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Climate-Modulated Volume Transport through the Coral Triangle and
its Impacts on Larval Connectivity

by

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ABSTRACT OF THE DISSERTATION

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Possessing complex bathymetry and regional circulation, the Coral Triangle (CT) is also the epicenter of marine biodiversity. Understanding regional circulation and the effects of intra-annual, seasonal and interannual processes on this circulation has important ramifications for larval transport, particularly in the context of changing climate. Using the Coral Triangle implementation of the Regional Ocean Modeling System (CT-ROMS), volume transport time series are assessed at 30 key passages throughout the region. Generally, seasonality seems to be the main modulator of volume transport along the South China Sea Throughflow (SCSTF), while the Indonesian Throughflow (ITF) volume transport is primarily influenced by interannual and secular changes in circulation. However, a ridge regression model which uses

El Niño Southern Oscillation (ENSO), Indian Ocean Dipole (IOD) and Pacific Decadal Oscillation (PDO) as explanatory variables is able to explain a significant portion of the volume transport through SCSTF passages.

Many oceanic species have larval stages which behave similarly to passive particles; being able to track these passive particles and understand where they might go under certain oceanic conditions provides us information that researchers cannot easily obtain *in situ*. TRACMASS trajectory model (TRACMASS), an offline particle tracking code, is used to track passive particles for 20, 40, 60, 80, and 100 days in order to assess decadal and interannual variability in particle retention, and the ability of particular ecoregions to function as particle sources and sinks along the South China Sea Returnflow (SCSRF) and the ITF. Due to the complexity in regional circulation, results are often localized to particular ecoregions. However, particle retention is generally higher during El Niño conditions along the SCSRF and during the 1980s along the ITF. Generally, our results highlight the need for networks of Marine Protected Areas (MPAs) and dynamic MPAs including temporary, migratory, zoned and gear-restricted MPAs. In order for any of these management strategies to be successful, the social and political challenges of a given location need to be considered, and representatives of

all stakeholder groups need to be included in management decisions.

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Acronyms

CORE-II Coordinated Ocean-ice Reference Experiments Phase II.

CT Coral Triangle.

CT-ROMS the Coral Triangle implementation of the Regional Ocean Modeling System.

CTI Coral Triangle Initiative.

DMI Dipole Mode Index.

ENSO El Niño Southern Oscillation.

EOF Empirical Orthogonal Function.

IBMs Individual-based models.

IOD Indian Ocean Dipole.

IS Indonesian seas.

ITF Indonesian Throughflow.

MERRA Modern Era-Retrospective Analysis for Research Applications.

MLR multiple linear regression.

MPAs Marine Protected Areas.

NEC North Equatorial Current.

ONI Oceanic Niño Index.

PDO Pacific Decadal Oscillation.

PDOI PDO index.

PLD pelagic larval duration.

PSDs power spectral densities.

ROMS Regional Ocean Modeling System.

SCS South China Sea.

SCSRF South China Sea Returnflow.

SCSTF South China Sea Throughflow.

SODA Simple Ocean Data Assimilation.

SSH sea surface height.

SSHa sea surface height anomalies.

SST sea surface temperature.

SSTa sea surface temperature anomalies.

Sv Sverdrups.

TRACMASS TRACMASS trajectory model.

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Chapter 1

Introduction

Many aquatic species, from fish (e.g. Riginos and Victor, 2001) to corals (e.g. Wood et al., 2014), bivalves (e.g. Fay et al., 1983) to crustaceans (e.g. Shanks, 2009) around the world possess pelagic larval stages. Understanding the influences of ocean currents on larval transport and distribution is vital to making sound management decisions to protect species of interest, both now and into the future. Connectivity, the idea that larvae from one place (a source) move under the influence of ocean currents (and potentially locomotion) and settle in another (a sink), can be impacted by many factors including the length of time the larvae are in the water column (pelagic larval duration, pelagic larval duration (PLD)), currents and eddies, larval swimming speeds, species reproductive method and periodicity, metabolic rates, energetic stores, presence of appropriate substrate for settlement, mortality rates, and

temperature regimes; all of these factors can have major impacts on larval transport, and, thus, connectivity. Understanding how these factors impact connectivity is vital to protecting sources and sinks that are integral to species survival, particularly in the context of changing climate. Here, we model passive particles with a variety of pelagic larval durations in order to encompass connectivities representative of a variety of species' pelagic larval life histories.

Larval transport is difficult to study *in situ*, as tracking particles is complicated at best for extended periods of time and is labor-intensive and expensive; furthermore, study areas may lack data describing the physical environment, due to underreporting and cloud cover, resulting in patchy satellite products. Laboratory studies of larvae experimentally determine biological parameters like swimming speed, metabolic stores, preferred settling substrate material, mortality rates, and preferred water temperatures (e.g. Hodgson, 1985; Harii et al., 2002; Cumbo et al., 2012). These values can then be used to inform biophysical models which can better predict larval connectivity. Here, we take the Regional Ocean Modeling System (ROMS) and couple it to the particle tracking code TRACMASS offline to create our biophysical model.

In contrast to *in situ* studies, biophysical modeling provides widespread regional coverage, allows millions of particles to be followed at once for as long as the researcher desires, and is efficient to run compared to labor-intensive *in situ* studies. While the number of “larvae” followed in these models is frequently much less than is released during a spawning event, the number of particles released in the model can still be sufficient to achieve significance in statistical analysis. Furthermore, biophysical models allow for simplifying assumptions to be made and for the influence of one variable (such as PLD) or a specific combination of variables (such as PLD and time of release) to be studied without the addition of confounding variables and stochastic processes inherent to the real world.

ROMS has been used for numerous modeling experiments worldwide, and the implementation used in the current study, CT-ROMS, was previously validated in Castruccio et al. (2013). ROMS solves the hydrostatic primitive equations and has a terrain-following vertical coordinate system and free surface; model variables are calculated on a Arakawa C-grid, using finite-difference numerical methods (see Shchepetkin and McWilliams, 2003). ROMS is forced by Coordinated

Ocean-ice Reference Experiments Phase II (CORE-II), is provided open boundary conditions by the Simple Ocean Data Assimilation (SODA) and the Modern Era-Retrospective Analysis for Research Applications (MERRA), and uses an interpolated product from 30-second resolution SRTM30_PLUS bathymetric data for its bathymetry (Large and Yeager, 2009; Carton et al., 2000; Marchesiello et al., 2001; Rienecker et al., 2011). CT-ROMS has a 5 km by 6 km horizontal resolution, with the model domain covering 95°E to 170°E and 25°S to 25°N (Figure 1.1) and rotated approximately 14° clockwise from due East. TRACMASS is a Lagrangian particle tracking scheme which utilizes horizontal velocity fields from a regional circulation model, here CT-ROMS, to calculate particle trajectories offline. Differential equations relating velocity and function are solved by TRACMASS via linear interpolation of the velocity field in both time and space (Doos et al., 2013).

The model domain in the present study surrounds the Coral Triangle (CT, Figure 1, demarcated by orange line) which encompasses six main countries: Indonesia, Malaysia, Philippines, Timor Leste, Papua New Guinea, and the Solomon Islands. The South China Sea (SCS), Sulu, Celebes, Java, Banda, Arafura, and Timor Seas are also found within the model domain. In addition, the western equatorial Pacific is

an important confluence of major ocean currents including the North Equatorial Current (NEC) and Countercurrent, the South Equatorial Current and Countercurrent, the Mindinao and Halmahera Eddies, the New Guinea Coastal Current, the Kuroshio Current, the Indonesian Throughflow ITF and the South China Sea Throughflow SCSTF.

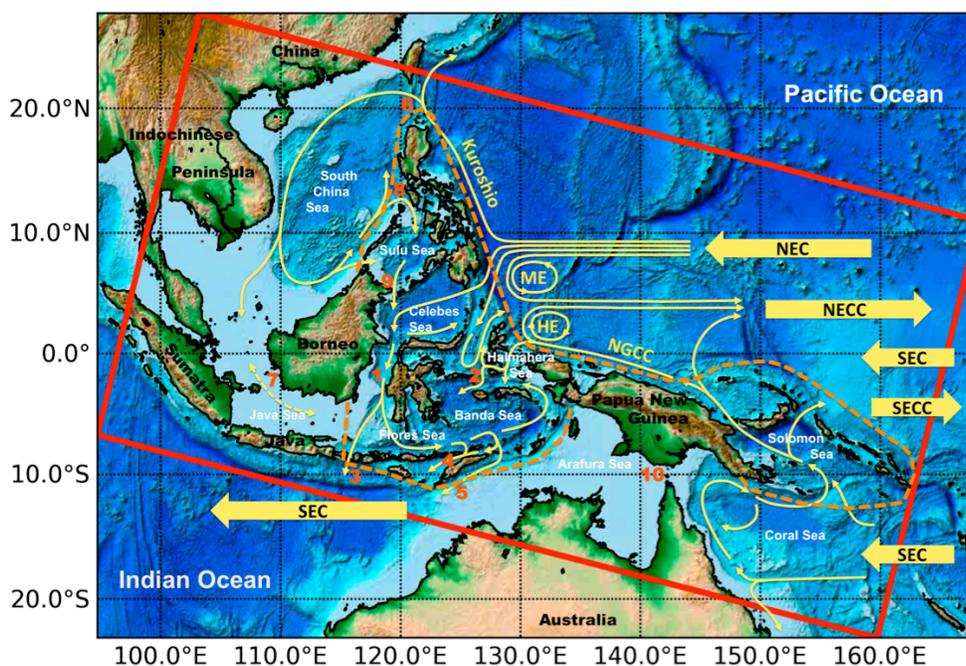


Figure 1.1: The Coral Triangle. The dotted orange line indicates the Coral Triangle region, while the solid red line indicates the model domain, from Castruccio et al., 2013.

In addition to the numerous currents which converge at and flow through the CT, atmospheric and oceanic phenomena including intra-annual monsoons (e.g., Gordon and Susanto, 1998), and interannual

processes such as El Niño Southern Oscillation (ENSO; e.g., Gordon et al., 2010), the Indian Ocean Dipole (IOD; e.g., Zhou et al., 2015), and the Pacific Decadal Oscillation (PDO; e.g., Wu, 2013) contribute to regional circulation. Previous work has shown that ENSO corresponds to interannual variability in sea surface temperature (SST) and sea surface height (SSH) anomalies within the CT, with cooling/warming and decreased/increased volume transport experienced during El Niño/La Niña conditions (Meyers, 1996; Gordon and Susanto, 1998; Sprintall et al., 2004; Susanto and Gordon, 2005). IOD events also lead to increased ITF transport, by generating an eastward pressure gradient due to an increased sea level in the eastern Indian Ocean (Yuan et al., 2011). Finally, positive phases of PDO shift the NEC bifurcation northward, weaken the Kuroshio current, and increase volume transport into the SCSTF, while negative PDO phases are characterized by a southward shift of the NEC bifurcation, and a strengthening of the NEC, North Equatorial Countercurrent, Kuroshio and Mindanao currents (Wu, 2013; Yu and Qu, 2013; Hu et al., 2015; Soumya et al., 2015).

Ecologically, the CT is of particular importance because it is the epicenter of biodiversity worldwide, home to 47 species of mangroves, 30%

of the world's coral reefs, and >2000 species of fish (Hoegh-Guldberg et al., 2009; Spalding et al., 2010; Allen, 2008). In addition, the CT provides food and jobs for millions of people around the world, while also providing nurseries for important commercial fisheries (Nagelkerken et al., 2000). And, the CT is economically relevant, with its marine ecosystems contributing approximately \$1.2 trillion USD per year to the gross domestic product (Bank, 2014b). Reefs and mangroves of particular importance should be protected through restriction of certain activities or gear usage in these locations, temporary closure of threatened fisheries, and/or creation of marine protected areas (MPAs). However, protecting those areas deemed particularly important, either from an ecological or an economical standpoint, is complicated through the municipal, regional and international politics of the CT, leaving many areas with little to no enforcement of imposed regulations (Christie et al., 2016). In order to more effectively protect the world's natural resources, studies such as the present one need to be conducted to better inform the placement of MPAs, releasing those which are no longer meeting target goals and creating more effective management strategies such as forming networks of MPAs, temporary or migratory MPAs, or zoned MPAs. Finally, making management decisions which are supported by the local populaces will help facilitate

the enforcement of the regulations that are in place.

