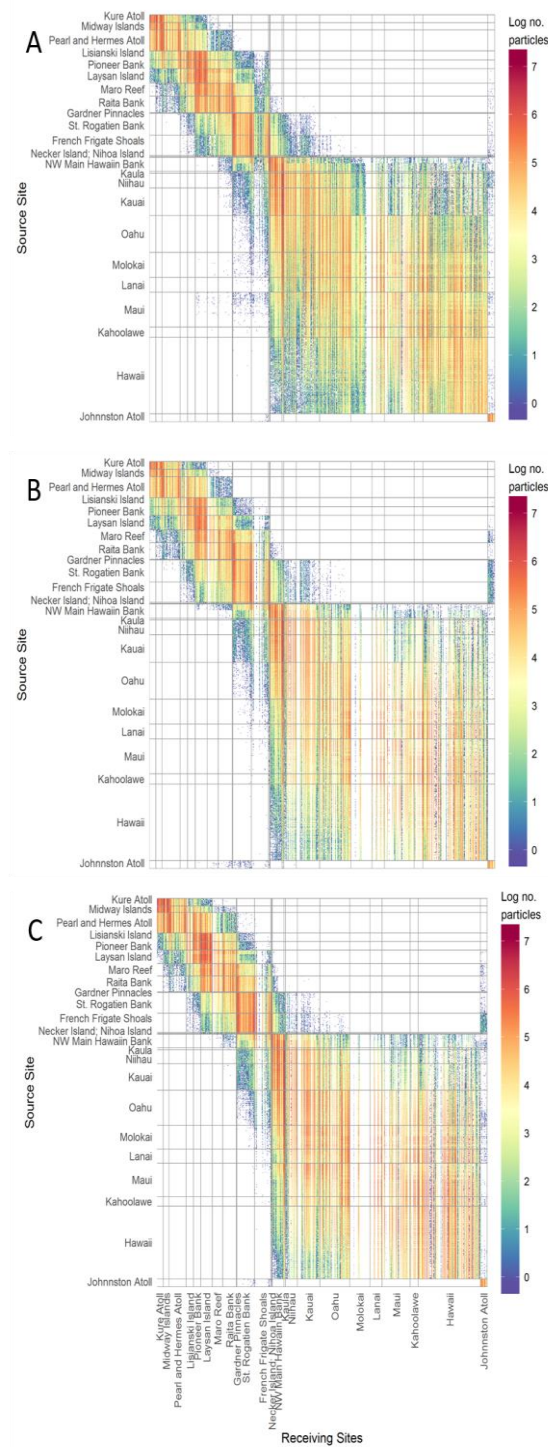


Figure 4. Total transport matrices ( $T_{ij}$ ) for Normal (a), El Niño (b) and La Niña (c) years for all sites. White areas show a zero exchange of particles. Gray lines delineate the 24 regional island groupings seen in Figure 6. Self-recruitment falls along the diagonal.

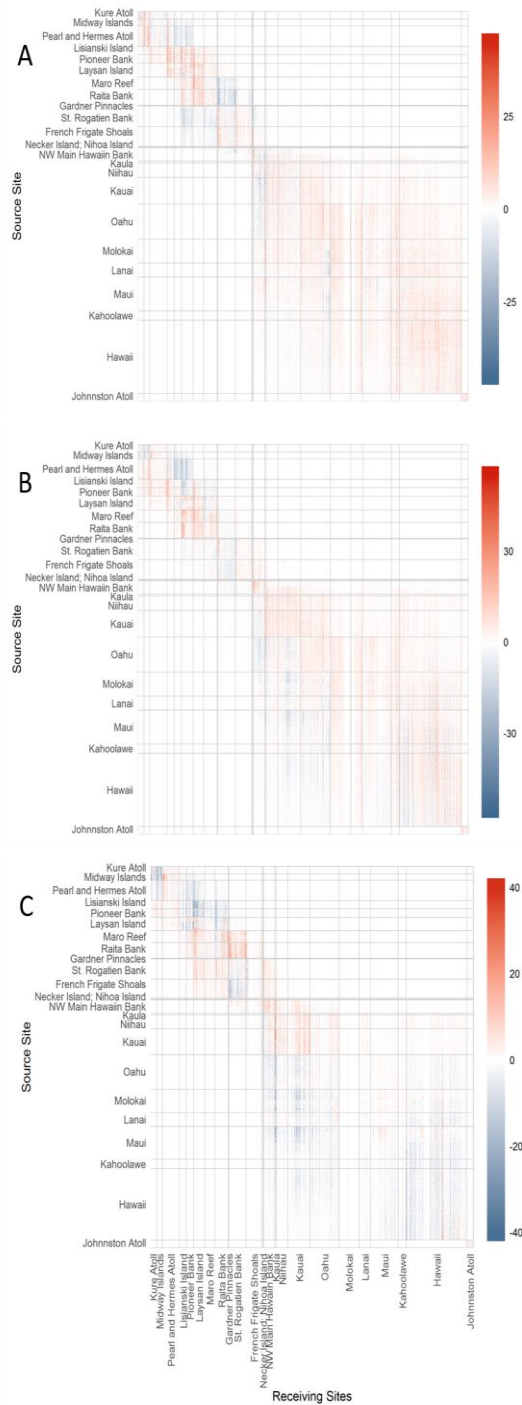


Figure 5. Difference matrix for total number of particles transported ( $T_{ij}$ ) at all sites for (a) Normal - El Niño, (b) Normal - La Niña, and (c) El Niño - La Niña. Red colors indicate the first listed state having more particles transported, blue indicate the second state having more particles transported. White denotes no difference between the two matrices. Gray lines delineate the 24 regional groupings seen in Figure 6. Please note the difference in scales

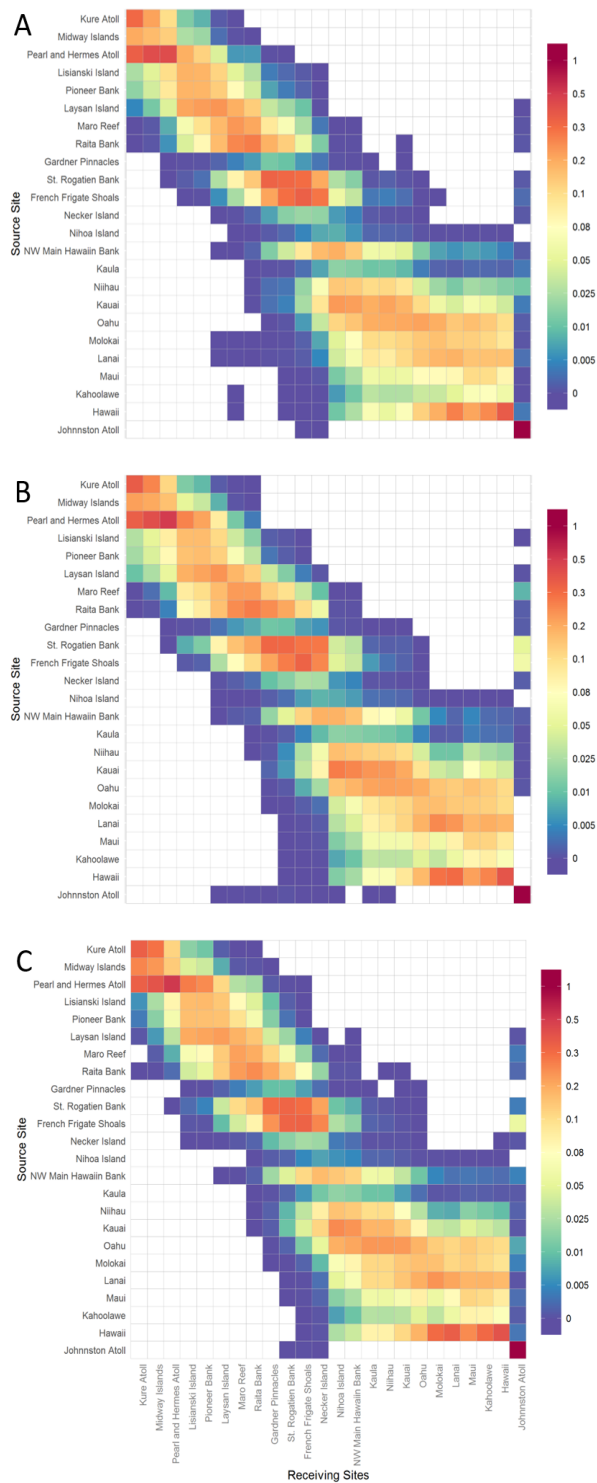


Figure 6. Regional potential upstream probability matrices ( $C_{ij}$ ) for a) Normal, b) El Niño, and c) La Niña years. White numbers indicate a zero connectivity. Diagonal of matrix represent self-recruitment and columns add up to one.



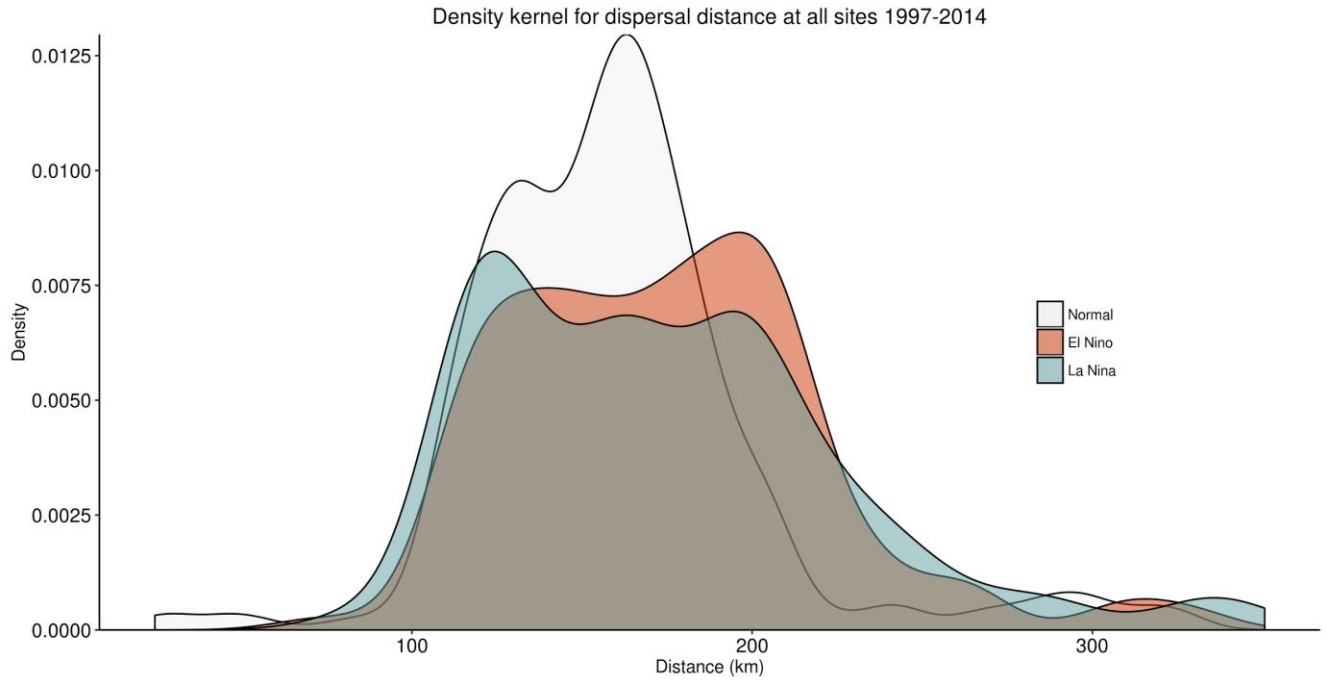


Figure 7. Dispersal distance density kernels for all sites during the three different ENSO states. Brown color shows where all three ENSO states overlap.

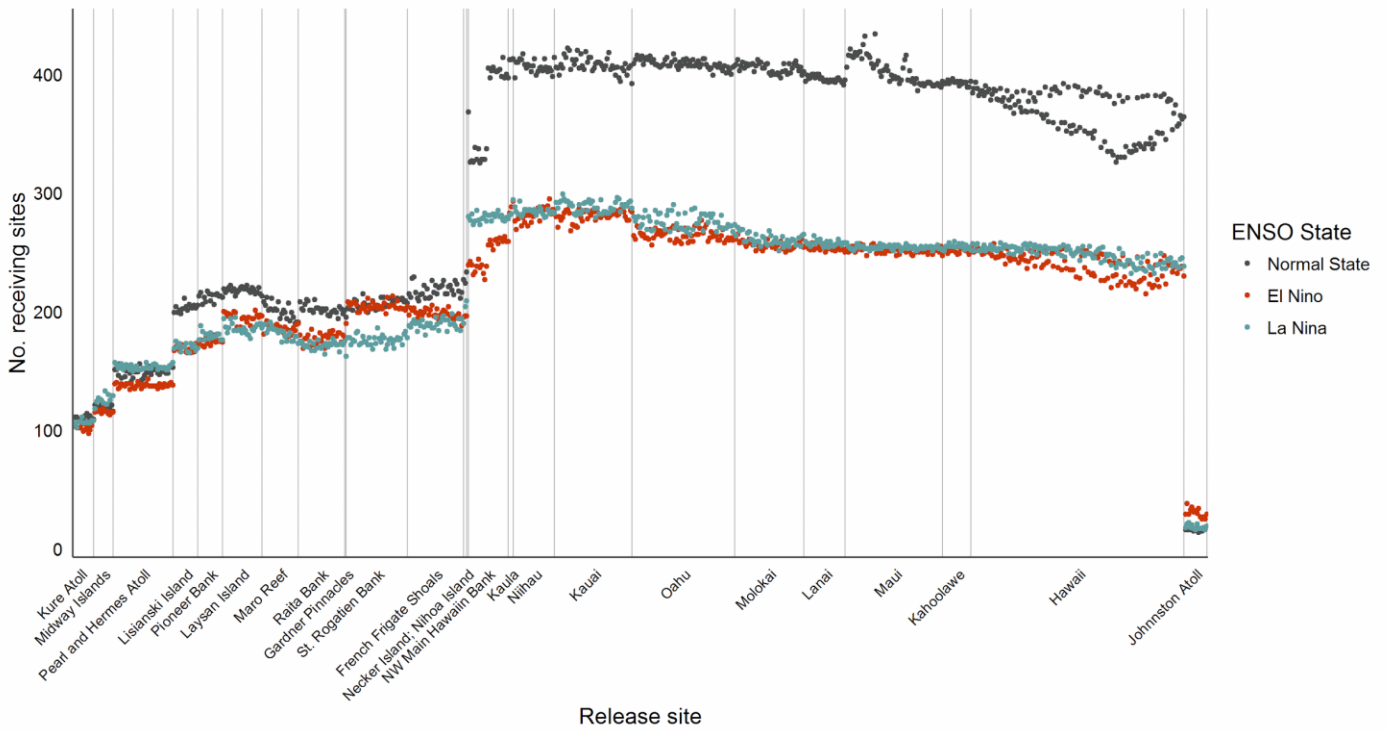


Figure 8. Number of downstream connections for particles released from the 687 habitat sites for each of the three ENSO states. Gray lines delineate the 24 regional island groupings seen in Figure 6.