Anthropogenic threats to reefs include overfishing, sediment deposition from coastal development, increased CO₂ emissions, river runoff carrying excess nutrients, marine-sourced pollution from shipping, bleaching from sunscreen use, and unsustainable tourism (Burke et al., 2011). In addition, climate change threatens reefs as well through ocean acidification (making the formation of calcium carbonate more difficult and leaving the reefs more vulnerable to storms) and increased sea surface temperatures (leading to thermal stress, coral bleaching, susceptibility to disease and changes in reproductive capability for reef organisms; Burke et al., 2011). Whether or not coral reefs can evolve rapidly enough to accommodate this change in background temperature is a matter of debate (e.g. Hughes et al., 2003; Donner et al., 2005; Palumbi et al., 2014; Kleypas et al., 2016).

The present study uses the CT implementation of ROMS (CT-ROMS) to characterize the means, standard deviations, secular changes and frequency content of volume transport time series from 30 key passages throughout the CT from 1958-2007. These results are discussed in Chapter 2. In Chapter 3, TRACMASS, which takes horizontal ve-

locity fields from CT-ROMS, is used to calculate trajectories offline for particles released year-round following lunar periodicity from all coral reef grid cells located within 43 ecoregions in the CT model domain (based on Veron et al., 2009) over three five-year periods. These trajectories are then used to assess connectivity changes during different ENSO phases for ecoregions along the SCSTF after 20-, 40-, 60-, 80- and 100-day PLDs. Chapter 4 uses the same set of particle trajectories from the three five-year periods to assess secular and decadal changes in connectivity along the ITF. These five-year periods are taken from the 1960s, 1980s and 2000s. Chapter 5 presents a summary of our results as well as concluding remarks.

Chapter 2

Climate-Modulated Volume Transport in the Coral Triangle

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Abstract

The western equatorial Pacific is one of the most complex regions in the world, possessing elaborate bathymetry, geography and current systems. Understanding the regional interplay among monsoons, seasonality, and interannual processes is crucial to understanding how regional circulation has continued to change along with changing climate. The present study uses a high-resolution model of the Coral Triangle (CT) to assess the relative contributions of intra-annual, seasonal, interan-

¹This chapter is in review to *Journal of Geophysical Research: Oceans*

nual, and secular processes through 30 key passages throughout the CT from 1960-2007. Significant, secular changes in volume transport are present along the Indonesian Throughflow (ITF) but are lacking along the South China Sea Throughflow (SCSTF). Furthermore, a multiple linear regression model uses indices for the Indian Ocean Dipole, El Niño Southern Oscillation and Pacific Decadal Oscillation to reconstruct volume transport through 13 of the 30 study transects, with these 13 passages lying along the SCSTF, not the ITF. These results suggest fundamentally different modes controlling these two different transport pathways. Possible explanations for these fundamental transport differences include North Equatorial Current migration and opposing two-layer flow between the Indian Ocean-bound ITF at depth and the Pacific Ocean-bound surface flow of the South China Sea Return-flow through the Molucca and Celebes Seas and Makassar Strait.

2.1 Introduction

Recognized as a bottleneck in the ocean's thermohaline circulation (Gordon, 2005), the western equatorial Pacific has an important impact on atmospheric circulation, transferring heat from ocean to atmosphere (Neale and Slingo, 2003). The Coral Triangle (CT; Figure 1.1)

is a geographic region within the western equatorial Pacific that encompasses Indonesia, Malaysia, the Philippines, the Solomon Islands, Papua New Guinea, and Timor-Leste. Characterized by complex geometry, bathymetry, and regional dynamics (Gordon et al., 2003), the CT is bordered by the confluence of several major ocean currents (the North and South Equatorial Currents, North and South Equatorial Counter-currents, and the Kuroshio Current) and provides a key exchange of water and nutrients between the Indian and Pacific Oceans.

Central to regional circulation, the Indonesian Throughflow (ITF) is the low-latitude pathway which transports warm, relatively fresh water from the Pacific to the Indian Ocean, traveling down through the Celebes Sea and Makassar Strait (Figure 1.1, Passage 1) and out through Lombok (Figure 1.1, Passage 3), Ombai (Figure 1.1, Passage 4), and Timor Straits (Figure 1.1, Passage 5). Similarly, the South China Sea Throughflow (SCSTF) dominates circulation of warmer, fresher water through the South China Sea, down through Karimata Strait (Figure 1.1, Passage 7), and outflows to the Indian Ocean, again via Lombok, Ombai, and Timor Straits. The South China Sea Return-flow returns to the Pacific at the surface by flowing northward through Makassar Strait, while the ITF flows southward through Makassar

Strait at depth (as shown in Figure 1.1, Passage 1), opposing the direction of the South China Sea Returnflow (Qu et al., 2009).

The Indo-Pacific warm pool is a body of water that is situated along the equatorial region of the western Pacific and Indian Oceans. Fluctuations in the warm pool along the CT's eastern edge are modulated by El Niño Southern Oscillation (ENSO; McPhaden, 1999) and are thought to contribute to changes in regional circulation, with cooling/warming experienced during El Niño/La Niña conditions and eastward/westward migration of the warm pool. In addition, a recent study by Kleypas et al. (2015) investigated the temperature-related regional effects of ENSO in the CT and found high levels of severe bleaching during the 1998-1999 La Niña event, with heat stress events more frequent during La Niña events. These systematic changes in ocean temperatures and circulation are particularly important to marine organisms such as coral, which rely on ocean currents to transport larvae and are thermally sensitive.

Understanding past hydrodynamics within and surrounding the CT is necessary to anticipate future changes in regional circulation. Here, we provide a description of regional volume transport throughout the

CT. To our knowledge, this is the first long-term regional study to investigate the impact of interannual and secular processes on regional circulation over half a century (1958-2007). Having a better understanding of systematic changes in regional physics is vital to making more informed management decisions to protect the ecologically complex and climatically sensitive coral reefs. To this end, we assess secular changes and interactions of interannual processes in volume transport throughout the CT over the last half-century.

2.2 Theory

ENSO and the Indian Ocean Dipole (IOD) are well-known interannual processes that may drive interannual variability in volume transport (Zhou et al., 2015). ENSO has already been shown to correspond to interannual variability in SST and SSH anomalies in the study region. Two experimental studies influential in understanding the effects of ENSO on volume transport through Makassar and other key ITF passages are ARLINDO (Gordon and Susanto, 1998) and INSTANT (Sprintall et al., 2004). During the ARLINDO study (1996-1998), a strong correlation was observed between ENSO phases and Makassar transport, with slower velocity values recorded during El Niño con-

ditions and higher velocity values (2.5 times higher) during La Niña conditions (Gordon and Susanto, 1998; Susanto and Gordon, 2005).

This research was continued and expanded during the 2004-2006 INSTANT program (Sprintall et al., 2004). A strong ENSO phase did not occur during the INSTANT program; however, Gordon et al. (2008) found that the peak in mean volume transport occurred during a weak La Niña condition with a one-week lag that was moderately correlated with the ENSO index (0.42). Gordon et al. (2010) also suggested that the other passages in the study were heavily influenced by the strong, positive IOD signal in 2006, which led to an increase in transport to the Indian Ocean.

Increased transport is seen through the rest of the ITF during La Niña (e.g., Meyers, 1996). This increase is thought to be due to an increased tilt of the sea surface between the Pacific and Indian Oceans due to westward migration of the warm pool during La Niña (Meyers, 1996). Unlike the ITF, the SCSTF, beginning at Luzon Strait, experiences increased transport during El Niño conditions (Qu et al., 2006a; Tozuka et al., 2009). The mechanism for this increased transport during El Niño is an increased transport of the NEC, leading to northward

migration of the NEC bifurcation, strengthening the Mindanao Current and weakening the Kuroshio Current, thus allowing more Pacific water through Luzon (Liu et al., 2006).

IOD events influence volume transport in the CT, due to decreased sea level in the eastern Indian Ocean, leading to an eastward pressure gradient and increased ITF transport (Yuan et al., 2011). IOD events also generate coastal Kelvin waves which propagate northward through the ITF along Sumatra and Java (Yuan and Liu, 2009). This propagation of Kelvin waves could facilitate communication of the IOD signal into the western equatorial Pacific, and, by continued propagation to the eastern tropical Pacific, impact interannual climate variations the following year and cause upwelling anomalies in the cold tongue (Yuan et al., 2013).

While IOD and ENSO are major contributors to regional interannual variability on timescales less than 10 years, Pacific Decadal Oscillation (PDO) influences decadal changes in the regional climate and ocean current systems in which the CT is embedded. Warm (positive) phases of PDO are characterized by weakened trade winds, weaker Walker circulation and a northward shift of the NEC bifurcation due to anoma-

lous southerly winds near the Philippines (Wu, 2013), inducing a weakened Kuroshio current and weakened equatorial circulation overall (Hu et al., 2015). A weakening of the Kuroshio leads to increased transport through Luzon Strait and into the SCSTF, with increased westerly wind anomalies in the equatorial Pacific (Soumya et al., 2015; Yu and Qu, 2013). During cold (negative) phases of PDO, the NEC bifurcation shifts southward. Due to increased easterly winds, Luzon Strait transport decreases (Yu and Qu, 2013), while the NEC, North Equatorial Countercurrent, Kuroshio, and Mindanao currents all strengthen.

The remainder of this paper characterizes the mean volume transport, trends and interannual variability in transport through 30 straits in the CT over the 1960-2007 time period. Section 2.3 describes the numerical simulation of the CT, provides model validation, and describes the analyses used in the present study. Section 2.4 presents the results for the mean, trend, and spatial and temporal variability in transport through the 30 study passages in the CT. Finally, Section 2.5 discusses these results.

2.3 Methods

Model output from the Coral Triangle implementation of the Regional Ocean Modeling System (CT-ROMS; Castruccio et al., 2013) is used to study volume transport in the CT over the 1958-2007 time period. The first two years of the model run are not analyzed, as they allow the upper ocean to reach dynamical equilibrium. The remaining 48 years are used to create monthly volume transport time series at 30 key passages throughout the CT.

To provide an introductory characterization of the region, means, standard deviations, and power spectral densities of volume transport time series are examined for these passages. Secular changes in volume transport are evaluated using linear trends to determine whether or not any long-term, systematic changes in circulation have occurred. A multiple linear regression model is formulated using ENSO, IOD, and PDO as explanatory variables to reconstruct the interannual variability in volume transport through the 30 passages.

2.3.1 Numerical simulation of the Coral Triangle

The Regional Ocean Modeling System (ROMS) is used for a variety of modeling applications around the world, both coastal and basin-wide in scale (e.g., Curchitser et al., 2005; Di Lorenzo, 2003; Haidvogel et al., 2000). CT-ROMS solves the hydrostatic primitive equations, with a terrain-following vertical coordinate system and a free surface. Model variables, including temperature, salinity and velocity, are calculated on a staggered, curvilinear, Arakawa C-grid using finite-difference numerical methods. For more information regarding the detailed algorithms governing ROMS, see Shchepetkin and McWilliams (2003); Shchepetkin and McWilliams (2005); and Shchepetkin and McWilliams (2009).

CT-ROMS has a 5 km by 6 km horizontal resolution (1280 x 640 grid points), covering the region between 95°E and 170°E and between 25°S and 25°N (Figure 1.1). The domain has been rotated approximately 14° clockwise from due East to better cover the CT region, while maximizing the percentage of oceanic points. Model bathymetry is generated by interpolating 30-second resolution SRTM30_PLUS bathymetric data.

CORE-II provides an extensive list of atmospheric surface fields that

are sampled four times a day, with a spatial resolution of 2.5° that is used to force CT-ROMS (Large and Yeager, 2009). The SODA analysis provides lateral oceanic boundary conditions for temperature, salinity, and velocity using a hybridized nudging and radiation approach (Carton et al., 2000; Marchesiello et al., 2001), and MERRA provides surface boundary conditions for sea-level pressure and precipitation and heat budget terms like short-wave and long-wave radiation and air temperature (Rienecker et al., 2011). The model was run from 1958-2007, producing a multi-decadal time series enabling dynamical inferences on long, climatically relevant time scales.

2.3.2 Validation of the CT-ROMS simulation

The CT-ROMS simulation covering the period 2004-2006 was previously validated by comparing CT-ROMS model output to known volume transport values from the INSTANT experiment (Castruccio et al., 2013). Overall agreement was generally good with known transport values for the Indonesian Throughflow and Makassar, Lifamatola, and Lombok Straits. Somewhat greater discrepancy was seen at Ombai Strait and Timor Passage. Geometric and topographic discrepancies in the model implementation are a potential concern in this region. At this horizontal resolution, the model has limited ability to resolve

sharp changes in flow direction around, for example, Timor-Leste and Pulau Wetar, thereby influencing the partitioning of flow between Ombai Strait and Timor Passage (see Castruccio et al. (2013), for a more in-depth discussion).

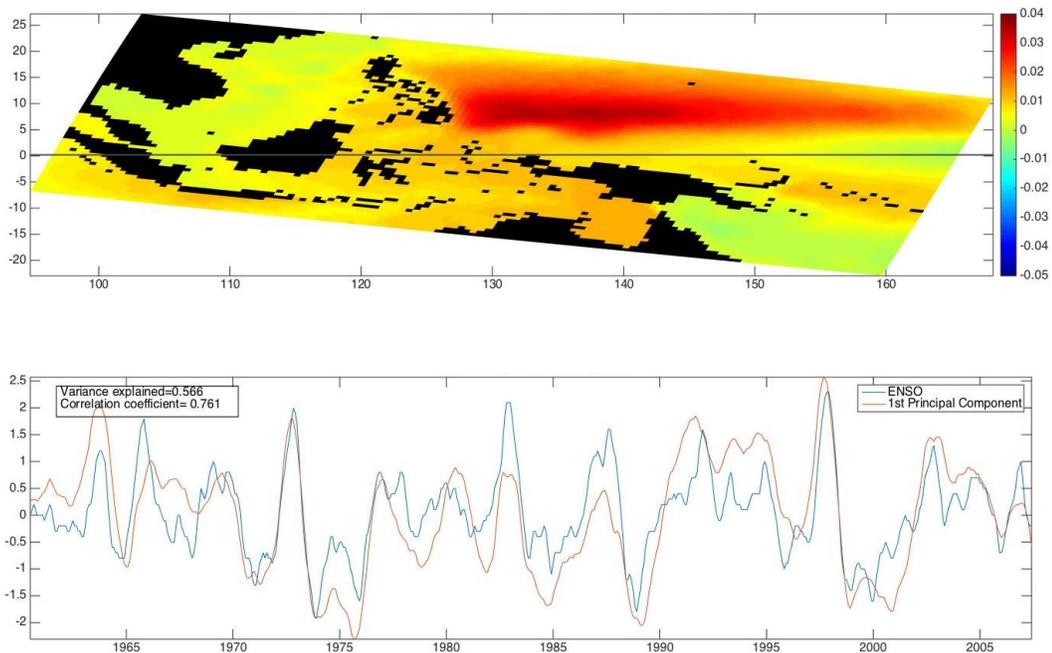


Figure 2.1: EOF1 for SSHa in the CT. The upper panel depicts the spatial pattern of EOF1. Time series have been demeaned and filtered with a 13-month boxcar filter. The lower panel depicts the time series from the 1st EOF, again filtered with a 13-month boxcar filter, in red and the ENSO time series in blue. ENSO and the time series from the first EOF are well-correlated ($R = 0.761$). The 1st EOF explains 56.6% of the overall variance.

As a subsequent step in model validation, we have performed Empirical Orthogonal Function (EOF) analysis using single value decomposition on sea surface height anomalies (SSHa) from the model output. Prior to EOF analysis, we de-trend and filter the time series using

a 13-month boxcar filter to isolate the interannual frequency content. The spatial pattern for the first EOF mode (EOF1) agrees with typical representations of SSHa seen during ENSO conditions and explains a significant portion of the total variance (0.566; Figure 2.1). The first principle component time series is well-correlated with the Oceanic Nino Index ($r= 0.761$), confirming the ability of the model to capture the ENSO signal in SSHa.

The first SSHa EOF, which depicts ENSO in the present study, agrees qualitatively with previous work (Soumya et al., 2015; Nidheesh et al., 2013). However, the present results show a stronger signal to the east of the Philippines than has been seen in either of the previous two studies. Additionally, Kleypas et al. (2015) found that the first EOF mode of sea surface temperature anomalies from the same CT-ROMS output explained 44% of the total variance and correlated well with ENSO ($r=0.70$).

In addition to capturing the ENSO signal, CT-ROMS is also able to reproduce the seasonal cycle (Figure 2.2) and, perhaps more importantly, the IOD (Figure 2.3) in sea surface temperature anomalies (SSTa). The first EOF mode in SSTa, when a 7-month filtering win-

low is applied, corresponds to the seasonal cycle, while the second EOF mode corresponds to IOD. The second principle component and IOD are well-correlated ($R = 0.506$), demonstrating the ability of the model to accurately capture the IOD signal. The second EOF explains 11.8% of the overall variance.

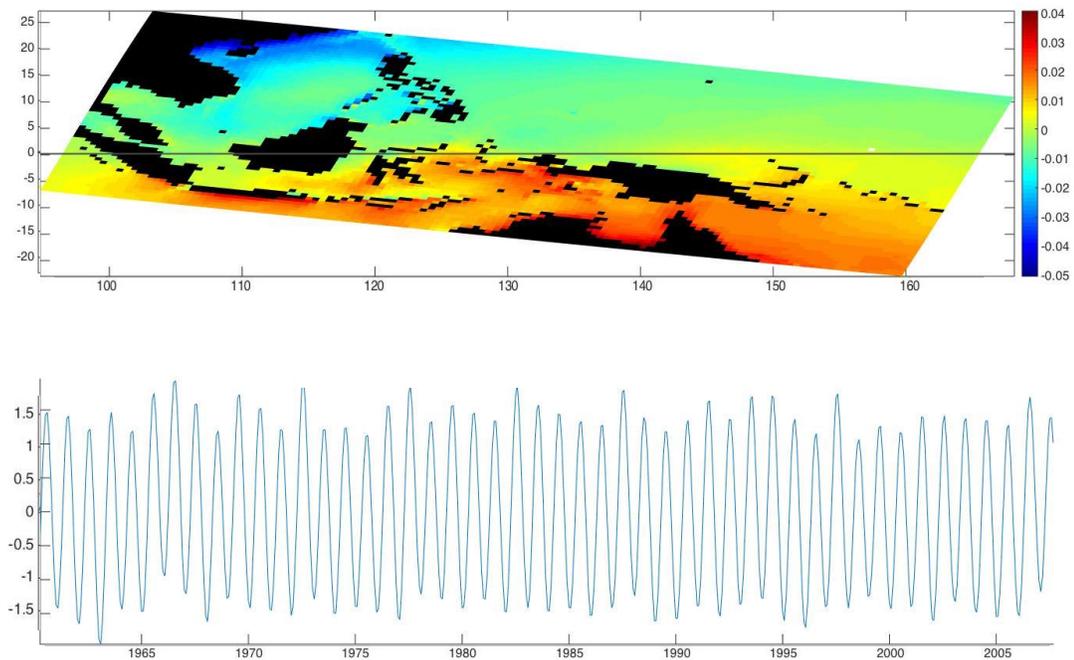


Figure 2.2: EOF1 for SSTa in the CT. The upper panel depicts the spatial pattern of EOF1, which corresponds to the seasonal cycle. Time series have been demeaned and filtered with a 7-month boxcar filter. The lower panel depicts the time series from the 1st EOF in blue, again depicting the seasonal cycle.

2.3.3 Power Spectral Density Calculation

To qualitatively assess the relative contributions of interannual and seasonal variability, power spectral densities (PSDs) are computed for the 30 straits. The PSDs characterize the heterogenous, rich spectral con-

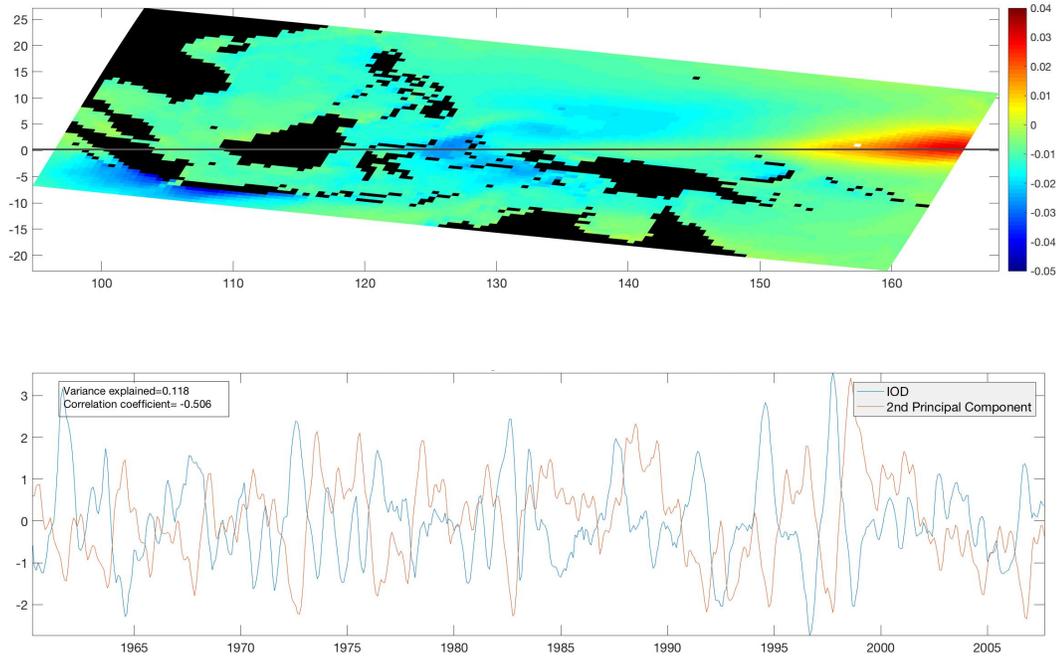


Figure 2.3: EOF2 for SSTa in the CT. The upper panel depicts the spatial pattern of EOF2, which corresponds to the IOD. Time series have been demeaned and filtered with a 7-month boxcar filter. The lower panel depicts the time series from the 2nd EOF, representing the IOD.

tent of the region. PSDs are computed using a Fast Fourier transform of the de-trended data. Interannual frequencies are defined as any frequency less than 0.9 cycles per year, seasonal cycles as 0.9-1.1 cycles per year, and intra-annual cycles as 1.1-3 cycles per year.

2.3.4 Multiple Linear Regression Model

To assess the combined effects of interannual processes on regional volume transport, we formulate a linear regression model which uses ENSO, IOD, and PDO climate indices as explanatory variables to pre-

dict volume transport. As discussed previously, these climate indices are not independent of one another. Correlations between Oceanic Niño Index (ONI) and Dipole Mode Index (DMI), and between ONI and PDO index (PDOI) are statistically significant (Table 1), producing multicollinearity.