# CHAPTER 5

---

## Synopsis

---

### 5.1 Background and dissertation goal

Despite decades of research, the factors that drive larval dispersal and population connectivity remain hotly debated (Weersing & Toonen 2009, White et al. 2010, Rivera et al. 2011, Selkoe & Toonen 2011, Selkoe et al. 2016a; Selkoe et al. 2016b). It has long been assumed that larval stages of marine organisms act as passive particles that are moved by ocean currents and thus the pelagic larval duration (PLD) determines the dispersal ability or range size of marine organisms. The assumption that larvae acted as passive particles at the mercy of ocean currents resulted in a universal belief that all marine populations were open. Around the turn of the century we started reevaluating that hypothesis as a growing number of studies proved that assumption false (Lester et al. 2007, Leis 2007, Selkoe & Toonen 2011, Mora et al. 2012, Selkoe et al. 2016a). Scientists showed that dispersal takes place over much smaller scales than previously thought, and self-recruitment is much more common (Swearer et al. 2002, Jones et al. 2005, Concepcion et al. 2014). Behavior was thought to play a large role in these findings, and when behavior was incorporated into biophysical dispersal models, they showed self-

recruitment rates similar to ones observed in the field. We can all agree that population connectivity is complex with many physical and biological factors determine dispersal range and connectivity patterns. Compounding the complexity of identifying underlying drivers of connectivity is the variable nature of the seascape, and studies showing that drivers are highly site and species specific (López-Duarte et al. 2012, Holstein et al. 2014, Liggins et al. 2015).

In some systems physical oceanographic factors (seascape) determine dispersal patterns (Baums et al. 2006, White et al. 2010, Liggins et al. 2015), while in others it is timing of spawning events (Donahue et al. 2015) or behavior (Huebert & Sponaugle 2009, Drake et al. 2011, 2013, Sundelöf & Jonsson 2012, Robins et al. 2013, Bidegain et al. 2013). In Hawai'i, modeled connectivity studies have shown directional dispersal towards the northwest with limited dispersal from the NWHI into the MHI (Friedlander et al. 2009) and that Johnston acts as a gateway to Hawai'i (Kobayashi 2006, Friedlander et al. 2009). However, these studies used only a few years' worth of realistic currents, making generalizations difficult.

The aim of this dissertation was to characterize modeled potential connectivity in Hawai'i. Firstly, I wanted to ground-truth an existing particle tracking model using in situ larval distribution data for use throughout this dissertation. Secondly, I wanted to create a comprehensive map over larval connectivity in the Hawaiian Archipelago, and thirdly, I wanted to see if and how connectivity patterns change during ENSO events.

## 5.2 Complete connectivity map

Comparing larval distributions obtained during field surveys with modeled larval distributions for the same period of time, I showed that a simple biophysical model with no behavior can predict larval distributions to a high degree when corrected for simple variables like gear avoidance (i.e. moon

illumination). Being able to ground-truth the model is imperative in interpreting the model output, thus this was an important first step that laid the groundwork for the remainder of the dissertation.

Connectivity in the northwestern Hawaiian Islands (NWHI) is predominantly physics driven and we see connectivity breaks (regions of limited dispersal) in regions of strong flows that correspond with observed genetic breaks (Toonen et al. 2011). Dispersal was predominantly towards the northwest, indicating that the MHI contribute larvae to the NWHI, but reciprocal connections are less likely. The connectivity map allowed me to determine that the upper limit on geographic distance of dispersal was 150 km, important information for managers when determining the geographic scale for Marine Spatial Planning (MSP) efforts. Agreement in dispersal and connectivity patterns and geographic scales over which connectivity operates for the NWHI have emerged from studies using vastly different methods: Lagrangian particle tracking models (Chapter 3), Eulerian spatially explicit individual based model (Friedlander et al. 2009) and population genetics (Toonen et al. 2011, Selkoe et al. 2014), and lends confidence in our findings.

While modeled potential connectivity showed congruence with genetic connectivity in the NWHI, our simplistic model could not reconcile the genetic patterns in the MHI. This may be due to discrepancies in the timescale over which the genetic studies and transport modeling determined connectivity (evolutionary vs. ecological), or indicate a mismatch between potential and realized connectivity. Because complex interactions between the larvae and its fluid environment determine realized population connectivity, it is likely that behavioral factors, mortality or growth and development rates trump seascape influences in the MHI. The MHI are heavily populated and human impacts on marine habitats through pollution and habitat degradation (Puritz & Toonen 2011, Selkoe et al. 2016a) have explained genetic structure and are strong contenders in explaining the discrepancies between the well-connected MHI in our model and observed genetic structure.

### 5.3 Robustness of connectivity patterns

Connectivity patterns for the Hawaiian Archipelago proved robust with respect to the type and resolution of circulation model used to move particles. A strong isolation by distance pattern was observed for both Archipelago wide simulations, and general connectivity patterns for the MHI remained robust throughout (Chapter 3; Appendix A). Higher resolution models showed an increase in number of connections, but with low dispersal probabilities. The MHI showed more sensitive to the type of model used than the resolution of the current model, however these differences were minimal. Vaz (2012) reported similar patterns of dispersal for different spatial resolutions of the same current mode around Hawai'i, lending confidence to our findings.

The availability of high resolution models that also have a long temporal domain are limited, thus knowing that the connectivity patterns described in chapter 3 are robust with respect to current model resolution allowed me to utilize a longer time series from a coarser resolution circulation model to look at longer term climate oscillations.

### 5.4 El Niño changes patterns of exchange

I show that changes in the frequency of El Niño events will affect potential connectivity in Hawai'i (Chapter 4). During El Niño, new dispersal pathways open up with distant habitat sites, while connectivity it islands in the well-connected MHI are reduced. Connections between Moloka'i and islands in the archipelago are drastically reduced during El Niño years, potentially rendering Moloka'i the most sensitive island to climate change in the MHI. If connectivity is reduced to the extent that is argued here, a special management plan focused on building resilience for Moloka'i is warranted.

Kobayashi (2006) showed that Johnston acted as a gateway to Hawai'i, however during his study

only one year of currents were available (2003), thus generalizations of patterns were difficult. Kobayashi (2006) identified a connection between Johnston Atoll and Hawai'i, but that connection was only present during winter months. The year of currents he had available spanned Jan 2003-Jan 2004, which was (by our definition) straddle an El Niño year and a Normal state year. Kobayashi only observed the connection with Hawai'i during winter of 2003, which was the El Niño state year. The results discussed in chapter 4 confirmed Kobayashi's (2006) findings, and importantly, showed that the connection with Johnston is not constant. Rather, the connection with the MHI only exists during El Niño years, which is important in the light of climate change when El Niño might become more common.

Additionally, I showed that during normal state years Johnston acts as an outpost, something that had not previously been shown in modeling studies, but was known through population genetic studies (Skillings et al. 2011). During Normal years Johnston Atoll receives larvae from all of the MHI and islands in the center of the archipelago, while during El Niño years the connection with the Big Island, Maui Nui and O'ahu is not present. With the possible expansion of PMNM to include Johnston Atoll these dispersal pathways are important when devising an effective management plan.

## 5.5 Management implications and future directions

To better understand drivers on the island level conducting finer scale studies in areas of concern, such as Moloka'i and throughout the MHI, are warranted. Indeed, efforts are underway to characterize connectivity in Kāne'ohe Bay, O'ahu (by Jerolmon, McManus, Powell, et al.), off west Hawai'i (by Wong-Ala, Neuheimer, Powell, et al.), around Maui (by Storlazzi et al.) and on Moloka'i (by Wren, Toonen, Jia, et al.) using high resolution current models and highly parameterized 3D spatially explicit individual based models (IBMs). Hopefully these higher resolution studies allow us to determine island scale drivers of connectivity in the Main Hawaiian Islands that a simplistic physics driven model

was not able to resolve.

However, the more complex the IBM doesn't necessarily mean the more accurate it is. Since most biophysical models lack the spatial resolution needed to identify temporally short mesoscale features in the ocean, such as thin layers (Woodson et al. 2012), we are not capable of modeling resulting larval behaviors. Multidisciplinary studies that incorporate modeled connectivity along with seascape genetics/genomics and physical and biological factors can tell us more than the individual pieces alone of what drives connectivity in the ocean (Selkoe et al. 2016a). In recent studies combining seascape genetics/genomics and dispersal modeling with seascape features and demographic parameters, seascape factors such as ocean currents and habitat availability have shown to be important drivers of genetic connectivity. For example, in Hawai'i, a recent study comparing allelic richness for 47 different species across the archipelago showed that the amount and quality of available habitat was a determining factor of genetic structure (Selkoe et al. 2016a).

For regions with persistent and dominating hydrological features, such as strong currents and jets, large scale patterns of connectivity can be inferred from simplistic biophysical models. I showed that modeled connectivity in the NWHI were consistent with genetic patterns of connectivity, and breaks were located in regions with strong zonal flows (Chapter 3). Similarly, Abesamis et al. (2016) showed that in the Philippines, the Bohol Jet is the primary driver in shaping the spatial structuring of reef fish assemblages. They compared connectivity patterns from a simplistic biophysical dispersal with species assemblages and habitat variables. They attributed the Bohol Jet with connecting sites upstream of the jet as well as creating a barrier to dispersal with sites outside the influence of the jet. For Hawaii, the observed regions with limited exchange in the NWHI created by zonal jets, suggest that Papahānaumokuākea Marine National Monument (PMNM) is best managed in multiple units and not as a whole. I suggest that management units should not exceed 150 km in length because connectivity past that distance is limited in a single generation. Studies both in Hawai'i and in the Caribbean have



demonstrated similar distances to dispersal (Cowen et al. 2006, Friedlander et al. 2009).

Biophysical models are powerful tools to study population connectivity and gain a deeper understanding of population dynamics and transport of marine larvae (Metaxas & Saunders 2009, Kough et al. 2013). The need for accurate biophysical models in marine conservation is constantly growing. With a changing climate and ever growing human population, the strain on our oceans is increasing, and an ecosystem based management (EBM) approach is needed to replace a more traditional single-species management approaches (Christie et al. 2007). Creating networks of marine reserves spaced apart enough that larval exchange is still possible is one approach in ensure healthy marine populations in the future (Gerber et al. 2005). We know that the larval stage of many marine organisms will be affected by climate change (Stumpp et al. 2011, Rosa et al. 2012, Byrne et al. 2013), and recent studies utilize biophysical dispersal models and parameterized them using results from research on larvae in future ocean conditions (Lett et al. 2010). Although this can give us valuable insight into future population connectivity patterns, it is important to be cautious when interpreting output from such models (Brander et al. 2013). Thus, identifying drivers of diversity on various scales (both regional scale like the Hawaiian Archipelago, and smaller, island scale) allows us to best manage our resources, and ensure that our reefs have a continued high biodiversity and resilience to withstand stressors from human use and climate change.

# APPENDIX A

---

## Hawai‘i connectivity circulation model comparisons

---

### A.1 Methods

#### *A.1.1 HYCOM*

The HYbrid Coordinate Ocean Model (HYCOM) is a global primitive equation ocean circulation model run by the HYCOM consortium (Bleck 2002; Chassignet et al. 2009). The Hybrid coordinate refers to the model's vertical coordinate system which varies based on the vertical structure on the ocean. It is density following (isopycnic) in the stratified ocean, pressure following (level) in the surface mixed layer and terrain-following (sigma) in coastal areas and on shelf seas.

#### *A.1.2 Connectivity Matrices*

Connectivity matrices were generated for the 8km global HYCOM driven dispersal simulation, as well as for the 4km regional Hawai‘i HYCOM driven simulation. For the full archipelago simulations we used the habitat definitions in the main manuscript and released 50 particles from 687 sites each day for five years (May 1, 2009-May 2014). For the MHI domain we used a subset of the coral reef habitat for

the smaller geographic domain, releasing 50 particles from each of the 406 habitat pixels every day from May 2, 2009-May 25, 2014.

Forward matrices report the final locations of particles released at a given island, as measured by the percent of successfully settled particles released from the source site ( $i$ ) that “settled” at the receiving site ( $j$ ) and can be written in the following equation:

$$P_{ij \text{ (forward)}} = S_{ij} / \sum S_i$$

## A.2 Results

Archipelago wide simulation yielded similar probability matrixes for model runs using 0.08 HYCOM (Fig A4) and regional MITgcm, despite having different resolutions. The global HYCOM for the Hawaii region showed a greater connectivity between more distant islands than did MITgcm. Johnston atoll showed consistently high levels of self-recruitment (close to 100%) with no discernible influx of propagules from Hawai'i.

### A.2.1 *Difference Matrices for the Hawaiian Archipelago*

Comparing the differences between transport model runs using 0.08° HYCOM vs. regional (0.04°) MITgcm currents, the rearward probability matrix (Fig A5b) show a stronger correlation ( $r=0.9259$ ) than the forward matrix (Fig. A5a) ( $r=0.9123$ ). Within the matrices, the forward transport probabilities are more different in the MHI indicated by the larger values in the difference matrix (Fig A5a), whereas rearward probabilities show greater differences in the NWHI. In the forward matrix, 0.08° HYCOM overestimates probabilities for the whole archipelago, except for the center of the archipelago where MITgcm shows higher probabilities or transport. This is most apparent around St. Rogatien and its banks, but also in Moloka'i, and somewhat around Laysan and Raita. In the rearward matrix (Fig. A5b),

0.08° HYCOM show higher probability between more distant locations, and show distant connections that are not present in the regional MITgcm runs.

#### *A.2.2 Difference Matrices for the Main Hawaiian Islands*

The forward potential connectivity matrix comparing MITgcm and 0.04° HYCOM for the Main Hawaiian Islands (MHI) are most similar ( $r=0.9102$ ) (Fig A7A1). Curiously, 0.08° HYCOM and 0.04° MITgcm forward matrices ( $r=0.8584$ ) (Fig A7B1) are slightly more similar than the 0.08° and 0.04° HYCOM ( $r=0.8315$ ) (Fig A7C1). The 0.08° HYCOM seems to overestimate connectivity compared to 0.04° HYCOM and 0.04° MITgcm throughout the MHI, except for Moloka'i and Lāna'i in the 0.04° HYCOM comparison.