Table 2.1: Correlation between climate indices; * indicate statistical significance at the 95% Confidence Level

Correlation	Correlation Coefficient
ONI & PDO	0.424*
ONI & IOD	0.277*
PDO & IOD	0.0331

Multicollinearity is accounted for in the linear regression model using ridge regression (Myers, 1990), a biased estimation technique, which reduces the variance and increases the stability of the regression coefficients by biasing the regression model coefficients through implementation of a constant shrinkage parameter, κ , which varies among the 30 constructed models. This shrinkage parameter is selected by examining the ridge trace, which plots the regression coefficients from standardized regressors against the shrinkage parameter κ . An appropriate κ is selected for the model of each transect at the point where all of the regression coefficients from the standardized regressors are sufficiently stable in the ridge trace. This selection of κ is used to alter the corre-

lation matrix in the orthogonal case to

$$(\mathbf{X}'\mathbf{X} + \kappa\mathbf{I})\mathbf{b}_R = \mathbf{X}'\mathbf{y} \quad (2.1)$$

which is rewritten, solving for \mathbf{b}_R (Myers, 1990):

$$\mathbf{b}_R = (\mathbf{X}'\mathbf{X} + \kappa\mathbf{I})^{-1}\mathbf{X}'\mathbf{y}. \quad (2.2)$$

which varies among the 30 constructed models.

The time series of three monthly climate indices are individually lagged to allow up to 36 months of signal propagation to create a series of models at each passage. Yuan et al. (2011) found that IOD-induced transport anomalies can be found within the Indo-Pacific for at least a year following the IOD event. And, Yu and Qu (2013) found high correlation between Luzon Strait transport in the upper layer and PDO with a 7-year lag and postulated that this distal process is communicated to Luzon Strait via subtropical mode waters. Using these two papers as endpoints, we select a maximum lag of 36 months, as this allows several years for the ENSO signal (and other signals) to propagate through the region, but for consecutive ENSO events to still be distinguishable.

We compute volume transport time series at the 30 passages and

filter them using a 13-month Butterworth filter to remove seasonal and intra-annual frequency content. We then compute Pearson correlation coefficients between each climate index and the volume transport at each of the 30 passages and find the maximum correlation coefficient between each climate index and the volume transport time series for each passage. The correlation coefficients are computed using effective degrees of freedom to account for autocorrelation between consecutive temporal data points. We select models which have lags ± 5 months away from the month causing the maximum correlation, as this 11-month selection of models defines the peak correlation event. Of these 11 models, we choose the model with the best F-statistic for each strait.

We then apply ridge regression to the model with the best F-statistic for each of the 30 passages, allowing the lags at a given passage, as well as between passages, to be independent of one another. Once ridge regression produces the coefficients for the new linear regression model, we then multiply these coefficients by their respective climate indices to produce a reconstructed volume transport time series at each of the thirty passages. Finally, we correlate the reconstructed volume transport time series against the original filtered monthly time series to assess how well the ridge regression linear model is able to reproduce

volume transport at a given passage.

2.4 Results

2.4.1 Regional Overview: Mean Transports

Volume transport time series from CT-ROMS for 30 passages over the 1960-2007 time period are computed as a metric for circulation and water body connectivity and analyzed for interannual and long-term temporal variability and systematic spatial patterns. Our intent is to quantify, as much as possible, the roles of forcing by large-scale atmosphere/ocean processes (e.g., ENSO) in regional circulation and temperature.

Using CT-ROMS, averaged monthly transport time series at thirty passages are obtained. These thirty passages inter-connect four sub-regions within the CT: the South China Sea, the Sulu Sea, the Sulawesi (Celebes) Sea, and the Southeastern CT (Figure 2.4). These include passages that are known to be key to flow through the CT and encompass the passages studied in Castruccio et al. (2013). The thirty passages are characterized by a variety of geometric shapes and sizes (e.g., widths, sill depths, etc.). The mean volume transports for the

thirty passages over 1960-2007 are shown in Figure 2.4. No spatial pattern is evident in the volume transport means, unsurprising given the heterogeneous characteristics of the various passages (i.e., nearby regional circulation, local winds, bathymetry, passage width, etc.).

2.4.2 Trends

We examine secular changes in volume transport using endpoints of the best-fit linear trend lines for the 30 passages. The volume transport time series from four representative passages demonstrate variability in transect trends, as well as interannual, seasonal, and intra-annual signals in the PSDs content. The secular change in transport for Makassar Strait shows an increase of 6.41 Sverdrups (Sv) toward the Indian Ocean, a significant change in volume transport (Figure 2.5, top panel). The large secular change seen at Makassar Strait qualitatively agrees with recent results showing a 3-4 Sv increase in transport towards the Indian Ocean, providing support for the substantial increases in transport seen at some of the passages in the CT (Lee et al., 2015). The large increase in Makassar's 2000 transport follows the protracted La Niña event of 1998-2000 and agrees with results from Lee et al., 2015, which found a significant increase in Makassar transport following the 2005-2006, 2007-2008, and 2008-2009 La Niña events, and which has been

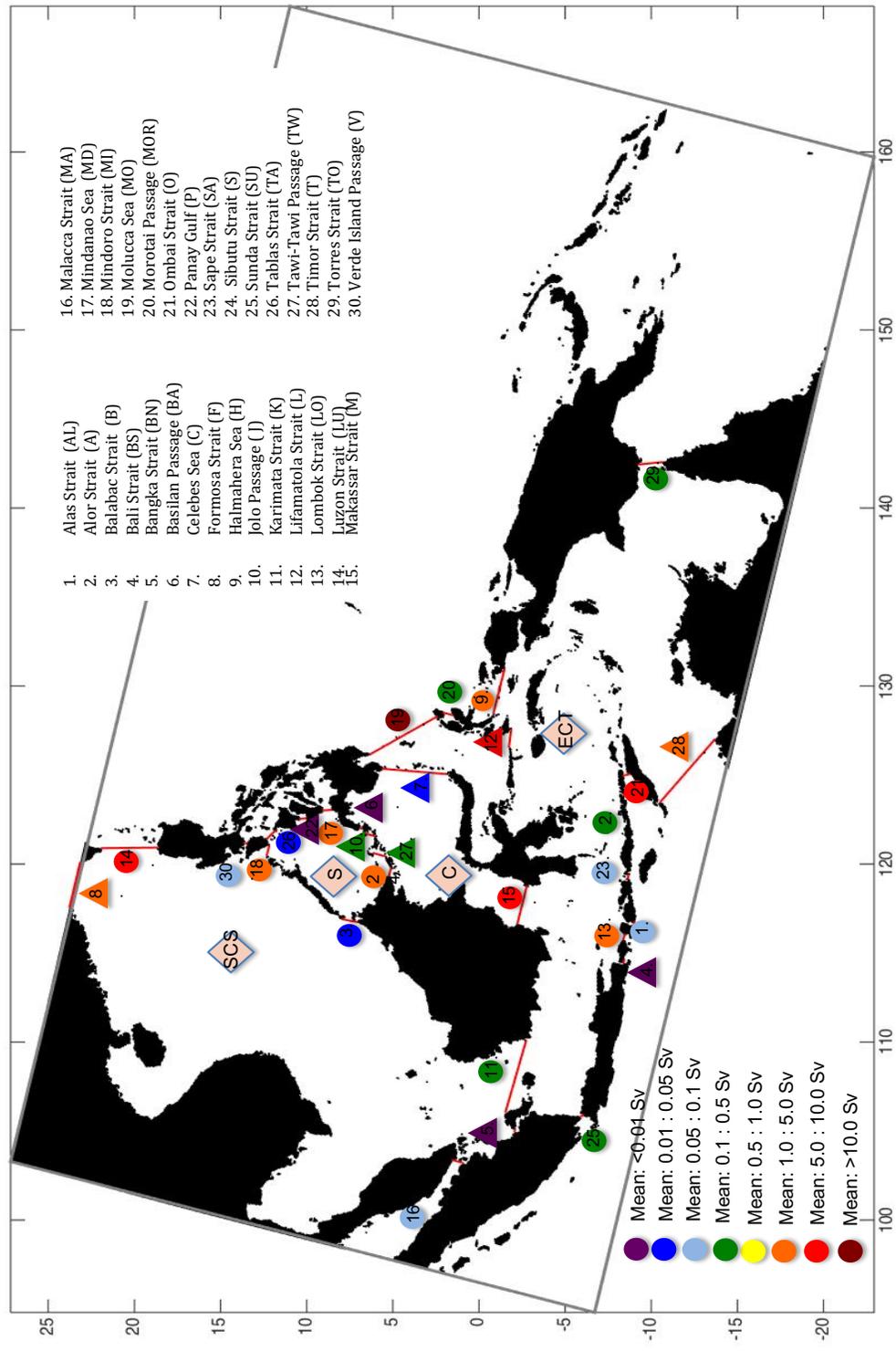


Figure 2.4: Magnitude of mean volume transport for 30 key passages throughout the CT (1960–2007) in Sv indicated by colored dots. The color key for the amount of transport for a given strait depicts small transport values in cool colors and large transport values in warm colors. Pacific-ward flow is indicated by triangles, while Indian-ward flow is indicated by diamonds. Beige diamonds indicate the 4 sub-basins of the CT.

noted elsewhere in the literature (e.g. Meyers, 1996; Tillinger and Gordon, 2009). Makassar is characterized by rich frequency content, having significant contributions from the interannual (blue-shaded), seasonal (green), and intra-annual (red) frequencies bands (Figure 2.5, bottom panel).

In addition to secular and interannual signals, some straits also experience noticeable biannual and seasonal changes in volume transport. Not investigated here, these biannual signals could be due to semianual propagation of Kelvin waves from the Indian Ocean, resulting from westerly winds during monsoonal shifts (Potemra and Schneider, 2007).

Changes similar to those seen in Makassar volume transport are seen at Lifamatola, Molucca, and Timor Straits (Figure 2.6). Like Makassar, Timor Strait experiences a significant increase in transport, greater than 10 Sv, toward the Indian Ocean over the 48 years of the model study. Like Makassar, Timor Strait is also characterized by rich frequency content and has significant contributions from interannual, seasonal and intra-annual signals in the PSD (Figure 2.6, bottom panel).

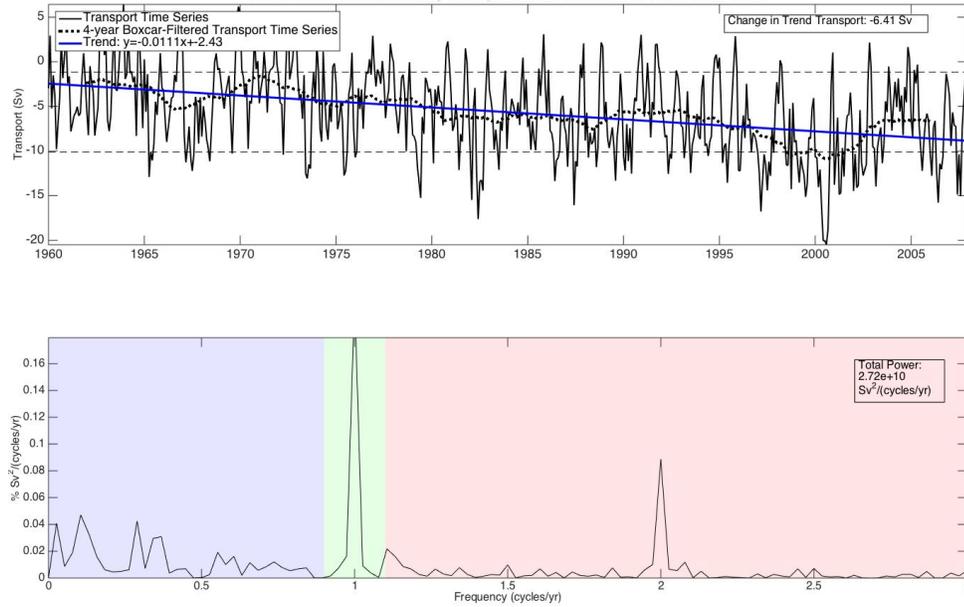


Figure 2.5: Monthly transport time series of Makassar Strait from 1960-2007. The unfiltered time series is shown in the top panel by the solid black line, the trend by the solid blue line, and \pm one standard deviation away from the mean is indicated by the dashed black lines. The blue box indicates 0-0.9 cycles/year, the green box indicates 0.9-1.1 cycles/year and the red box indicates 1.1-3 cycles/year.

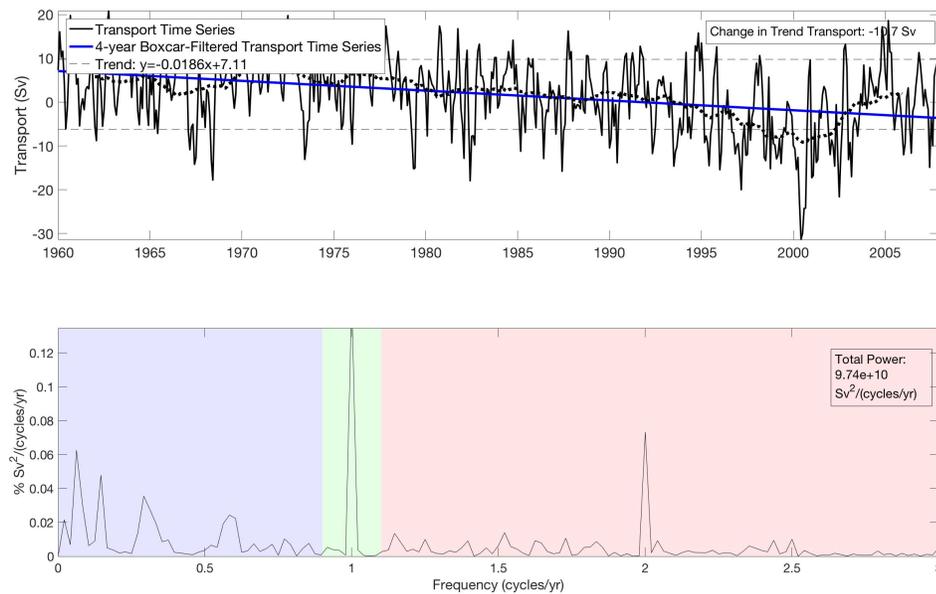


Figure 2.6: Monthly transport time series of Timor Strait from 1960-2007. The unfiltered time series is shown in the top panel by the solid black line, the trend by the solid blue line, and \pm one standard deviation away from the mean is indicated by the dashed black lines. The blue box indicates 0-0.9 cycles/year, the green box indicates 0.9-1.1 cycles/year and the red box indicates 1.1-3 cycles/year.

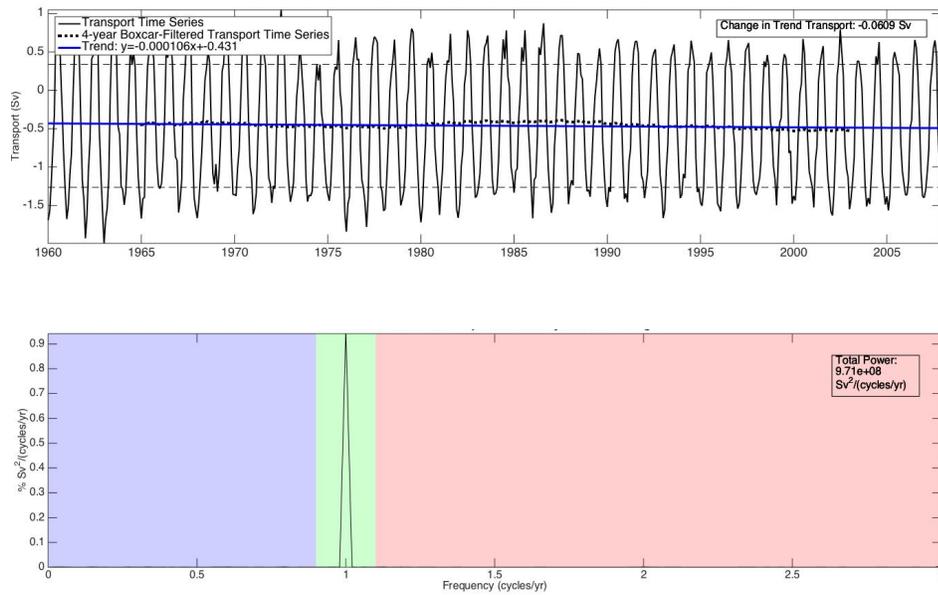


Figure 2.7: Monthly transport time series of Karimata Strait from 1960-2007. The unfiltered time series is shown in the top panel by the solid black line, the trend by the solid blue line, and \pm one standard deviation away from the mean is indicated by the dashed black lines. The dotted black line indicates a 4-year running mean. The blue box indicates 0-0.9 cycles/year, the green box indicates 0.9-1.1 cycles/year and the red box indicates 1.1-3 cycles/year.

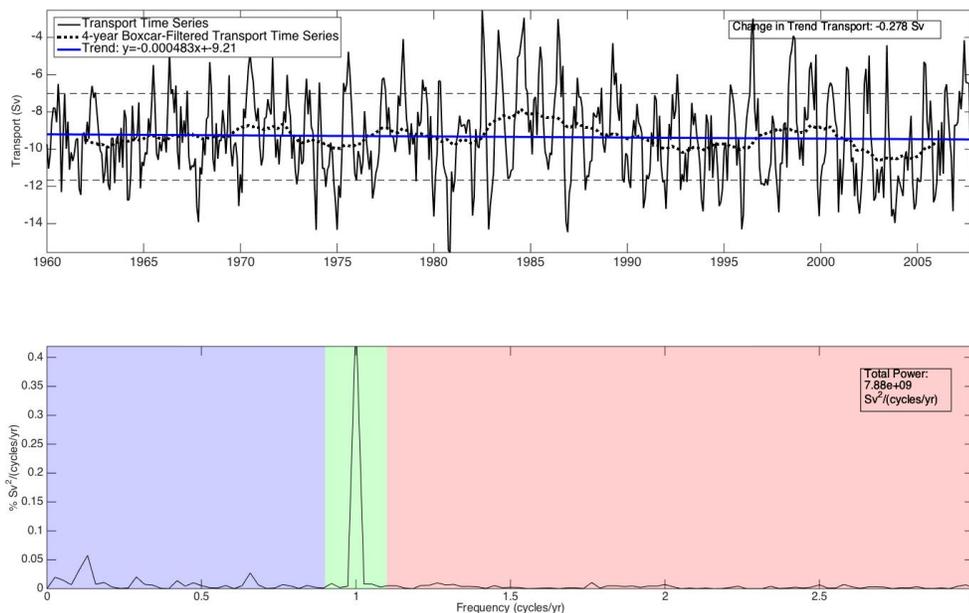


Figure 2.8: Monthly transport time series of Luzon Strait from 1960-2007. The unfiltered time series is shown in the top panel by the solid black line, the trend by the solid blue line, and \pm one standard deviation away from the mean is indicated by the dashed black lines. The dotted black line indicates a 4-year running mean. The blue box indicates 0-0.9 cycles/year, the green box indicates 0.9-1.1 cycles/year and the red box indicates 1.1-3 cycles/year.

Conversely, Lombok experiences a slight decrease in transport of approximately 0.5 Sv (not shown), and there is little change in volume transport at other straits, including Karimata and Luzon (Figures 2.7 and 2.8). In contrast to Timor and Makassar Straits, Karimata Strait (Figure 2.7) is almost exclusively driven by seasonal changes in transport, as indicated both by the transport time series and the PSD. A very weak decadal modulation could be suggested by the dotted black line, but its energy content is negligible when viewed in the context of the seasonal signal.

Like Karimata, Luzon Strait (Figure 2.8) also has a negligible secular change in volume transport and does experience significant seasonal modulation (green), as depicted by the PSD. However, Luzon transport also has a rich interannual content, as is evident both by the transport time series and the PSD (blue). What is perhaps most noteworthy is the decadal signal that is seen in the 4-year running mean time series. This decadal signal in Luzon transport was also evident in Yu and Qu (2013), which found a decadal contribution from PDO to Luzon Strait transport.

Of the thirty passages examined in this study, eight of these pas-

sages experience significant changes in volume transport. These eight passages lie along the ITF, suggesting an overall long-term increase in transport through the ITF. Of these eight passages, only Lombok experiences decreased transport toward the Indian Ocean of approximately 0.5 Sv, possibly due to changes in flow partitioning between the SCSTF and its return flow to the Pacific Ocean. The remaining seven passages all experience significant increases in transport towards the Indian Ocean: Halmahera experiences an increase of 1.1 Sv; Makassar, Ombai, Lifamatola, and Celebes an increase of 5.0-10.0 Sv, and Molucca and Timor an increased volume transport greater than 10.0 Sv (Figure 2.9). Significant increases in volume transport (> 0.5 Sv) toward the Indian Ocean along the SCSTF are absent.

2.4.3 Space and time variability

The interactions of interannual and decadal processes (ENSO, IOD, and PDO) are also investigated to assess the contributions of these processes when combined. To assess if the ridge regression model is able to improve upon the correlations between the original volume transport time series and individual climate indices, two criteria are used. First, the correlation coefficient between the reconstructed and filtered volume transport time series for a given passage must be greater than 0.3, and,

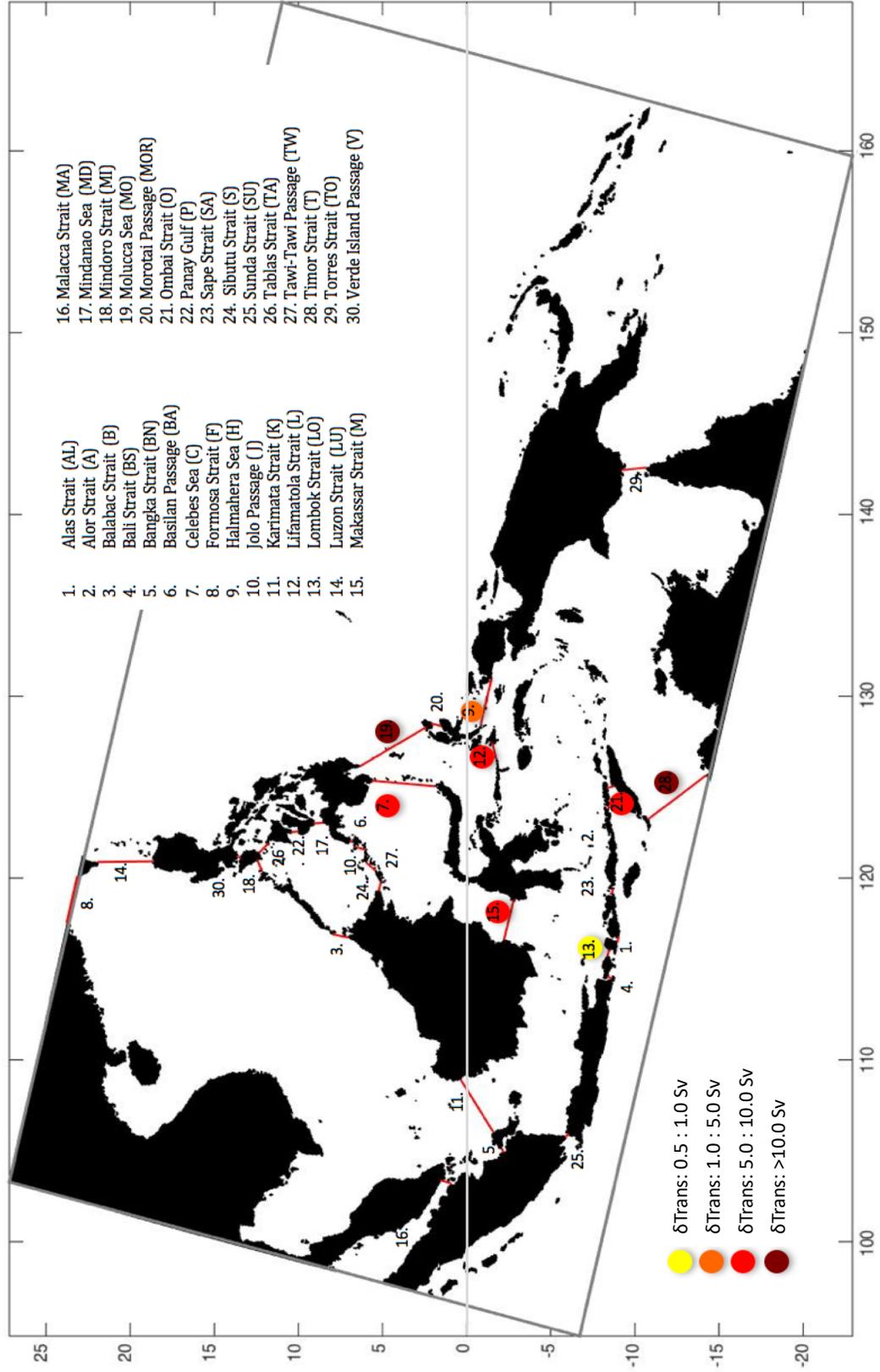


Figure 2.9: Change in Volume Transport (1960-2007) in Sv as indicated by colored dots. The legend for the color-scale is located in the lower left hand corner. Straits with no dot have insignificant trends in transport. Straits with significant changes in volume transport over the study period are located along the ITF.

second, this correlation coefficient must be at least 0.1 larger than the correlation coefficients between each of the three lagged climate indices and the original filtered time series for that passage. A model must meet both of these criteria to be able to successfully reconstruct interannual volume transport content. As such, we were able to successfully reconstruct 13 out of the 30 study passages, with the climate indices successfully explaining the interannual volume transport through the SCSTF but not the ITF (Figure 2.10).