Rearward connectivity differs in patterns of correlation strength between models compared to forward connectivity. Rearward difference matrices show that the two resolutions of HYCOM have the strongest correlation ( $r=0.974$ )(Fig A7C2). The 0.04° MITgcm and 0.04° HYCOM show slightly less agreement ( $r=0.9533$ ) (Fig A7A2) than 0.08° HYCOM and 0.04° MITgcm ( $r=0.9305$ ) (Fig A7B2). Disagreements between models in rearward matrices vary more than the forward matrices; there is not one model that overestimates potential connectivity for the whole MHI.

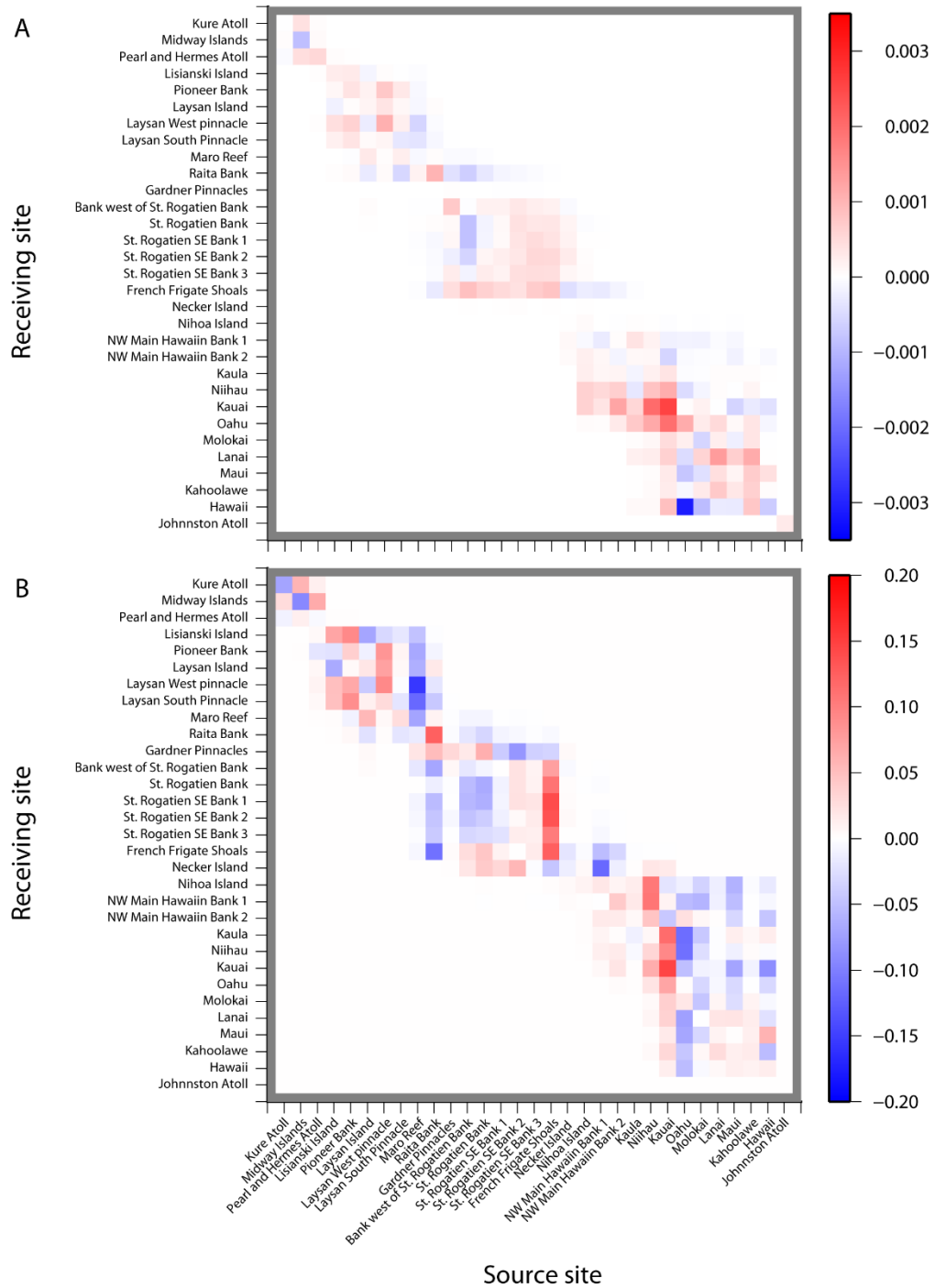


Figure A1. Difference matrices comparing (A) forward and (B) rearward “settlement” probabilities between year round particle releases and releases during May - June only. Red indicated year round probabilities were higher and blue colors indicate releases during May - June only had higher probability of transport. White indicate no probability of transport.

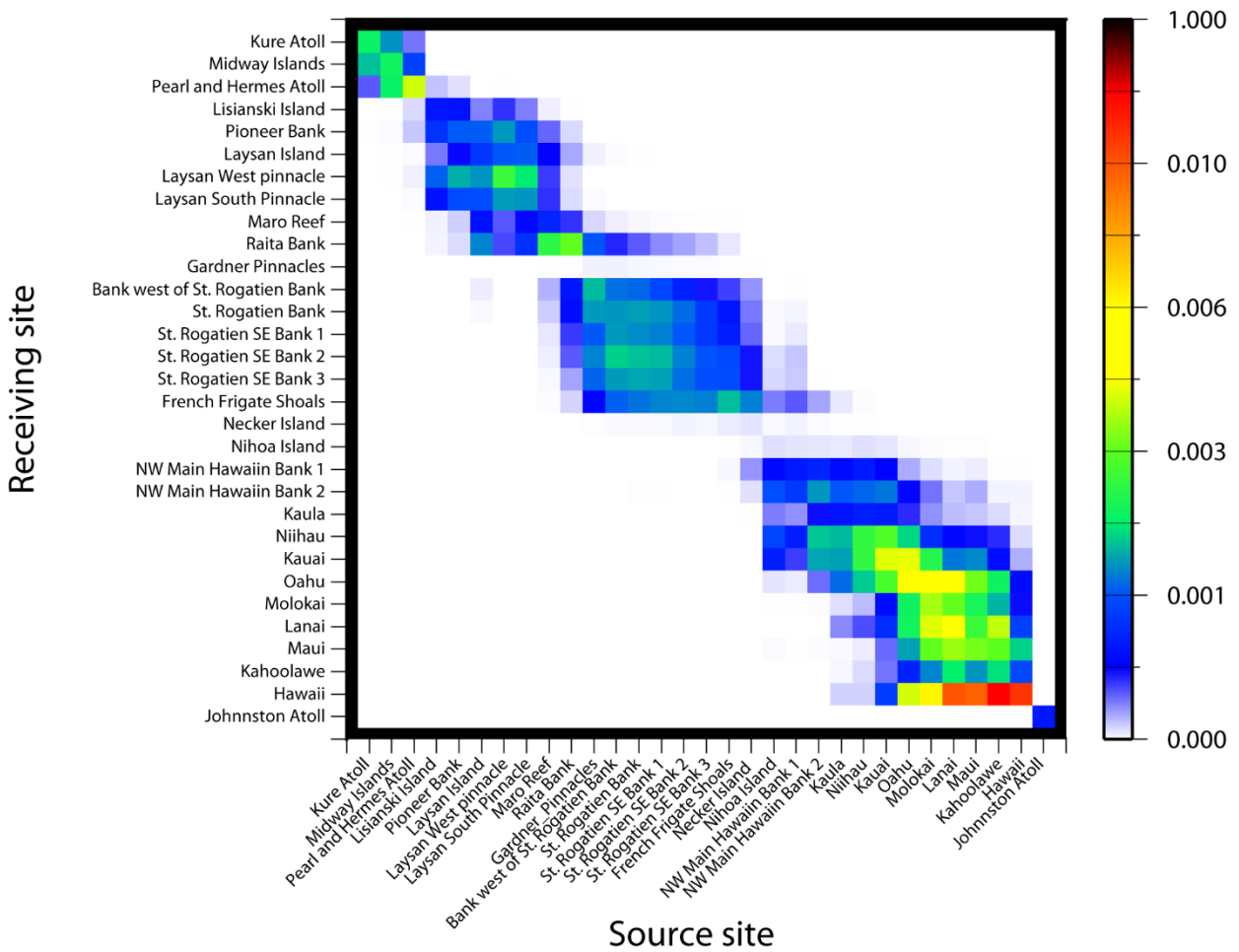


Figure A2. Forward probability matrix for the model run using MITgcm currents. Colored tiles represent probability of transport from source sites to receiving sites. White areas indicate no probability of transport between source and receiving sites

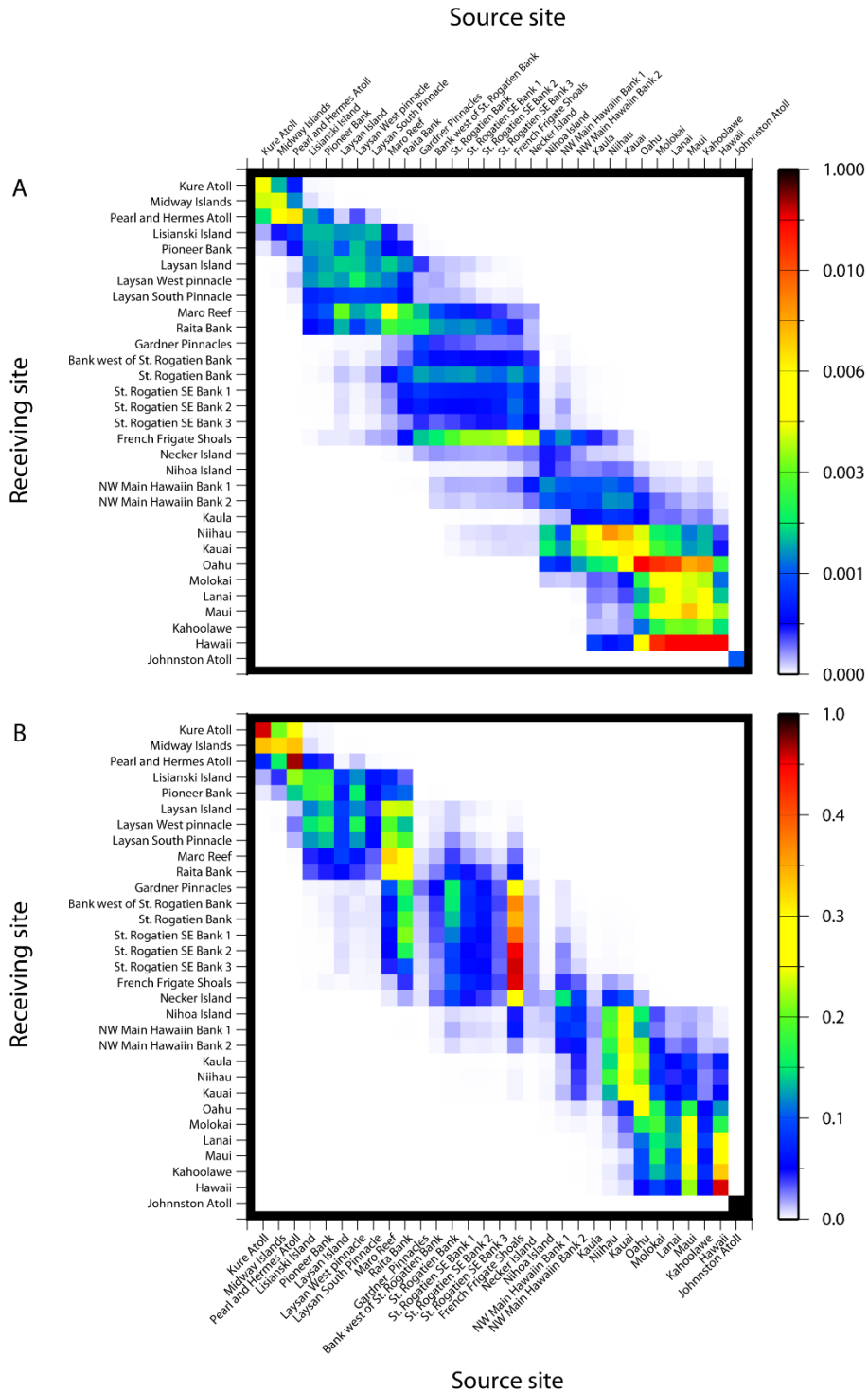


Figure A3. Potential connectivity matrices for particle tracking model run using 0.08° HYCOM currents for (A) forward probabilities and (B) rearward probabilities. Colored tiles represent probability of transport from source sites to receiving sites, scaled after receiving site with each row adding up to zero. White represents a zero probability of connectivity.

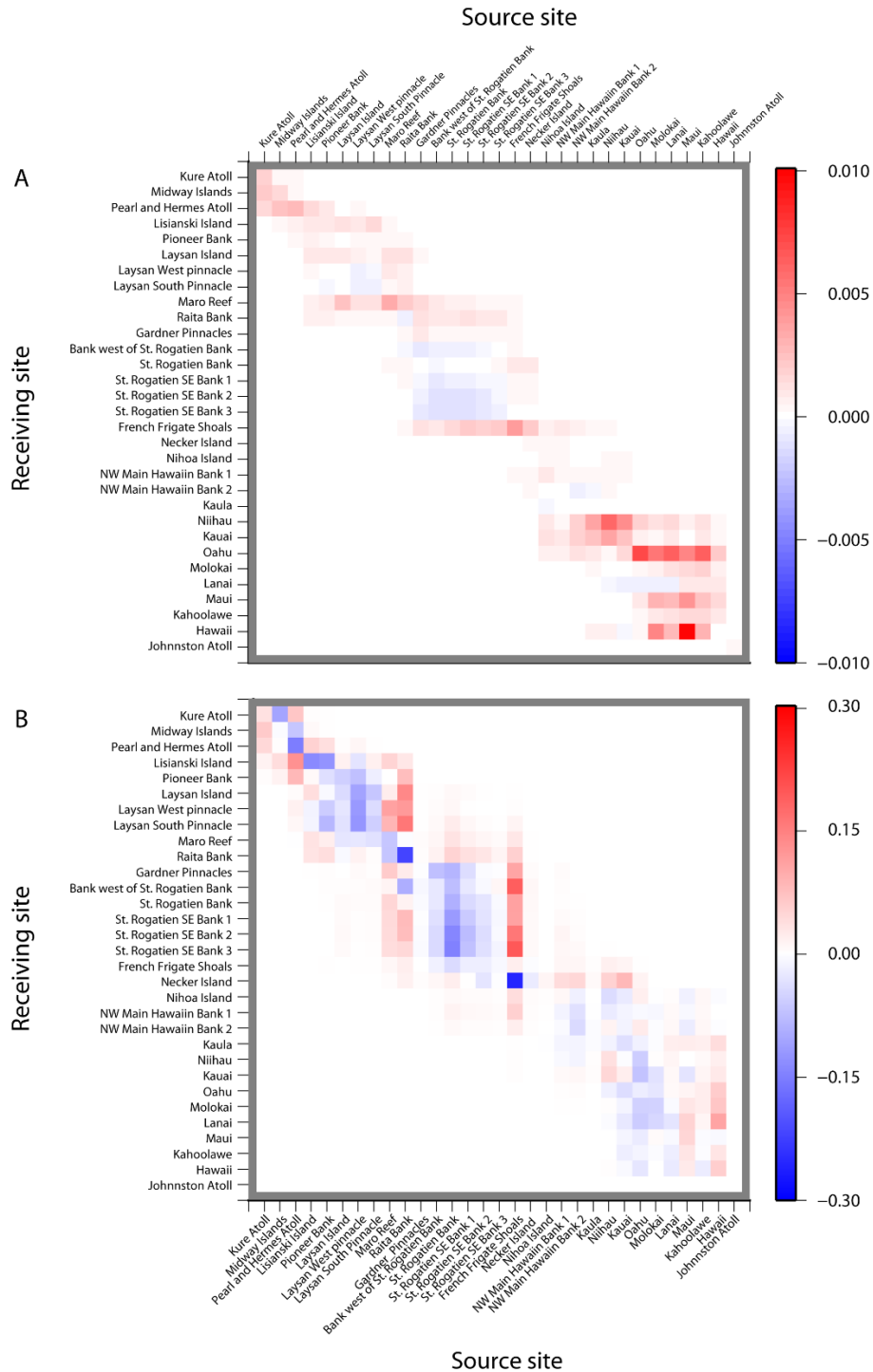


Figure A4. Difference matrices comparing (A) forward and (B) rearward transport probabilities between year round releases in the dispersal model run using 0.08° HYCOM and regional (0.04°) MITgcm. Red indicated HYCOM driven probabilities were higher and blue colors indicate the MITgcm driven model run had higher probability of transport. White indicate no probability of transport.



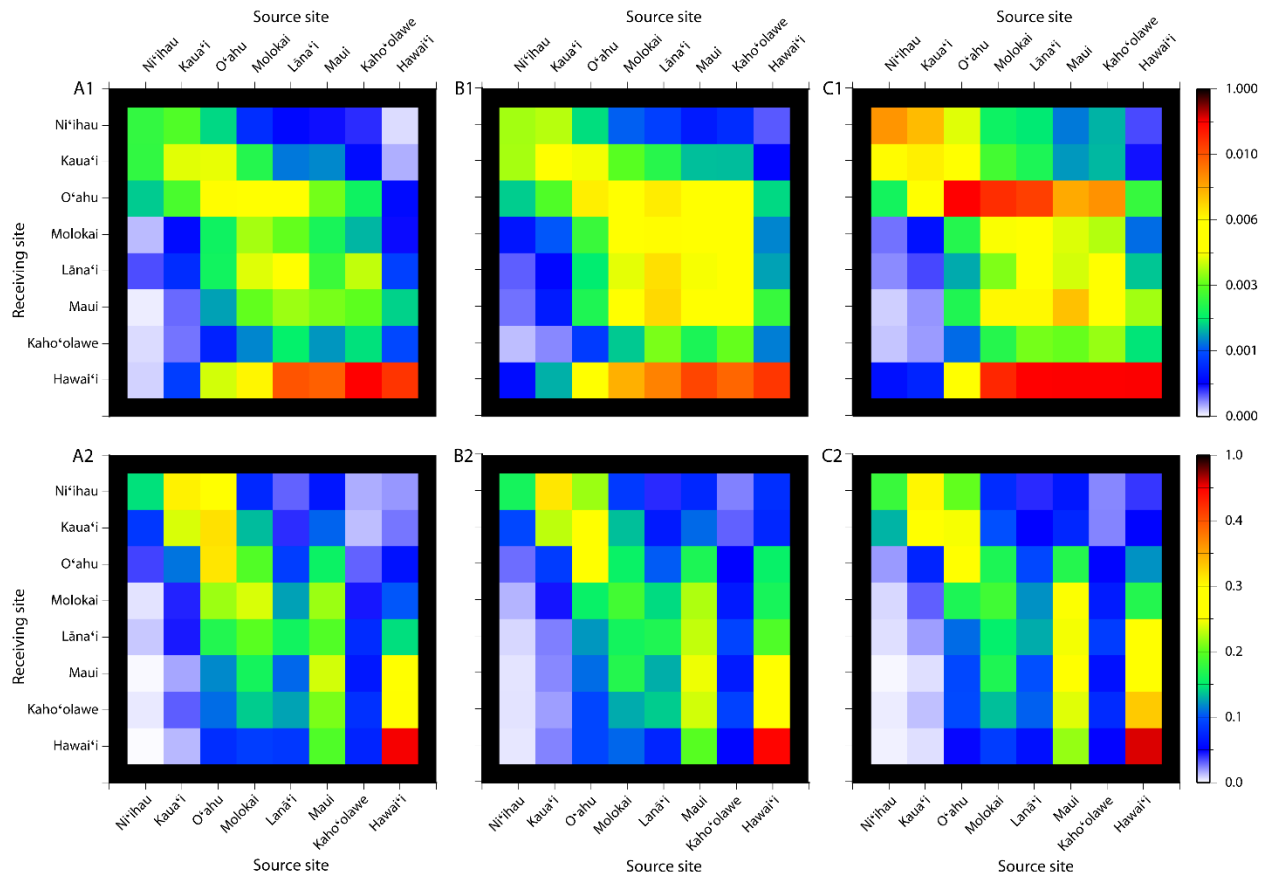


Figure A5. Probability matrices for forward (A1, B1, C1) and rearward (A2, B2, C2) potential connectivity for the Main Hawaiian Islands for three transport model runs. (A) is a subset of Fig 2a for the MHI, (B) shows probabilities from a model run using regional 0.04° HYCOM currents, and (C) is a MHI subset of figure A4. Colored tiles represent probability of transport from source sites to receiving sites. Forward matrices are scaled after receiving site with each row adding up to zero. White represents a zero probability of connectivity.

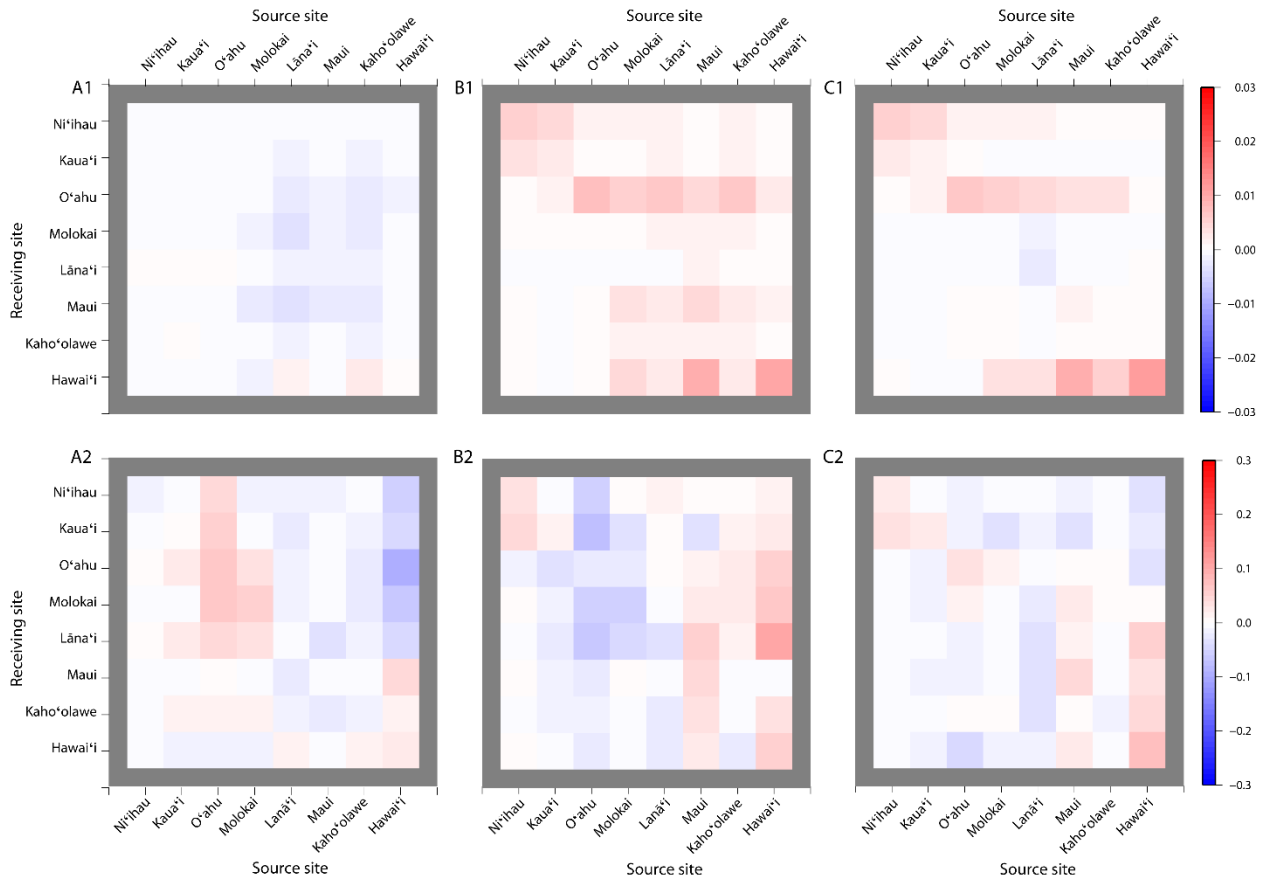


Figure A6. Difference matrices for the Main Hawaiian Islands for forward (A1, B1, C1) and rearward (A2, B2, C2) transport probabilities for year round releases in the dispersal model run between the regional MITgcm and 0.04 HYCOM (A), between 0.08° HYCOM and regional (0.04°) MITgcm (B) and between the two resolutions of HYCOM (C). Red colors indicated 0.08° HYCOM driven probabilities were higher in (B) and (C) and MITgcm in (A). Blue colors indicate the MITgcm driven model run had higher probability of transport in (B) and 0.04 HYCOM in (A) and (C). White represents no probability of transport.

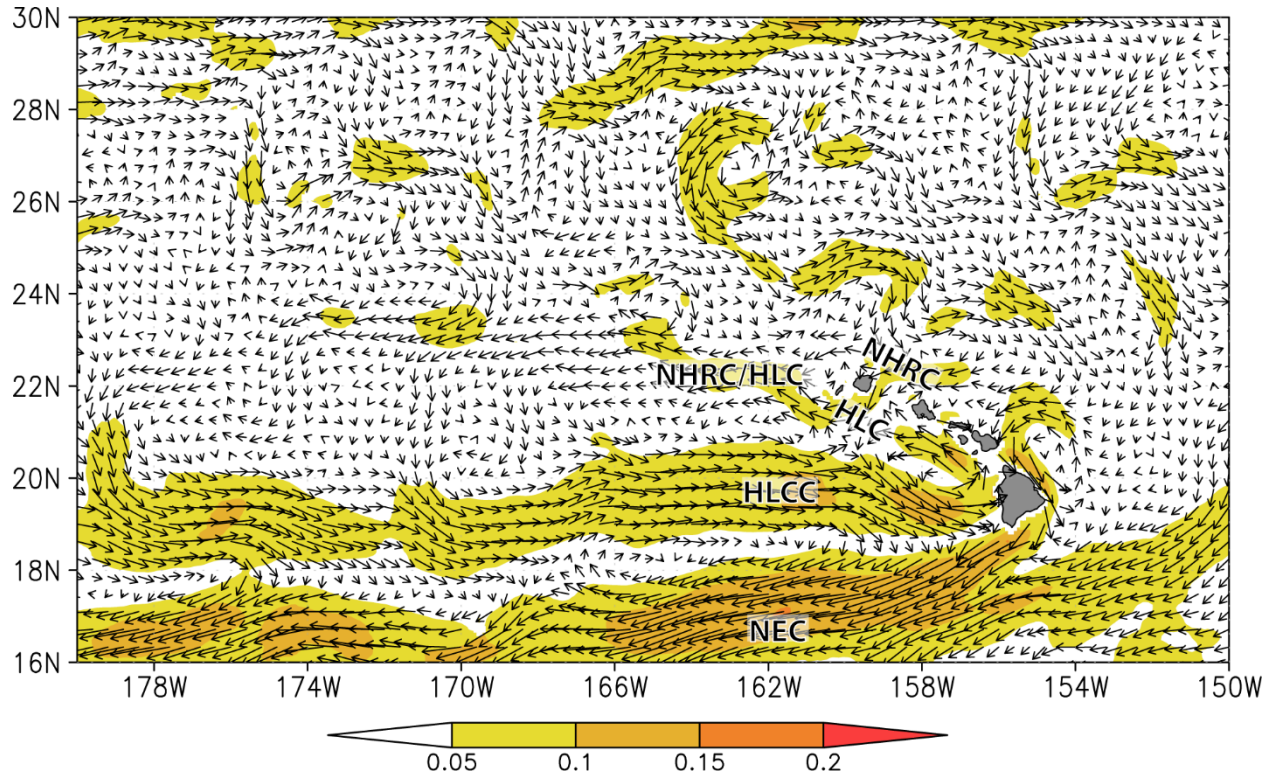


Figure A7. Map showing averaged surface circulation from global 0.08 HYCOM generated data for the Hawaiian Archipelago. Major surface currents are marked. Zonal flows in the NWHI are not present in this dataset.