2.5 Discussion

A recent paper proposed a long-term southward shift in the NEC bifurcation, causing a strengthening of the Kuroshio Current (Hu et al., 2015), which has previously been correlated to decreased Luzon Strait transport, as well as decreased transport through the rest of the SCSTF (Nan et al., 2013). In the current study, a similar decrease in SCSTF is not observed. Rather, we observed slight increases in transport along the upper SCSTF, with greater, significant increases downstream, where the ITF and SCSTF join. However, from 1993-2007, we observe a decrease in transport through Luzon Strait of 0.013 Sv/yr, compared to a decreased 1993-2010 Luzon transport of 0.24 Sv/yr in Nan et al.

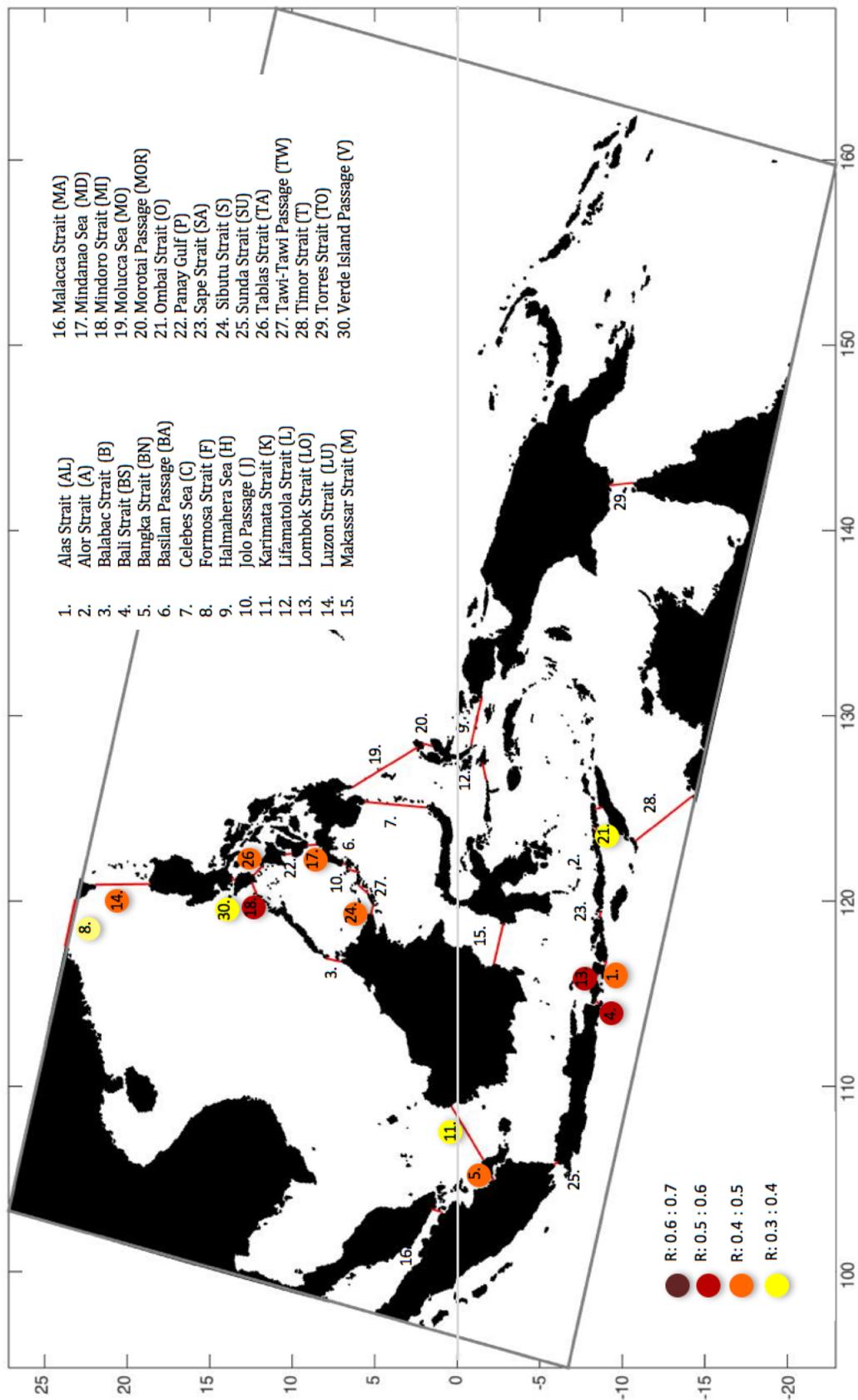


Figure 2.10: Maximum correlation coefficients between volume transport time series (S_v) and reconstructed volume transport time series from the ridge regression analysis (1962-2005). The legend for the color scale is located in the lower left hand corner. Straits with no dot have insignificant trends in transport. Straits with significant changes in volume transport over the study period are located along the SCSTF.

(2013).

The lack of a long-term decrease in SCSTF transport could be due to PDO influence. Yu and Qu (2013) found previously that Luzon Strait transport was well-correlated to PDO and that during positive PDO phases a northward migration of the NEC bifurcation and strengthening of the Luzon Strait transport occurred. And, it appears that Luzon experiences a long-term increase in transport, with cyclic variability due to PDO influences; during the period from 1993-2010, the Luzon transport seen in Yu and Qu (2013) seemed to decrease. The results of the present study are then consistent with this interpretation.

Although the regression model is able to capture interannual variability in transport through the SCSTF, it is not able to do so along the ITF. This is not to suggest an absence of PDO and ENSO signal in the ITF transport. To the contrary, a larger fraction of the total transport is due to interannual content in the ITF transport, relative to the SCSTF transport, as seen in Figure 2.11. Generally, the passages along the ITF experience a significant portion of their total transport at interannual periods, due to interannual Pacific variability. At these passages, the contribution of interannual content is equal

to or greater than the seasonal contribution. This is in contrast to the transport through the SCSTF which is generally characterized by a predominant seasonal cycle and weak interannual and intra-annual contributions (Figure 2.11). While significant interannual changes in transport along the SCSTF are captured by the multiple linear regression (MLR) model, significant secular changes are seen along the ITF, suggesting two fundamentally different modes of regional transport.

El Niño conditions lead to northward migration of the NEC bifurcation, and weakening of the Kuroshio current occurs, increasing SCSTF transport (Xiang-Hui and Fei, 2014). Positive PDO conditions, which cause a northward shift of the NEC bifurcation and weakened Kuroshio and Mindanao currents, have existed since 1976 (Zhao et al., 2015), also increasing SCSTF transport. In addition, increased occurrences of El Niño events would result in increased SCSTF transport, although a previous study suggested that ENSO only contributes significantly to the migration of the NEC bifurcation under negative PDO conditions (Wu, 2013). However, long-term trends and migration towards a more La Niña-like mean state (Luo et al., 2012) could be responsible for an overall southward migration of the NEC bifurcation and strengthening of the Kuroshio, weakening the SCSTF on secular timescales, leading to

more modest increases in volume transport through the SCSTF, compared to those seen in the ITF. This would explain why the SCSTF experiences significant changes in volume transport at interannual frequencies and why the ridge regression model “works”, while the SCSTF does not experience significant secular changes in volume transport.

It is the interactions between the PDOI and ONI, in particular, that characterize the interannual and secular content of the transports through these two pathways. Under positive PDO conditions, experienced since 1976 (Zhao et al., 2015), ITF transport would be expected to decrease (Feng et al., 2011). With the increased occurrence of El Niño conditions, the ITF would also experience decreased transport. At interannual frequencies, then, the ITF would be expected to experience the same significant changes in transport at interannual frequencies as the SCSTF. As the equatorial Pacific moves towards a more La Niña-like mean state (Luo et al., 2012), long-term increases in volume transport through the ITF would be expected. In addition, the last two decades have experienced strengthening of the Pacific subtropical cells (Feng et al., 2011), causing a further multi-decadal increase in ITF transport. The combination of these multi-decadal processes results in a net increase in transport through the ITF, opposing the overall de-

creased transport due to interannual effects.

The inability of the MLR model to accurately reconstruct transport through the ITF could also be due to the opposing dynamics of the SCSRF flowing northward through Makassar Strait and out Molucca Strait at the surface, while ITF water flows down through Makassar and Molucca Straits at thermocline depths (Qu et al., 2005). These opposing flows could result in destructive interference between the interannual signals in the volume transport of the pathways or smearing of the interannual signal, making it harder for the MLR model to accurately reconstruct the interannual signal in the volume transport over the entire water column. This could also explain why the MLR model was able to correctly predict significant interannual content at Lombok and Ombai Straits in the presence of significant trends. Here, outflow from the SCSTF and the ITF could combine, allowing for interannual and secular signals to manifest.