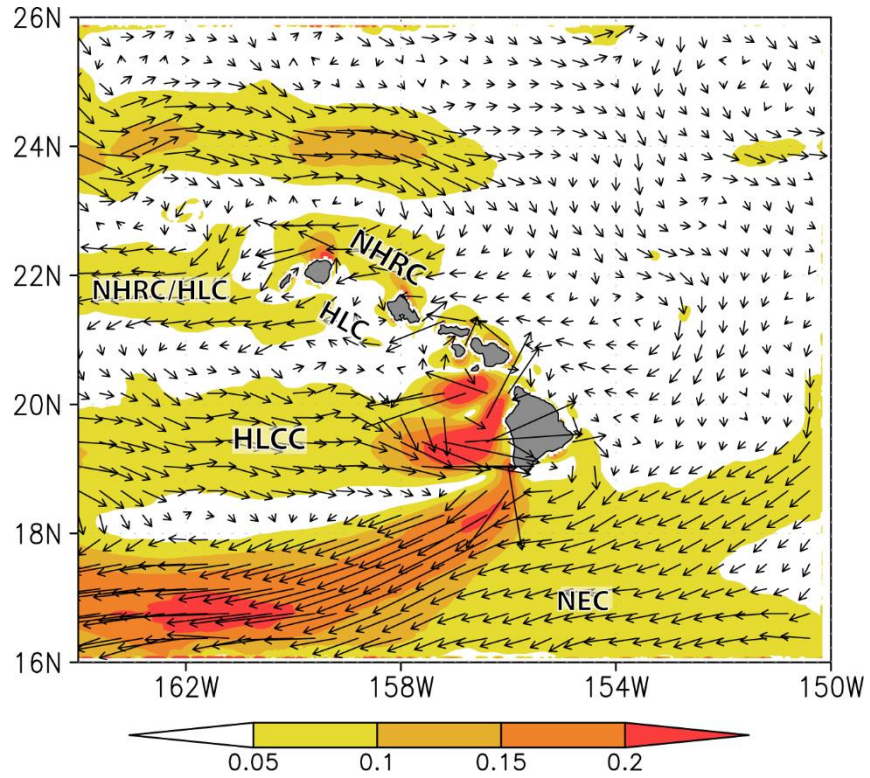


Figure A8. Map showing averaged surface circulation from the regional 0.04 HYCOM generated data for the Main Hawaiian Islands. Major surface currents are marked.

# APPENDIX B

---

## ENSO connectivity matrices

---

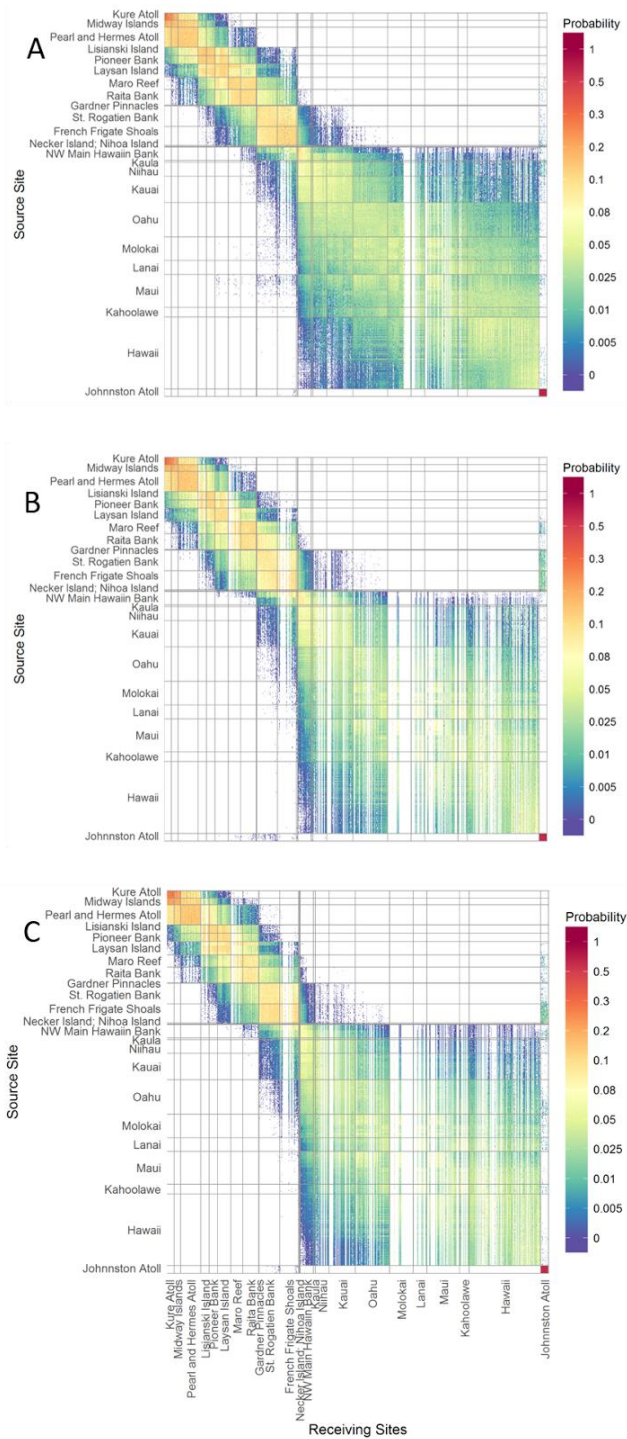


Fig B1. Potential upstream probability matrices ( $C_{ij}$ ) for Normal (a), El Niño (b) and La Niña (c) years. White areas show a zero probability of connections. Gray lines delineate the 24 regional groupings. Self-recruitment falls along the diagonal.

---

References

---

- Abesamis, R. A., Stockwell, B. L., Bernardo, L. P. C., Villanoy, C. L., & Russ, G. R. (2016). Predicting reef fish connectivity from biogeographic patterns and larval dispersal modelling to inform the development of marine reserve networks. *Ecological Indicators*, *66*, 534–544.
- Almany, G. R., Berumen, M. L., Thorrold, S. R., Planes, S., & Jones, G. P. (2007). Local Replenishment of Coral Reef Fish Populations in a Marine Reserve. *Science*, *316*, 742–744.
- Anadón, J. D., del Mar Mancha-Cisneros, M., Best, B. D., & Gerber, L. R. (2013). Habitat-specific larval dispersal and marine connectivity: implications for spatial conservation planning. *Ecosphere*, *4*, 1–15.
- Bahr, K. D., Jokiel, P. L., & Rodgers, K. S. (2015). The 2014 coral bleaching and freshwater flood events in Kāneʻohe Bay, Hawaiʻi. *PeerJ*, *3*, e1136.
- Baird, A. H., Guest, J. R., & Willis, B. L. (2009). Systematic and Biogeographical Patterns in the Reproductive Biology of Scleractinian Corals. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 551–571.
- Baltz, K., Field, J., Ralston, S., & Sakuma, K. (2002). Operations Manual - Juvenile Rockfish Recruitment Survey Trawling Protocols. Southwest Fisheries Science Center, NOAA fisheries, unpublished report.
- Battista, T. A., Costa, B. M., & Anderson, S. M. (2007). *Shallow-water benthic habitats of the main eight Hawaiian Islands*. Silver Spring, MD: NOAA Technical Memorandum NOS NCCOS 61, Biogeography Branch.
- Baums, I. B., Paris, C. B., & Chérubin, L. M. (2006). A bio-oceanographic filter to larval dispersal in a reef-building coral. *Limnology and Oceanography*, *51*, 1969–1981.
- Bidegain, G., Bárcena, J. F., García, A., & Juanes, J. A. (2013). LARVAHS: Predicting clam larval dispersal and recruitment using habitat suitability-based particle tracking model. *Ecological Modelling*, *268*, 78–92.

- Bidigare, R. R., Benitez-Nelson, C., Leonard, C. L., Quay, P. D., Parsons, M. L., Foley, D. G., & Seki, M. P. (2003). Influence of a cyclonic eddy on microheterotroph biomass and carbon export in the lee of Hawaii. *Geophysical Research Letters*, *30*, 1318.
- Bird, C. E. (2006). *Aspects of community ecology on wave-exposed rocky Hawaiian coasts*. University of Hawai'i at Mānoa.
- Bird, C. E., Holland, B. S., Bowen, B. W., & Toonen, R. J. (2007). Contrasting phylogeography in three endemic Hawaiian limpets (*Cellana* spp.) with similar life histories. *Molecular Ecology*, *16*, 3173–3186.
- Bleck, R. (2002). An oceanic general circulation model framed in hybrid isopycnic-Cartesian coordinates. *Ocean Modelling*, *4*, 55–88.
- Boehlert, G. W., & Mundy, B. C. (1996). *Ichthyoplankton vertical distributions near Oahu, Hawai'i, 1985–1986: data report*. NOAA Technical Memoir. NMFS-SWSC-235: 1–148.
- Botsford, L. W., Brumbaugh, D. R., Grimes, C., Kellner, J. B., Largier, J., O'Farrell, M. R., ... Wespestad, V. (2009). Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. *Reviews in Fish Biology and Fisheries*, *19*, 69–95.
- Bowen, B. W. (2016). The Three Domains of Conservation Genetics: Case Histories from Hawaiian Waters. *The Journal of Heredity*, *107*, 309–317.
- Bradbury, I. R., & Bentzen, P. (2007). Non-linear genetic isolation by distance: implications for dispersal estimation in anadromous and marine fish populations. *Marine Ecology Progress Series*, *340*, 245–257.
- Bradbury, I. R., Laurel, B., Snelgrove, P. V. R., Bentzen, P., & Campana, S. E. (2008). Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. *Proceedings of the Royal Society of London B: Biological Sciences*, *275*, 1803–1809.
- Brander, K., Neuheimer, A., Andersen, K. H., & Hartvig, M. (2013). Overconfidence in model projections. *ICES Journal of Marine Science: Journal Du Conseil*, *70*, 1065–1068.
- Browman, H. I., Stergiou, K. I., Browman, C. H. I., Cury, P. M., Hilborn, R., Jennings, S., ... Zeller, D. (2004). Perspectives on ecosystem-based approaches to the management of marine resources. *Marine Ecology Progress Series*, *274*, 269–303.
- Burgess, S. C., Nickols, K. J., Griesemer, C. D., Barnett, L. A. K., Dedrick, A. G., Satterthwaite, E. V., ... Botsford, L. W. (2014). Beyond connectivity: How empirical methods can quantify population persistence to improve marine protected-area design. *Ecological Applications: A Publication of the Ecological Society of America*, *24*, 257–270.
- Burgess, S. C., Treml, E. A., & Marshall, D. J. (2012). How do dispersal costs and habitat selection influence realized population connectivity? *Ecology*, *93*, 1378–1387.
- Bushnell, M. E., Claisse, J. T., & Laidley, C. W. (2010). Lunar and seasonal patterns in fecundity of an indeterminate, multiple-spawning surgeonfish, the yellow tang *Zebrasoma flavescens*. *Journal of Fish Biology*, *76*, 1343–1361.



- Byrne, M., Lamare, M., Winter, D., Dworjanyn, S. A., & Uthicke, S. (2013). The stunting effect of a high CO<sub>2</sub> ocean on calcification and development in sea urchin larvae, a synthesis from the tropics to the poles. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *368*, 20120439.
- Cai, W., Borlace, S., Lengaigne, M., van Rensch, P., Collins, M., Vecchi, G., ... Jin, F.-F. (2014). Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change*, *4*, 111–116.
- Calabrese, J. M., & Fagan, W. F. (2004). A Comparison-Shopper's Guide to Connectivity Metrics. *Ecological Applications: A Publication of the Ecological Society of America*, *2*, 529–536.
- Campbell, L., Liu, H., Nolla, H. A., & Vaulot, D. (1997). Annual variability of phytoplankton and bacteria in the subtropical North Pacific Ocean at Station ALOHA during the 1991–1994 ENSO event. *Deep Sea Research Part I: Oceanographic Research Papers*, *44*, 167–192.
- Cane, M. A. (1983). Oceanographic events during El Niño. *Science*, *222*, 1189–1195.
- Cane, M. A. (1986). El Niño. *Annual Review of Earth and Planetary Sciences*, *14*, 43–70.
- Capotondi, A., Wittenberg, A. T., Newman, M., Lorenzo, E. D., Yu, J.-Y., Braconnot, P., ... Yeh, S.-W. (2015). Understanding ENSO Diversity. *Bulletin of the American Meteorological Society*, *96*, 921–938.
- Carson, H. S., López-Duarte, P. C., Rasmussen, L., Wang, D., & Levin, L. A. (2010). Reproductive timing alters population connectivity in marine metapopulations. *Current Biology: CB*, *20*, 1926–1931.
- Cesar, H., Burke, L., & Pet-Soede, L. (2003). The economics of worldwide coral reef degradation. Retrieved from <http://agris.fao.org/agris-search/search.do?recordID=GB2013202743>
- Chassignet, E., Hurlburt, H., Metzger, E. J., Smedstad, O., Cummings, J., Halliwell, G., ... Wilkin, J. (2009). US GODAE: Global Ocean Prediction with the HYbrid Coordinate Ocean Model (HYCOM). *Oceanography*, *22*, 64–75.
- Chavanne, C., Flament, P., Lumpkin, R., Dousset, B., & Bentamy, A. (2002). Scatterometer observations of wind variations induced by oceanic islands: Implications for wind-driven ocean circulation. *Canadian Journal of Remote Sensing*, *28*, 466–474.
- Cheal, A. J., Delean, S., Sweatman, H., & Thompson, A. A. (2007). Spatial synchrony in coral reef fish populations and the influence of climate. *Ecology*, *88*, 158–169.
- Christie, M. R., Tissot, B. N., Albins, M. A., Beets, J. P., Jia, Y., Ortiz, D. M., ... Hixon, M. A. (2010). Larval connectivity in an effective network of marine protected areas. *PloS One*, *5*, e15715.
- Christie, P., Fluharty, D. L., White, A. T., Eisma-Osorio, L., & Jatulan, W. (2007). Assessing the feasibility of ecosystem-based fisheries management in tropical contexts. *Marine Policy*, *31*, 239–250.
- Chu, P. S. (1995). Hawaii rainfall anomalies and El Niño. *Journal of Climate*, *8*, 1697–1703.

- Chu, P. S., & Wang, J. (1997). Tropical Cyclone Occurrences in the Vicinity of Hawaii: Are the Differences between El Niño and Non-El Niño Years Significant? *Journal of Climate*, *10*, 2683-2689.
- Clague, D. A., & Dalrymple, G. B. (1987). The Hawaiian-Emperor volcanic chain. Part I. Geologic evolution. *Volcanism in Hawaii*, *1*, 5-54.
- Claisse, J. T., Kienzle, M., Bushnell, M. E., Shafer, D. J., & Parrish, J. D. (2009a). Habitat- and sex-specific life history patterns of yellow tang *Zebrasoma flavescens* in Hawaii, USA. *Marine Ecology Progress Series*, *389*, 245-255.
- Claisse, J. T., McTee, S. A., & Parrish, J. D. (2009b). Effects of age, size, and density on natural survival for an important coral reef fishery species, yellow tang, *Zebrasoma flavescens*. *Coral Reefs*, *28*, 95-105.
- Clarke, T. A. (1983). Comparison of abundance estimates of small fishes by three towed nets and preliminary results of the use of small purse seines as sampling devices. *Biological Oceanography*, *2*, 311-340.
- Clarke, T. A. (1991). *Larvae of nearshore fishes in oceanic waters near Oahu, Hawaii*. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.
- Collins, M., An, S.-I., Cai, W., Ganachaud, A., Guilyardi, E., Jin, F.-F. F., ... Wittenberg, A. (2010). The impact of global warming on the tropical Pacific Ocean and El Niño. *Nature Geoscience*, *3*, 391-397.
- Concepcion, G. T., Baums, I. B., & Toonen, R. J. (2014). Regional population structure of *Montipora capitata* across the Hawaiian Archipelago. *Bulletin of Marine Science*, *90*, 257-275.
- Cooley, S. R., Kite-Powell, H. L., & Doney, S. C. (2009). Ocean Acidification's Potential to Alter Global Marine Ecosystem Services. *Oceanography*, *22*, 172-181.
- Cowen, R. K., Gawarkiewicz, G., Pineda, J., Thorrold, S. R., & Werner, F. E. (2007). Population Connectivity in Marine Systems An Overview. *Oceanography*, *20*, 14-21.
- Cowen, R. K., Lwiza, K. M. M., Sponaugle, S., Paris, C. B., & Olson, D. B. (2000). Connectivity of marine populations: open or closed? *Science*, *287*, 857-859.
- Cowen, R. K., Paris, C. B., Olson, D. B., & Fortuna, J. L. (2015). The role of long distance dispersal versus local retention in replenishing marine populations. *Gulf and Caribbean Research*, *14*, 129-137.
- Cowen, R. K., Paris, C. B., & Srinivasan, A. (2006). Scaling of Connectivity in Marine Populations. *Science*, *311*, 522-527.
- Cowen, R. K., & Sponaugle, S. (2009). Larval Dispersal and Marine Population Connectivity. *Annual Review of Marine Science*, *1*, 443-466.
- Crandall, E. D., Treml, E. A., & Barber, P. H. (2012). Coalescent and biophysical models of stepping-stone gene flow in neritid snails. *Molecular Ecology*, *21*, 5579-5598.

- DeMartini, E. E., Wren, J. L. K., & Kobayashi, D. R. (2013). Persistent spatial patterns of recruitment in a guild of Hawaiian coral reef fishes. *Marine Ecology Progress Series*, *485*, 165–179.
- Donahue, M. J., Karnauskas, M., Toews, C., & Paris, C. B. (2015). Location Isn't Everything: Timing of Spawning Aggregations Optimizes Larval Replenishment. *PloS One*, *10*, e0130694.
- Drake, P. T., Edwards, C. A., & Barth, J. A. (2011). Dispersion and connectivity estimates along the U.S. west coast from a realistic numerical model. *Journal of Marine Research*, *69*, 1–37.
- Drake, P. T., Edwards, C. A., Morgan, S. G., & Dever, E. P. (2013). Influence of larval behavior on transport and population connectivity in a realistic simulation of the California Current System. *Journal of Marine Research*, *71*, 317–350.
- Drazen, J. C., De Forest, L. G., & Domokos, R. (2011). Micronekton abundance and biomass in Hawaiian waters as influenced by seamounts, eddies, and the moon. *Deep-Sea Research. Part I, Oceanographic Research Papers*, *58*, 557–566.
- Eble, J. A., Toonen, R. J., & Bowen, B. W. (2009). Endemism and dispersal: comparative phylogeography of three surgeonfishes across the Hawaiian Archipelago. *Marine Biology*, *156*, 689–698.
- Eble, J. A., Toonen, R. J., Sorenson, L., Basch, L. V., Papastamatiou, Y. P., & Bowen, B. W. (2011). Escaping paradise: larval export from Hawaii in an Indo-Pacific reef fish, the yellow tang *Zebrasoma flavescens*. *Marine Ecology Progress Series*, *428*, 245–258.
- FAO. (2014). *The State of World Fisheries and Aquaculture (SOFIA)*. Rome: Food and agriculture organization of the United Nations.
- Flament, P., Kennan, S., Lumpkin, R., Sawyer, M., & Stroup, E. D. (1996). *Ocean atlas of Hawai'i: regional processes*. University of Hawaii.
- Fogarty, M. J., & Botsford, L. W. (2007). Population connectivity and spatial management of marine fisheries. *Oceanography*, *20*, 112–123.
- Foley, M. M., Halpern, B. S., Micheli, F., Armsby, M. H., Caldwell, M. R., Crain, C. M., ... Emmett Duffy, J. (2010). Guiding ecological principles for marine spatial planning. *Marine Policy*, *34*, 955–966.
- Fox, H. E., Haisfield, K. M., Brown, M. S., Stevenson, T. C., Tissot, B. N., Walsh, W. J., & Williams, I. D. (2012). Influences of oceanographic and meteorological features on reef fish recruitment in Hawai'i. *Marine Ecology Progress Series*, *463*, 259–272.
- Franklin, E. C., Jokieli, P. L., & Donahue, M. J. (2013). Predictive modeling of coral distribution and abundance in the Hawaiian Islands. *Marine Ecology Progress Series*, *481*, 121–132.
- Friedlander, A., Kobayashi, D. R., Bowen, B. W., Meyers, C., Papastamatiou, Y. P., DeMartini, E. E., ... Hilting, A. (2009). Connectivity and integrated ecosystem studies. In A. M. Friedlander, K. Keller, L. Wedding, A. Clarke, & M. Monaco (Eds.), *A Marine Biogeographic Assessment of the Northwestern Hawaiian Islands*. NOAA Technical Memorandum NOS NCCOS 84. (pp. 291–330). Silver Spring, MD: Prepared by NCCOS's Biogeography Branch in cooperation with the Office of National Marine Sanctuaries Papahānaumokuākea Marine National Monument.

- Friedlander, A. M., & DeMartini, E. E. (2002). Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian Islands: the effects of fishing down apex predators. *Marine Ecology Progress Series*, 230, e264.
- Friedlander, A. M., Keller, K., Wedding, L., Clarke, A., & Monaco, M. (Eds.). (2009). *A marine biogeographic assessment of the Northwestern Hawaiian Islands*. NOAA Technical Memorandum NOS NCCOS 84 (p. 363). Silver Springs, MD: NCCOS's Biogeography Branch in cooperation with the Office of National Marine Sanctuaries Papahānaumokuākea Marine National Monument. Retrieved from <https://coastalscience.noaa.gov/datasets/e98/docs/nwhi-2009.pdf>
- Gaines, S. D., White, C., Carr, M. H., & Palumbi, S. R. (2010). Designing marine reserve networks for both conservation and fisheries management. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 18286–18293.
- Gerber, L. R., Beger, M., McCarthy, M. A., & Possingham, H. P. (2005). A theory for optimal monitoring of marine reserves. *Ecology Letters*, 8, 829–837.
- Glynn, P. W., Maté, J. L., & Baker, A. C. (2001). Coral bleaching and mortality in Panama and Ecuador during the 1997–1998 El Niño–Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982–1983 event. *Bulletin of Marine Science*.
- Grigg, R. (1981). Acropora in Hawaii. Zoogeography. *Pacific Science*, 35, 15–24.
- Halpern, B. S., Lester, S. E., & Kellner, J. B. (2009). Spillover from marine reserves and the replenishment of fished stocks. *Environmental Conservation*, 36, 268–276.
- Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., ... Watson, R. (2008). A global map of human impact on marine ecosystems. *Science*, 319, 948–952.
- Harrison, C. S., Siegel, D. A., & Mitarai, S. (2013). Filamentation and eddy–eddy interactions in marine larval accumulation and transport. *Marine Ecology Progress Series*, 472, 27–44.
- Hastings, A., & Botsford, L. W. (2006). Persistence of spatial populations depends on returning home. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 6067–6072.
- Hellberg, M. E. (2009). Gene Flow and Isolation among Populations of Marine Animals. *Annual Review of Ecology, Evolution, and Systematics*, 40, 291–310.
- Hijmans, R. J. (2015). geosphere: Spherical Trigonometry (Version R package version 1.3-13). Retrieved from <http://cran.r-project.org/package=geosphere>
- Hilborn, R. (2011). Future directions in ecosystem based fisheries management: A personal perspective. *Fisheries Research*, 108, 235–239.
- Hoegh-Guldberg, O. (2011). Coral reef ecosystems and anthropogenic climate change. *Regional Environmental Change*, 11, 215–227.

- Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., ... Hatziolos, M. E. (2007). Coral reefs under rapid climate change and ocean acidification. *Science*, *318*, 1737–1742.
- Holstein, D. M., Paris, C. B., & Mumby, P. J. (2014). Consistency and inconsistency in multispecies population network dynamics of coral reef ecosystems. *Marine Ecology Progress Series*, *499*, 1–18.
- Hourigan, T. F., & Reese, E. S. (1987). Mid-ocean isolation and the evolution of Hawaiian reef fishes. *Trends in Ecology & Evolution*, *2*, 187–191.
- Huebert, K. B., & Sponaugle, S. (2009). Observed and simulated swimming trajectories of late-stage coral reef fish larvae off the Florida Keys. *Aquatic Biology*, *7*, 207–216.
- Hughes, T. P. (1990). Recruitment limitation, mortality, and population regulation in open systems: a case study. *Ecology*, *71*, 12–20.
- Hughes, T. P., Baird, A. H., Bellwood, D. R., Card, M., Connolly, S. R., Folke, C., ... Roughgarden, J. (2003). Climate Change, Human Impacts, and the Resilience of Coral Reefs. *Science*, *301*, 929–933.
- Jia, Y., Calil, P. H. R., Chassignet, E. P., Metzger, E. J., Potemra, J. T., Richards, K. J., & Wallcraft, A. J. (2011). Generation of mesoscale eddies in the lee of the Hawaiian Islands. *Journal of Geophysical Research*, *116*, C11009.
- Jokiel, P. L., & Brown, E. K. (2004). Global warming, regional trends and inshore environmental conditions influence coral bleaching in Hawaii. *Global Change Biology*, *10*, 1627–1641.
- Jokiel, P. L., Brown, E. K., Friedlander, A., Ku'ulei Rodgers, S., & Smith, W. R. (2004). Hawai'i Coral Reef Assessment and Monitoring Program: Spatial Patterns and Temporal Dynamics in Reef Coral Communities. *Pacific Science*, *58*, 159–174.
- Jones, G. P., Almany, G. R., Russ, G. R., Sale, P. F., Steneck, R. S., Van Oppen, M. J. H., & Willis, B. L. (2009). Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs*, *28*, 307–325.
- Jones, G. P., Planes, S., & Thorrold, S. R. (2005). Coral reef fish larvae settle close to home. *Current Biology: CB*, *15*, 1314–1318.
- Jones, G. P., Srinivasan, M., & Almany, G. R. (2007). Population Connectivity and Conservation of Marine Biodiversity. *Oceanography*, *20*, 100–111.
- Kappel, C. V., Martone, R. G., & Duffy, J. E. (2006). Ecosystem-based management. *Encyclopedia of Earth*. Edited by CJ Cleveland. Environmental Information Coalition, National Council for Science and the Environment, Washington, DC, 1–4.
- Karl, D. M., Christian, J. R., Dore, J. E., Hebel, D. V., Letelier, R. M., Tupas, L. M., & Winn, C. D. (1996). Seasonal and interannual variability in primary production and particle flux at Station ALOHA. *Deep-Sea Research. Part II, Topical Studies in Oceanography*, *43*, 539–568.

- Kay, E. A., & Palumbi, S. R. (1987). Endemism and evolution in Hawaiian marine invertebrates. *Trends in Ecology & Evolution*, 2, 183–186.
- Kittinger, J. N., Dowling, A., Purves, A. R., Milne, N. A., & Olsson, P. (2011). Marine Protected Areas, Multiple-Agency Management, and Monumental Surprise in the Northwestern Hawaiian Islands. *Journal of Marine Biology*, 2011.
- Knight-Jones, E. W. (1953). Laboratory experiments on gregariousness during setting in *Balanus balanoides* and other barnacles. *The Journal of Experimental Biology*, 30, 584–598.
- Knowlton, N., & Jackson, J. B. C. (2008). Shifting baselines, local impacts, and global change on coral reefs. *PLoS Biology*, 6, e54.
- Kobayashi, D. R. (2006). Colonization of the Hawaiian Archipelago via Johnston Atoll: a characterization of oceanographic transport corridors for pelagic larvae using computer simulation. *Coral Reefs*, 25, 407–417.
- Kobayashi, D. R., & Polovina, J. J. (2006). Simulated seasonal and interannual variability in larval transport and oceanography in the Northwestern Hawaiian Islands using satellite remotely sensed data and computer modeling. *Atoll Research Bulletin*, 543, 365–390.
- Kool, J. T., Huang, Z., & Nichol, S. L. (2015). Simulated larval connectivity among Australia's southwest submarine canyons. *Marine Ecology Progress Series*, 539, 77–91.
- Kool, J. T., Moilanen, A., & Treml, E. A. (2012). Population connectivity: recent advances and new perspectives. *Landscape Ecology*, 28, 165–185.
- Kosaki, R. K., Pyle, R. L., Randall, J. E., & Irons, D. K. (1991). New records of fishes from Johnston Atoll, with notes on biogeography. *Pacific Science*, 45, 186–203.
- Kough, A. S., Paris, C. B., & Butler, M. J., IV. (2013). Larval Connectivity and the International Management of Fisheries. *PLoS One*, 8, e64970.
- Kritzer, J. P., & Sale, P. F. (2004). Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. *Fish and Fisheries*, 5, 131–140.
- Krupp, D. A. (1983). Sexual reproduction and early development of the solitary coral *Fungia scutaria* (Anthozoa: Scleractinia). *Coral Reefs*, 2, 159–164.
- Leis, J. M. (1982). Nearshore distributional gradients of larval fish (15 taxa) and planktonic crustaceans (6 taxa) in Hawai'i. *Marine Biology*, 72, 89–97.
- Leis, J. M. (2007). Behaviour as input for modelling dispersal of fish larvae: Behaviour, biogeography, hydrodynamics, ontogeny, physiology and phylogeny meet hydrography. *Marine Ecology Progress Series*, 347, 185–193.
- Leis, J. M., & Carson-Ewart, B. M. (2000). Behaviour of pelagic larvae of four coral-reef fish species in the ocean and an atoll lagoon. *Coral Reefs*, 19, 247–257.