Understanding the role of NEC bifurcation migration on Indo-Pacific transport is integral to determining the impact of future, global-scale climate change on regional dynamics. Future directions for research include attempting to demonstrate the relationship between NEC bi-

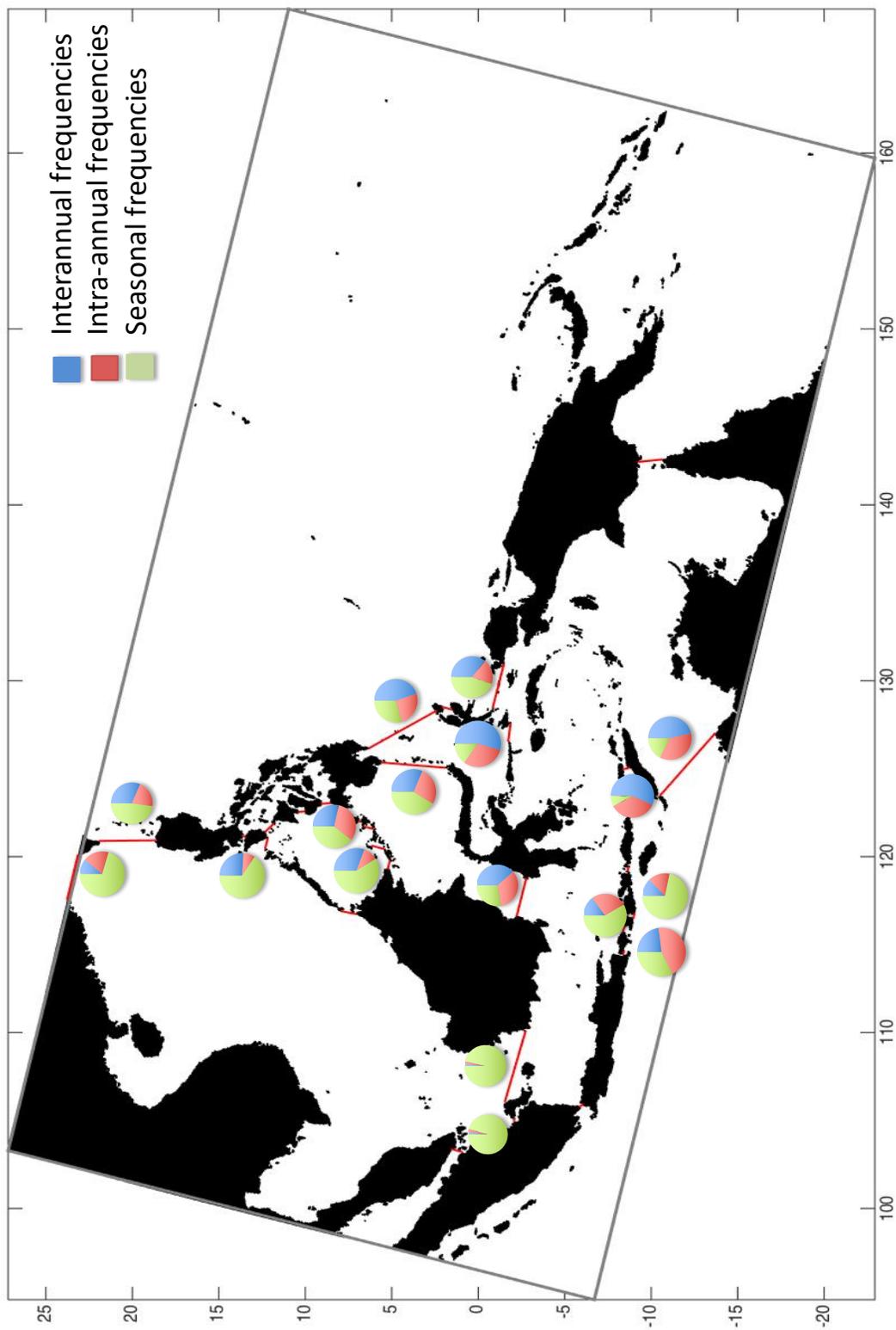


Figure 2.11: Pie charts representing the total power spectral density content at frequencies greater than 0 and less than 3 cycles per year, demeaned and detrended. Green wedges represent the seasonal cycle, blue wedges interannual content and red wedges intra-annual content. Generally, passages with the greatest seasonal content are seen along the SCSTF, and passages with the greatest interannual content are seen along the ITF.

furcation migration and modulation of Coral Triangle throughflow, and to further assess the ability of the MLR model to accurately predict transport through the ITF by attempting to predict the SCSRF at the surface and the ITF at thermocline depth by separating the water column into two layers. In particular, the ability of the model to predict the interannual content of the flows at the surface and at depth should be investigated. Understanding the cumulative effects of ENSO, IOD, and PDO, as well as secular changes in climate, on circulation through the CT provides better knowledge of the circulation that delicate coral reef ecosystems might experience under future climate scenarios and provides a context for how reef connectivity may evolve under changing climate.

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Chapter 3

ENSO-Modulated Variability in Ecoregion Connectivity in the South China and Indonesian Seas

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Abstract

The South China and Indonesian Seas are at the confluence of several major current systems and experience seasonal, annual, and interannual changes in circulation. These seas surround the Coral Triangle, one of the most important and threatened ecosystems in the world. The present study uses horizontal velocity fields from the Coral Triangle implementation of the Regional Ocean Modeling System (CT-ROMS) to

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calculate trajectories for passive particles released in coral reef locations within eight ecoregions in the South China and Indonesian Seas. Average particle retention, sources and sinks during El Niño and La Niña events are evaluated for each of these eight ecoregions after 20-, 40-, 60-, 80-, and 100-day pelagic larval durations. Our results demonstrate the difficulty in characterizing this dynamic region as a whole in the context of interannual climate variability. However, these results can be used to inform selection of localized areas for more detailed modeling studies which can better inform ecological management decisions that might emphasize protection of source or refugia reefs or that maximize biodiversity or the preservation of unique assemblages.

3.1 Introduction

The Coral Triangle (CT) region of the Indonesia/Philippines archipelago (Figure 1.1) is simultaneously one of the most dynamically complex and ecologically important regions in the world. The CT is the most biodiverse ecosystem in the world, including 35 percent of the world's coral reef fish species and 30 percent of the world's coral reefs (Hoegh-Guldberg et al., 2009). Unfortunately, it is simultaneously the most threatened reef system worldwide with 95 percent of its reefs listed as

threatened (Burke et al., 2011). Understanding the combined effects of circulation and ecologically-driven larval release strategy on regional connectivity is necessary to protect this fragile but important ecosystem.

The confluence of major ocean currents to the east, the South China Sea Returnflow (SCSRF) to the west, and the Indonesian Throughflow (ITF) through the CT all contribute to the region's complex dynamics (Figure 1.1). The SCSRF is seasonally modulated by monsoonal winds. The SCSRF, as described in Xu and Malanotte-Rizzoli (2013), is as follows. During boreal winter, surface water is transported into the South China Sea (SCS) through Luzon Strait from waters of the western equatorial Pacific, including the Kuroshio current, and heads southward along the Vietnam coastline. This current then splits, with a smaller branch flowing northwestward into the Gulf of Thailand, while the main flow continues southward out of Karimata Strait, and eastward into the Java Sea. The Southeast monsoon then drives the fresher SCS surface water northward into Makassar Strait over the saltier, southward-flowing ITF, setting up a northward pressure gradient and reducing net transport (Gordon et al., 2003; Sprintall et al., 2004). During summer, water flows upward into the SCS through Karimata

Strait, with a small branch turning into Malacca Strait and with the predominant flow heading eastward into the SCS basin. The surface flow then exits the SCS as the South China Sea Throughflow (SCSTF) through Luzon Strait (Wyrтки, 1961).

Some of the water transported through Luzon Strait exits the SCS through Mindoro Strait, rather than Karimata; this outflow is known as the Mindoro Strait outflow (Qu et al., 2006b). Having entered the Sulu Sea via Mindoro Strait, water can then exit the Sulu Sea and enter the Celebes Sea via the Sibutu Passage, allowing the SCS to directly influence the Celebes Sea (Qu et al., 2009). Flow through Mindoro is monsoonally modulated, flowing northward during the Northeast monsoon and southward during the Southwest monsoon (Wyrтки, 1961).

SCSTF transport is also modulated by ENSO. A weaker Kuroshio intrusion into Luzon Strait occurs during El Niño as a result of northward migration of the North Equatorial Current (NEC) bifurcation; conversely, the Kuroshio intrusion into Luzon strengthens during La Niña conditions and southward migration of the NEC bifurcation (Xiang-Hui and Fei, 2014; Ho et al., 2004). However, the total Luzon Strait transport is stronger during El Niño and weaker during La Niña con-

ditions (Qu et al., 2004). This communication of ENSO into the SCS through Luzon Strait effectively connects the SCS and Pacific Ocean on interannual timescales. Finally, an increase in Mindoro Strait transport could shift the NEC bifurcation southward, strengthening the Kuroshio intrusion (Qu et al., 2009). This migration of the NEC bifurcation and variation in the strength of the Kuroshio intrusion alter water column properties, thereby affecting larval environments and, potentially, altering connectivity at a population and regional scale.

Many larvae experience life in the water column from a predominantly passive perspective; that is, they do not swim faster than the currents in which they reside. As such, understanding the effects of interannual processes like ENSO on regional circulation is necessary to understanding potential fluctuations in regional connectivity as a function of these interannual processes. Larval connectivity places important constraints on the genetic variability and survival of populations (Cowen and Sponaugle, 2009) and is heavily influenced by circulation (e.g., Wood et al., 2014), winds (e.g., Cuif et al., 2014; Zhang et al., 2016), sea surface temperatures (e.g., Kleypas et al., 2016), predators and physical barriers to dispersal such as turbid, fresh-water plumes (e.g., Foster et al., 2012).

Understanding the likely environmental impacts of both anthropogenic and climate-related factors on larval connectivity is integral to mapping marine protected areas (MPAs) in locations that would maximize the survival of the metapopulation. Figueiredo et al. (2014) theorized that a majority of reefs will experience a several-fold decrease in larval dispersal as surface waters continue to warm under climate change. While this decrease in dispersal will potentially make reefs more responsive to conservation efforts, decreased dispersal also may increase reef recovery time following disturbances like hurricanes. These management decisions require information that can help identify potential refugia, such as biophysical and genetic modeling studies, to identify which reefs function as sources/sinks and which reefs are more genetically diverse and evolutionarily adaptive.

A previous connectivity study by Thompson et al. (2014) in the CT covering 1960-2006 found increased self-seeding in the Halmahera eddy region during La Niña, possibly as a result of southeastward Halmahera eddy migration. An overall decrease in self-seeding during La Niña conditions occurred throughout the CT, most likely as a result of increased Indonesian Throughflow (ITF) transport. However, after further anal-

ysis, they concluded that variability in connectivity was due to local, stochastic processes such as small-scale eddies.

The goal of this study is to assess how differences in pelagic larval duration (PLD) impact connectivity under different ENSO phases over the last half century. The remainder of this paper examines ecoregion connectivity as a function of particle retention, sources and sinks within eight ecoregions throughout the SCS and Indonesian seas (IS). Section 3.2 describes the models used in the study, as well as the modeling strategy used and how the connectivity and graph theory statistics were computed. Section 3.3 shows the particle retention, source/sink, and graph theory results for the eight ecoregions in the SCS and IS. Section 3.4 discusses these results.

3.2 Methods

This study uses model output from the Coral Triangle implementation of the Regional Ocean Modeling System (CT-ROMS; as described in Castruccio et al., 2013) to provide the necessary surface velocity fields as daily averages to the offline Lagrangian particle tracking model TRACMASS (Doos et al., 2013). Larval connectivity is a combination of be-

havior and transport. However, because larval behavior varies considerably across the many species of the CT, we chose to focus on just the transport part of connectivity and not include any specific behaviors. These particles were released year-round from forty-three ecoregions within the CT (Figure 3.1) in the spirit of Veron et al. (2009). Particle retention, sources and sinks were evaluated for an eight-ecoregion subset of the forty-three ecoregions from which particles were released and tracked.

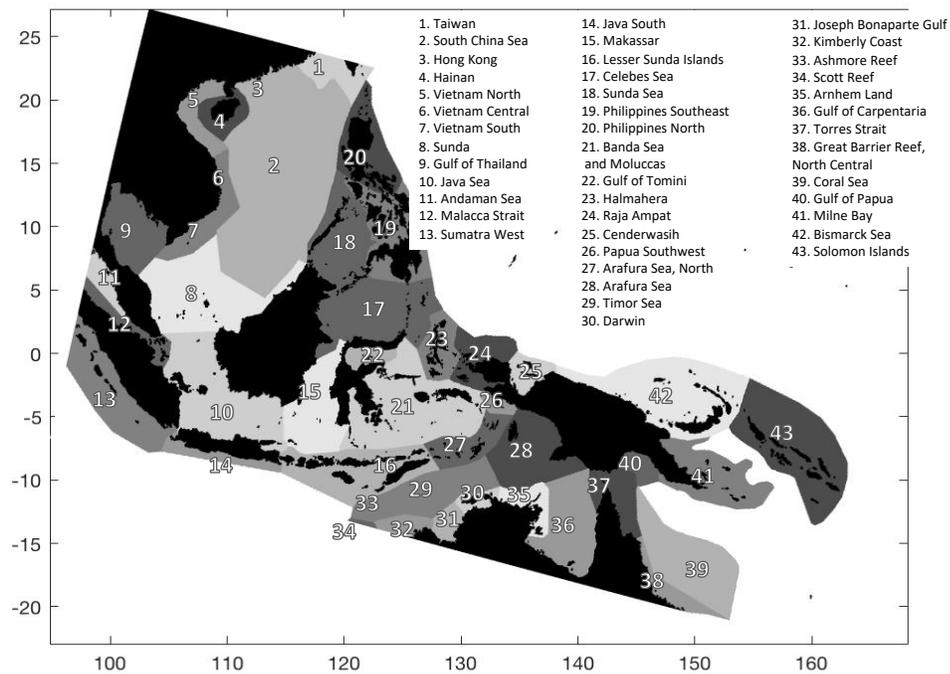


Figure 3.1: Forty-three ecoregions in the CT-ROMS domain, based on Veron et al. (2009).