- Leis, J. M., Caselle, J. E., Bradbury, I. R., Kristiansen, T., Llopiz, J. K., Miller, M. J., ... Warner, R. R. (2013). Does fish larval dispersal differ between high and low latitudes? *Proceedings of the Royal Society of London: Biological Sciences*, *280*, 20130327.
- Leis, J. M., Herwerden, L. V., & Patterson, H. M. (2011). Estimating Connectivity in Marine Fish Populations: What Works Best? *Oceanography and Marine Biology: An Annual Review*, *49*, 193–234.
- Leis, J. M., & Miller, J. M. (1976). Offshore distributional patterns of Hawaiian fish larvae. *Marine Biology*, *36*, 359–367.
- Leis, J. M., Paris, C. B., Irisson, J.-O., Yerman, M. N., & Siebeck, U. E. (2014). Orientation of fish larvae in situ is consistent among locations, years and methods, but varies with time of day. *Marine Ecology Progress Series*, *505*, 193–208.
- Lester, S. E., Costello, C., Halpern, B. S., Gaines, S. D., White, C., & Barth, J. A. (2013). Evaluating tradeoffs among ecosystem services to inform marine spatial planning. *Marine Policy*, *38*, 80–89.
- Lester, S. E., Tobin, E. D., & Behrens, M. D. (2007). Disease dynamics and the potential role of thermal stress in the sea urchin, i. *Canadian Journal of Fisheries and Aquatic Sciences. Journal Canadien Des Sciences Halieutiques et Aquatiques*, *64*, 314–323.
- Lett, C., Ayata, S.-D., Huret, M., & Irisson, J.-O. (2010). Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. *Progress in Oceanography*, *87*, 106–113.
- Levin, L. a. (2006). Recent progress in understanding larval dispersal: New directions and digressions. *Integrative and Comparative Biology*, *46*, 282–297.
- Liggins, L., Tremblay, E. A., Possingham, H. P., & Riginos, C. (2015). Seascape features, rather than dispersal traits, predict spatial genetic patterns in co-distributed reef fishes. *Journal of Biogeography*, *43*, 256–267.
- Lipcius, R. N., Eggleston, D. B., Schreiber, S. J., Seitz, R. D., Shen, J., Sisson, M., ... Wang, H. V. (2008). Importance of Metapopulation Connectivity to Restocking and Restoration of Marine Species. *Reviews in Fisheries Science*, *16*, 101–110.
- Lobel, P. S. (1989). Ocean current variability and the spawning season of Hawaiian reef fishes. *Environmental Biology of Fishes*, *24*, 161–171.
- Lobel, P. S. (2011). Transport of reef lizardfish larvae by an ocean eddy in Hawaiian waters. *Dynamics of Atmospheres and Oceans*, *52*, 119–130.
- Lobel, P. S., & Robinson, A. R. (1983). Reef fishes at sea: ocean currents and the advection of larvae (Vol. 1, pp. 29–38).
- Lobel, P. S., & Robinson, A. R. (1986). Transport and entrapment of fish larvae by ocean mesoscale eddies and currents in Hawaiian waters. *Deep-Sea Research. Part A, Oceanographic Research Papers*, *33*, 483–500.

- Lobel, P. S., & Robinson, A. R. (1988). Larval fishes and zooplankton in a cyclonic eddy in Hawaiian waters. *Journal of Plankton Research*, *10*, 1209.
- López-Duarte, P. C., Carson, H. S., Cook, G. S., Fodrie, F. J., Becker, B. J., Dibacco, C., & Levin, L. a. (2012). What controls connectivity? An empirical, multi-species approach. *Integrative and Comparative Biology*, *52*, 511–524.
- Lo-Yat, A., Simpson, S. D., Meekan, M., Lecchini, D., Martinez, E., & Galzin, R. (2011). Extreme climatic events reduce ocean productivity and larval supply in a tropical reef ecosystem. *Global Change Biology*, *17*, 1695–1702.
- Lumpkin, C. F. (1998). *Eddies and currents of the Hawaiian Islands*. University of Hawaii.
- Maragos, J. E., & Jokiell, P. L. (1986). Reef corals of Johnston Atoll: one of the world's most isolated reefs. *Coral Reefs*, *4*, 141–150.
- Marshall, D. J., Krug, P. J., Kupriyanova, E. K., Byrne, M., & Emlen, R. B. (2012). The biogeography of marine invertebrate life histories. *Annual Review of Ecology, Evolution, and Systematics*, *43*, 97.
- Marshall, J., Adcroft, A., Hill, C., Perelman, L., & Heisey, C. (1997). A finite-volume, incompressible Navier Stokes model for studies of the ocean on parallel computers. *Journal of Geophysical Research, C: Oceans*, *102*, 5753–5766.
- Maximenko, N. A., Bang, B., & Sasaki, H. (2005). Observational evidence of alternating zonal jets in the world ocean. *Geophysical Research Letters*, *32*, L12607.
- McLeod, K. L., & Leslie, H. M. (2009). *Ecosystem-based management for the oceans*. (K. L. McLeod & H. M. Leslie, Eds.) (Vol. 3, pp. 6–7). Washington D. C.: Island Press, Washington, DC, USA.
- Meekan, M. G., Carleton, J. H., McKinnon, A. D., Flynn, K., Furnas, M., & Others. (2003). What determines the growth of tropical reef fish larvae in the plankton: food or temperature? *Marine Ecology Progress Series*, *256*, 193–204.
- Metaxas, A., & Saunders, M. (2009). Quantifying the “Bio-” components in biophysical models of larval transport in marine benthic invertebrates: advances and pitfalls. *The Biological Bulletin*, *216*, 257–272.
- Methot, R. D. (1990). Synthesis model: An adaptable framework for analysis of diverse stock assessment data. INPFC Bull. 50: 259-277. In *Symposium on application of stock assessment techniques to Gadoids*.
- Meyer, C. G., Holland, K. N., Wetherbee, B. M., & Lowe, C. G. (2000). Movement patterns, habitat utilization, home range size and site fidelity of whitesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve. *Environmental Biology of Fishes*, *59*, 235–242.
- Meyer, C. G., Papastamatiou, Y. P., & Clark, T. B. (2010). Differential movement patterns and site fidelity among trophic groups of reef fishes in a Hawaiian marine protected area. *Marine Biology*, *157*, 1499–1511.



- Mitarai, S., Siegel, D. a., & Winters, K. B. (2008). A numerical study of stochastic larval settlement in the California Current system. *Journal of Marine Systems*, *69*, 295–309.
- Mitarai, S., Watanabe, H., Nakajima, Y., Shchepetkin, A. F., & McWilliams, J. C. (2016). Quantifying dispersal from hydrothermal vent fields in the western Pacific Ocean. *Proceedings of the National Academy of Sciences of the United States of America*. doi:10.1073/pnas.1518395113
- Mora, C., & Sale, P. F. (2002). Are populations of coral reef fish open or closed? *Trends in Ecology & Evolution*, *17*, 422–428.
- Mora, C., Treml, E. A., Roberts, J. J., Crosby, K., Roy, D., & Tittensor, D. P. (2012). High connectivity among habitats precludes the relationship between dispersal and range size in tropical reef fishes. *Ecography*, *35*, 89–96.
- Morgan, S. G. (2014). Behaviorally Mediated Larval Transport in Upwelling Systems. *Advances in Oceanography*, *2014*. doi:10.1155/2014/364214
- Muhling, B. A., & Beckley, L. E. (2007). Seasonal variation in horizontal and vertical structure of larval fish assemblages off south-western Australia, with implications for larval transport. *Journal of Plankton Research*, *29*, 967–983.
- Munday, P. L., Leis, J. M., Lough, J. M., Paris, C. B., Kingsford, M. J., Berumen, M. L., & Lambrechts, J. (2009). Climate change and coral reef connectivity. *Coral Reefs*, *28*, 379–395.
- Mundy, B. C. (2005). *Checklist of the fishes of the Hawaiian Archipelago* (Vol. 6). Bishop Museum Press.
- Murray-Smith, D. J. (2000). The inverse simulation approach: a focused review of methods and applications. *Mathematics and Computers in Simulation*, *53*, 239–247.
- National Weather Service Climate Prediction Center. (2016). Oceanic Nino Index (ONI). Retrieved from [http://www.cpc.ncep.noaa.gov/products/analysis\\_monitoring/ensostuff/ensoyears.shtml](http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml)
- Neuheimer, A. B., & Taggart, C. T. (2007). The growing degree-day and fish size-at-age: the overlooked metric. *Canadian Journal of Fisheries and Aquatic Sciences. Journal Canadien Des Sciences Halieutiques et Aquatiques*, *64*, 375–385.
- North, E. W., Schlag, Z., Hood, R. R., Li, M., Zhong, L., Gross, T., & Kennedy, V. S. S. (2008). Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. *Marine Ecology Progress Series*, *359*, 99–115.
- O'Connor, M. I., Bruno, J. F., Gaines, S. D., Halpern, B. S., Lester, S. E., Kinlan, B. P., & Weiss, J. M. (2007). Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 1266–1271.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., ... Wagner, H. (2015). *vegan: Community Ecology Package*. Retrieved from <https://cran.r-project.org/package=vegan>

- Olivar, M. P., & Sabate, A. (1997). Vertical distribution of fish larvae in the north-west Mediterranean Sea in spring. *Marine Biology*, *129*, 289–300.
- Padilla-Gamiño, J. L., & Gates, R. D. (2012). Spawning dynamics in the Hawaiian reef-building coral *Montipora capitata*. *Marine Ecology Progress Series*, *229*, 145–160.
- Paris, C. B., Atema, J., Irisson, J.-O., Kingsford, M., Gerlach, G., & Guigand, C. M. (2013). Reef odor: a wake up call for navigation in reef fish larvae. *PLoS One*, *8*, e72808.
- Patzert, W. C. (1969). *Eddies in Hawaiian waters*. DTIC Document.
- Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., ... Sainsbury, K. J. (2004). Ecosystem-Based Fishery Management. *Science*, *305*, 346–347.
- Pineda, J. S., Hare, J. A., & Sponaugle, S. (2007). Larval Transport and Dispersal in the Coastal Ocean and Consequences for Population Connectivity. *Oceanography*, *20*, 22–39.
- Pogson, G. H., Taggart, C. T., Mesa, K. A., & Boutilier, R. G. (2001). Isolation by distance in the Atlantic cod, *Gadus morhua*, at large and small geographic scales. *Evolution; International Journal of Organic Evolution*, *55*, 131–146.
- Polato, N. R., Concepcion, G. T., & Toonen, R. J. (2010). Isolation by distance across the Hawaiian Archipelago in the reef-building coral *Porites lobata*. *Molecular*, *19*, 4661–4677.
- Polovina, J. J., Kleiber, P., & Kobayashi, D. R. (1999). Application of TOPEX-POSEIDON satellite altimetry to simulate transport dynamics of larvae of spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands, 1993-1996. *Fishery Bulletin*, *97*, 132–143.
- Puritz, J. B., & Toonen, R. J. (2011). Coastal pollution limits pelagic larval dispersal. *Nature Communications*, *2*, 226.
- Putman, N. F., & He, R. (2013). Tracking the long-distance dispersal of marine organisms: sensitivity to ocean model resolution. *Journal of the Royal Society, Interface / the Royal Society*, *10*, 20120979.
- Qiu, B., & Durland, T. S. (2002). Interaction between an Island and the Ventilated Thermocline: Implications for the Hawaiian Lee Countercurrent. *Journal of Physical Oceanography*, *32*, 3408–3426.
- Qiu, B., Koh, D. A., Lumpkin, C., & Flament, P. (1997). Existence and formation mechanism of the North Hawaiian Ridge Current. *Journal of Physical Oceanography*, *27*, 431–444.
- Raff, R. A. (2008). Origins of the other metazoan body plans: the evolution of larval forms. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *363*, 1473–1479.
- Randall, J. E. (2007). *Reef and shore fishes of the Hawaiian Islands* (Vol. 1, p. 546). University of Hawaii Sea Grant College Program.
- Rasmuson, L. K., & Shanks, A. L. (2014). In situ observations of Dungeness crab megalopae used to estimate transport distances by internal waves. *Marine Ecology Progress Series*, *511*, 143–152.

- R Core Team. (2012). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.r-project.org/>
- Richmond, R. H., & Hunter, C. L. (1990). Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. *Marine Ecology Progress Series*, *60*, 185–203.
- Riginos, C., Douglas, K. E., Jin, Y., Shanahan, D. F., & Tremblay, E. A. (2011). Effects of geography and life history traits on genetic differentiation in benthic marine fishes. *Ecography*, *34*, 566–575.
- Riginos, C., & Liggins, L. (2013). Seascape Genetics: Populations, Individuals, and Genes Marooned and Adrift. *Geography Compass*, *7*, 197–216.
- Rivera, M. A. J., Andrews, K. R., Kobayashi, D. R., Wren, J. L. K., Kelley, C., Roderick, G. K., & Toonen, R. J. (2011). Genetic Analyses and Simulations of Larval Dispersal Reveal Distinct Populations and Directional Connectivity across the Range of the Hawaiian Grouper (*Epinephelus quernus*). *Journal of Marine Biology*, *2011*, 1–11.
- Robins, P. E., Neill, S. P., Giménez, L., Jenkins, S. R., & Malham, S. K. (2013). Physical and biological controls on larval dispersal and connectivity in a highly energetic shelf sea. *Limnology and Oceanography*, *58*, 505–524.
- Rosa, R., Pimentel, M. S., Boavida-Portugal, J., Teixeira, T., Trübenbach, K., & Diniz, M. (2012). Ocean warming enhances malformations, premature hatching, metabolic suppression and oxidative stress in the early life stages of a keystone squid. *PLoS One*, *7*, e38282.
- Roughgarden, J., Gaines, S., & Possingham, H. (1988). Recruitment dynamics in complex life cycles. *Science*, *241*, 1460–1466.
- Roughgarden, J., Iwasa, Y., & Baxter, C. (1985). Demographic theory for an open marine population with space-limited recruitment. *Ecology*, *66*, 54–67.
- Rousset, F. (1997). Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics*, *145*, 1219–1228.
- Ruttenberg, B. I. R. I., Hamilton, S. L. H. L., & Warner, R. R. W. R. (2008). Spatial and temporal variation in the natal otolith chemistry of a Hawaiian reef fish: prospects for measuring population connectivity. *Canadian Journal of Fisheries and Aquatic Sciences. Journal Canadien Des Sciences Halieutiques et Aquatiques*, *65*, 1181–1192.
- Sale, P. F. (1970). Distribution of larval Acanthuridae off Hawaii. *Copeia*, *1970*, 765–766.
- Sale, P. F. (1978). Coexistence of coral reef fishes—a lottery for living space. *Environmental Biology of Fishes*, *3*, 85–102.
- Sancho, G., Ma, D., & Lobel, P. S. (1997). Behavioral observations of an upcurrent reef colonization event by larval surgeonfish *Ctenochaetus strigosus* (Acanthuridae). *Marine Ecology Progress Series*, *153*, 311–315.

- Scheltema, R. S. (1971). Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *The Biological Bulletin*, *140*, 284–322.
- Seki, M. P., Lumpkin, R., & Flament, P. (2002). Hawaii cyclonic eddies and blue marlin catches: the case study of the 1995 Hawaiian International Billfish Tournament. *Journal of Oceanography*, *58*, 739–745.
- Seki, M. P., Polovina, J. J., Brainard, R. E., Bidigare, R. R., Leonard, C. L., & Foley, D. G. (2001). Biological enhancement at cyclonic eddies tracked with GOES Thermal Imagery in Hawaiian waters. *Geophysical Research Letters*, *28*, 1583–1586.
- Selkoe, K. A., D’Aloia, C. C., Crandall, E. D., Iacchei, M., Liggins, L., Puritz, J. B., ... Toonen, R. J. (2016b). A decade of seascape genetics: contributions to basic and applied marine connectivity. *Marine Ecology Progress Series*, *554*, 1–19.
- Selkoe, K. A., Gaggiotti, O. E., Bowen, B. W., Toonen, R. J., & ToBo Laboratory. (2014). Emergent Patterns of Population Genetic Structure for a Coral Reef Community. *Molecular Ecology*, *23*, 3064–3079.
- Selkoe, K. A., Halpern, B. S., Ebert, C. M., Franklin, E. C., Selig, E. R., Casey, K. S., ... Toonen, R. J. (2009). A map of human impacts to a “pristine” coral reef ecosystem, the Papahānaumokuākea Marine National Monument. *Coral Reefs*, *28*, 635–650.
- Selkoe, K. A., & Toonen, R. J. (2011). Marine connectivity: a new look at pelagic larval duration and genetic metrics of dispersal. *Marine Ecology Progress Series*, *436*, 291–305.
- Selkoe, K. A., Watson, J. R., White, C., Horin, T. B., Iacchei, M., Mitarai, S., ... Toonen, R. J. (2010). Taking the chaos out of genetic patchiness: seascape genetics reveals ecological and oceanographic drivers of genetic patterns in three temperate reef species. *Molecular Ecology*, *19*, 3708–3726.
- Selkoe, K.A., Gaggiotti, O., Trembl, E., Wren, J., Donovan, M., Hawaii Reef Connectivity Consortium, & Toonen, R. (2016a). The DNA of coral reef biodiversity: predicting and protecting genetic diversity of reef assemblages. *Proceedings of the Royal Society of London B: Biological Sciences*, *283*.
- Shanks, A. L. (2009). Pelagic larval duration and dispersal distance revisited. *The Biological Bulletin*, *216*, 373–385.
- Sharp, G. D. (1995). It’s about time: new beginnings and old good ideas in fisheries science. *Fisheries Oceanography*, *4*, 324–341.
- Siegel, D. A., Kinlan, B. P., Gaylord, B., & Gaines, S. D. (2003). Lagrangian descriptions of marine larval dispersion. *Marine Ecology Progress Series*, *260*, 83–96.
- Siegel, D. A., Mitarai, S., Costello, C. J., Gaines, S. D., Kendall, B. E., Warner, R. R., & Winters, K. B. (2008). The stochastic nature of larval connectivity among nearshore marine populations. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 8974–8979.

- Skillings, D. J., Bird, C. E., & Toonen, R. J. (2011). Gateways to Hawai'i: genetic population structure of the tropical sea cucumber *Holothuria atra*. *Journal of Marine Biology*, 2011. doi:10.1155/2011/783030
- Slocombe, D. S. (1993). Implementing ecosystem-based management. *Bioscience*, 43, 612–622.
- Sponaugle, S., Paris, C. B., Walter, K. D., Kourafalou, V., & D'Alessandro, E. (2012). Observed and modeled larval settlement of a reef fish to the Florida Keys. *Marine Ecology Progress Series*, 453, 201–212.
- Staaterman, E., & Paris, C. B. (2014). Modelling larval fish navigation: the way forward. *ICES Journal of Marine Science: Journal Du Conseil*, 71, 918–924.
- Staaterman, E., Paris, C. B., & Helgers, J. (2012). Orientation behavior in fish larvae: a missing piece to Hjort's critical period hypothesis. *Journal of Theoretical Biology*, 304, 188–196.
- Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S., & Lima, M. (2002). Ecological effects of climate fluctuations. *Science*, 297, 1292–1296.
- Stimson, J. S. (1978). Mode and timing of reproduction in some common hermatypic corals of Hawaii and Enewetak. *Marine Biology*, 48, 173–184.
- Stone, L., Rajagopalan, B., Bhasin, H., & Loya, Y. (1999). Mass coral reef bleaching: A recent outcome of increased El Nino activity? *Ecology Letters*, 2, 325–330.
- Strathmann, R. R. (1993). Hypotheses on the Origins of Marine Larvae. *Annual Review of Ecology and Systematics*, 24, 89–117.
- Stumpp, M., Wren, J. L. K., Melzner, F., Thorndyke, M. C., & Dupont, S. T. (2011). CO<sub>2</sub> induced seawater acidification impacts sea urchin larval development I: elevated metabolic rates decrease scope for growth and induce developmental delay. *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology*, 160, 331–340.
- Sundelöf, A., & Jonsson, P. R. (2012). Larval dispersal and vertical migration behaviour - a simulation study for short dispersal times. *Marine Ecology*, 33, 183–193.
- Swearer, S. E., Caselle, J. E., Lea, D. W., & Warner, R. R. (1999). Larval retention and recruitment in an island population of a coral-reef fish. *Nature*, 402, 799–802.
- Swearer, S. E., Shima, J. S., Hellberg, M. E., Thorrold, S. R., Jones, G. P., Robertson, D. R., ... Warner, R. R. (2002). Evidence of self-recruitment in demersal marine populations. *Bulletin of Marine Science*, 70, 251–271.
- Thorrold, S. R., Zacherl, D. C., & Levin, L. A. (2007). Population Connectivity and Larval Dispersal Using Geochemical Signatures in Calcified Structures. *Oceanography*, 20, 80–89.
- Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews of the Cambridge Philosophical Society*, 25, 1–45.

- Thresher, R. E., & Brothers, E. B. (1985). Reproductive Ecology and Biogeography of Indo-West Pacific Angelfishes (Pisces: Eomacanthidae). *Evolution; International Journal of Organic Evolution*.
- Timmers, M. A., Andrews, K. R., Bird, C. E., deMaintenton, M. J., Brainard, R. E., & Toonen, R. J. (2011). Widespread dispersal of the crown-of-thorns sea star, *Acanthaster planci*, across the Hawaiian Archipelago and Johnston Atoll. *Journal of Marine Biology*, 2011.
- Tissot, B. N., Walsh, W. J., & Hixon, M. A. (2009). Hawaiian Islands Marine Ecosystem Case Study: Ecosystem- and Community-Based Management in Hawaii. *Coastal Management: An International Journal of Marine Environment, Resources, Law, and Society*, 37, 255–273.
- Toonen, R. J., Andrews, K. R., Baums, I. B., Bird, C. E., Concepcion, G. T., Daly-Engel, T. S., ... Bowen, B. W. (2011). Defining boundaries for ecosystem-based management: a multispecies case study of marine connectivity across the Hawaiian Archipelago. *Journal of Marine Biology*, 2011, 1–13.
- Toonen, R. J., & Tyre, A. J. (2007). If larvae were smart: a simple model for optimal settlement behavior of competent larvae. *Marine Ecology Progress Series*, 349, 43–61.
- Toonen, R. J., Wilhelm, T. A., Maxwell, S. M., Wagner, D., Bowen, B. W., Sheppard, C. R. C., ... Friedlander, A. M. (2013). One size does not fit all: The emerging frontier in large-scale marine conservation. *Marine Pollution Bulletin*, 77, 7–10.
- Trembl, E. A., Ford, J. R., Black, K. P., & Swearer, S. E. (2015). Identifying the key biophysical drivers, connectivity outcomes, and metapopulation consequences of larval dispersal in the sea. *Movement Ecology*, 3, 17.
- Trembl, E. A., Halpin, P. N., Urban, D. L., & Pratson, L. F. (2008). Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. *Landscape Ecology*, 23, 19–36.
- Trembl, E. A., Roberts, J. J., Chao, Y., Halpin, P. N., Possingham, H. P., & Riginos, C. (2012). Reproductive output and duration of the pelagic larval stage determine seascape-wide connectivity of marine populations. *Integrative and Comparative Biology*, 52, 525–537.
- Vaz, A. C. (2012). *Here today, gone tomorrow: flow variability, larval dispersal and fisheries management in Hawai'i*. University of Hawai'i at Mānoa.
- Vaz, A. C., Richards, K. J., Jia, Y., & Paris, C. B. (2013). Mesoscale flow variability and its impact on connectivity for the island of Hawai'i. *Geophysical Research Letters*, 40, 332–337.
- Victor, B. C., Wellington, G. M., & Robertson, D. R. (2001). The effect of the El Niño–Southern Oscillation event on the distribution of reef-associated labrid fishes in the eastern Pacific Ocean. *Bulletin of Marine Science*.
- Walsh, W. J. (1987). Patterns of recruitment and spawning in Hawaiian reef fishes. *Environmental Biology of Fishes*, 18, 257–276.
- Warner, R. R., Swearer, S. E., & Caselle, J. E. (2000). Larval accumulation and retention: implications for the design of marine reserves and essential habitat. *Bulletin of Marine Science*, 66, 821–830.

- Watson, R. A., Nowara, G. B., Hartmann, K., Green, B. S., Tracey, S. R., & Carter, C. G. (2015). Marine foods sourced from farther as their use of global ocean primary production increases. *Nature Communications*, *6*, 7365.
- Watson, W., & Leis, J. M. (1974). *Ichthyoplankton of Kaneohe Bay, Hawaii: A One-year Study of Fish Eggs and Larvae*. University of Hawaii.
- Weersing, K., & Toonen, R. J. (2009). Population genetics, larval dispersal, and connectivity in marine systems. *Marine Ecology Progress Series*, *393*, 1–12.
- Weiss, J., Miller, J., Hirsch, E., Rooney, J., Wedding, L., & Friedlander, A. (2009). Geology and Benthic Habitats. In *A Marine Biogeographic Assessment of the Northwestern Hawaiian Islands*. NOAA Technical Memorandum NOS NCCOS 84. (pp. 65–154). Silver Spring, MD: Prepared by NCCOS's Biogeography Branch in cooperation with the Office of National Marine Sanctuaries Papahānaumokuākea Marine National Monument.
- Wellington, G. M., Glynn, P. W., Strong, A. E., Nauarrete, S. A., Wieters, E., & Hubbard, D. (2001). Crisis on coral reefs linked to climate change. *Eos*, *82*.
- Werner, F. E., Cowen, R. K., & Paris, C. B. (2007). Coupled biological and physical models: present capabilities and necessary developments for future studies of population connectivity. *Oceanography*, *20*, 54–69.
- Werner, F. E., Quinlan, J. A., Lough, R. G., & Lynch, D. R. (2001). Spatially-explicit individual based modeling of marine populations: A review of the advances in the 1990s. *Sarsia*, *86*, 411–421.
- Wessel, P., & Smith, W. H. F. (1991). Free software helps map and display data. *Eos Trans. AGU*, *72*, 445–446.
- Wetherbee, B. M., Holland, K. N., Meyer, C. G., & Lowe, C. G. (2004). Use of a marine reserve in Kaneohe Bay, Hawaii by the Giant trevally, *Caranx ignobilis*. *Fisheries Research*, *67*, 253–263.
- White, C., Selkoe, K. A., Watson, J., Siegel, D. A., Zacherl, D. C., & Toonen, R. J. (2010). Ocean currents help explain population genetic structure. *Proceedings. Biological Sciences / The Royal Society*, *277*, 1685–1694.
- White, J. W., Schroeger, J., Drake, P. T., & Edwards, C. A. (2014). The Value of Larval Connectivity Information in the Static Optimization of Marine Reserve Design. *Conservation Letters*, *7*, 533–544.
- Wilkinson, C. (2008). *Status of coral reefs of the world: 2008*. Townsville, Australia: Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre.
- Wolanski, E., & Kingsford, M. J. (2014). Oceanographic and behavioural assumptions in models of the fate of coral and coral reef fish larvae. *Journal of the Royal Society, Interface / the Royal Society*, *11*, 20140209.
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society. Series B, Statistical Methodology*, *73*, 3–36.

- Wood, S., Paris, C. B., Ridgwell, A., & Hendy, E. J. (2014). Modelling dispersal and connectivity of broadcast spawning corals at the global scale. *Global Ecology and Biogeography: A Journal of Macroecology*, *23*, 1–11.
- Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., ... Watson, R. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, *314*, 787–790.
- Wren, J. L. K., & Kobayashi, D. R. (2016). Exploration of the “larval pool”: development and ground-truthing of a larval transport model off leeward Hawai‘i. *PeerJ*, *4*, e1636.
- Wren, J. L. K., Kobayashi, D. R., Jia, Y., & Toonen, R. J. (in revision). Modeled population connectivity across the Hawaiian Archipelago. *PloS One*.
- Wright, S. (1943). Isolation by Distance. *Genetics*, *28*, 114–138.
- Wyrtki, K. (1975). El Nino-the dynamic response of the equatorial Pacific ocean to atmospheric forcing. *Journal of Physical Oceanography*, *5*, 572–584.
- Xie, S.-P., Deser, C., Vecchi, G. A., Collins, M., Delworth, T. L., Hall, A., ... Watanabe, M. (2015). Towards predictive understanding of regional climate change. *Nature Climate Change*, *5*, 921–930.
- Yeh, S.-W., Kug, J.-S., Dewitte, B., Kwon, M.-H., Kirtman, B. P., & Jin, F.-F. (2009). El Niño in a changing climate. *Nature*, *461*, 511–514.
- Yu, J.-Y., Zou, Y., Kim, S. T., & Lee, T. (2012). The changing impact of El Niño on US winter temperatures. *Geophysical Research Letters*, *39*, L15702.