3.2.1 Models

For the present study, the CT implementation of ROMS (CT-ROMS) was used as described in Chapter 2. Three five-year windows were selected from the CT-ROMS output, based on maximum variability in volume transport through thirty study passages throughout the CT over five-year intervals. Both Levene's test and the Brown-Forsythe test were used to test for maximum variability around the mean and median, respectively. Periods of high variability were selected from these results for the 1960s (April 1962-March 1967) and 1980s (October 1982-September 1987). In addition to meeting the criteria from the Levene's and Brown-Forsythe tests, these periods also exhibited significant ENSO events, with the 1960s window including one moderate and one severe El Niño event and one weak La Niña event, and with the 1980s window including one moderate and one very severe El Niño event and two weak La Niña events.

No period meeting the criteria from the Levene's and Brown-Forsythe tests was present during the 2000s; thus, the five-year period from September 1997-August 2002 was selected since it includes the very strong 1997-1998 El Niño and the moderate 1998-2000 and weak 2000-

2001 La Niñas. While the 1998-2000 La Niña events were moderate in strength, a recent study by Kleypas et al. (2015) investigating the regional effects of ENSO found high levels of severe bleaching during the 1998-1999 La Niña event, with heat stress events more frequent during La Niña events, making the selection of the 1997-2001 period appropriate. To investigate the effects of ENSO, ecoregion connectivity patterns during El Niño, La Niña, and ENSO neutral months were assessed.

The Lagrangian particle tracking scheme, TRACMASS, uses surface velocity fields from CT-ROMS to infer particle trajectories. The trajectories are calculated offline, allowing many more simulations to be conducted than would otherwise be possible if particle trajectories were obtained concurrently with the CT-ROMS simulation. TRACMASS calculates the analytical solutions to the differential equations relating velocity and location using linear interpolation in both time and space. For additional information on the details of TRACMASS, see Doos et al. (2013). TRACMASS has already been employed with CT-ROMS output for offline experimental runs, with results published in Thompson et al. (2018).

3.2.2 Model Release Strategy

The forty-three ecoregions within the CT, including the SCS and IS, are designated and named based on Veron et al. (2015). The eight-ecoregion subsample is selected based on previous work conducted in Chapter 2, which found that a significant portion of the interannual frequency content in the volume transport through passages along the SCSTF to the Pacific Ocean could be reconstructed by a multiple linear regression model which used the Oceanic Nino Index, Dipole Mode Index, and the Pacific Decadal Oscillation Index as explanatory variables. These passages include those circumscribing the SCS: Luzon and Formosa Straits to the north, Karimata and Bangka Straits to the south, as well as Mindoro Strait connecting the SCS to the Sulu Sea. Additional passages which were successfully reconstructed included Tablas Strait and Verde Island Passage in the Philippines; Sibutu Strait and Mindanao Sea connecting the Sulu Sea to the Celebes Sea; and Alas, Lombok and Bali Straits connecting the SCSTF to the Indian Ocean. Based on this work, ecoregions which encompass the primary transport pathways through the SCS and IS are selected to examine the effects of interannual processes, specifically ENSO, on ecoregion connectivity over the last half century. We refer to these eight ecoregions as Philip-

Philippines North, Taiwan, SCS, Sunda, Java Sea, Makassar, Celebes Sea, and Sulu Sea ecoregions (Figure 3.2).

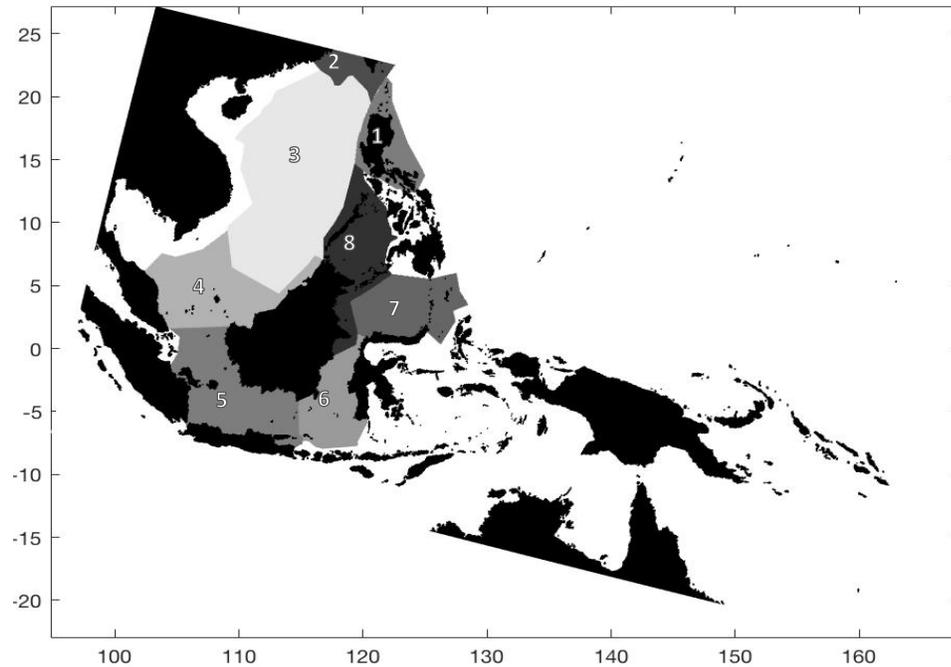


Figure 3.2: SCS and IS ecoregions: 1. Philippines North, 2. Taiwan, 3. SCS, 4. Sunda, 5. Java Sea, 6. Makassar, 7. Celebes Sea, 8. Sulu Sea.

Forty passive, surface-following particles were released at the surface of every grid cell with some reef coverage in the CT-ROMS model domain (Thompson et al., 2014). This number of particles is consistent with previous work using ROMS in the CTregion (e.g., Thompson et al. (2014) with 25 particles/grid cell; Dorman et al. (2016) with 50-200 particles/grid cell).

Based on a range of PLDs for a variety of reef species, short (20 days), moderate (40 and 60 days), and long PLDs (80 and 100 days) were examined (e.g., Harii et al., 2002; Richmond, 1988; Riginos and Victor, 2001). While larvae typically live under ideal conditions in culture and, consequently, metamorphose within a short time, it is noteworthy that genetic connectivity has been observed between distal reefs which suggests, in some cases, a much longer PLD. A recent modeling experiment found that infrequent connections were possible between East and West Pacific populations (Wood et al., 2014). In coral, survival, followed by successful settlement and metamorphosis, over these long time periods is possible through a combination of reduced oxygen consumption, reabsorption of organic matter, the presence of zooxanthellae, partial metamorphosis to a planktonic polyp capable of heterotrophic feeding, and the consumption of fat storage (Graham et al., 2008, 2013; Richmond, 1987). Aside from laboratory observations, known fat reserves and metabolic consumption rates place PLDs around 100 days for some coral species, such as *Pocillopora damicornis* (Richmond, 1987). Thus, long PLDs (greater than 100 days) are not only possible, but also are known for species depending on physiological characteristics and genetic diversity. However, species such as these are the exception rather than the norm; most species have relatively short PLDs as shown in

Figure 3.3, with increasingly fewer viable larvae as time progresses.

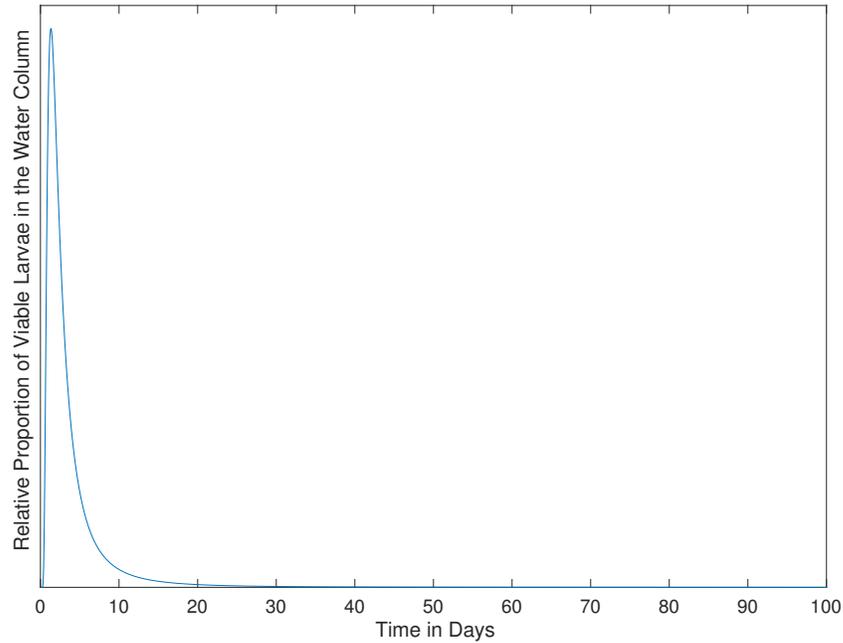


Figure 3.3: Larval probability distribution curve, depicting the relative proportion of larvae in the water column as a function of time. Most larvae settle out of the water column quickly, with only occasional individuals surviving for extended periods of time.

In the present study, particles are released year-round on day 6 following the new moon (in contrast to Thompson et al. (2014) which released particles annually during the April full moon) in order to coincide with a particular tidal cycle phase. Some corals such as *P. damicornis* are known to reproduce at this time within the study area (Cumbo et al., 2012), which inspired our release strategy. Our intent was not to represent one particular species but rather to gain a better under-

standing of regional connectivity in the mixed layer. How connectivity is mediated by the length of time the particles are in the water (analogous to the biological parameter, PLD) and how ENSO might impact this regional connectivity are our focus in the current paper.

3.2.3 Connectivity and Graph Theory Computations

Potential connectivity, here defined as the percentage of passive particles traveling from one ecoregion (source) to another (sink), is calculated for the 43 ecoregions of the equatorial western Pacific within the model domain. For each particle release, all of the particles are followed for the duration of the release (100 days) to one of the 43 ecoregions. The percentage of particles that travel to each of the 43 ecoregions, including the source ecoregion, of the total number of particles released is computed. These values are stored as 43x43 connectivity matrices for 20, 40, 60, 80, and 100 days after release. These connectivity matrices are then used to determine how “sourcy” or “sinky” an ecoregion is. “Sourciness” is defined as the number of ecoregions that a given ecoregion contributes particles to, while “sinkiness” is the number of ecoregions that contribute particles to a given ecoregion. Particle retention, defined as the percentage of particles that remained in a given ecoregion following release, is also calculated. If even one particle suc-

cessfully traveled from ecoregion A to ecoregion B, it was counted and contributed to the sourciness calculation. The same is true for sinkiness. Thus, these statistics include exceedingly rare events/connections. The sourciness, sinkiness, and particle retention for a given ecoregion are then plotted as pies, with the pie divided into 20-, 40-, 60-, 80-, and 100-day wedges, allowing us to depict the time evolution of sourciness, sinkiness, or particle retention for a given ecoregion, using code modified from Defne et al. (2016).

To explicitly depict connectivity differences among ENSO conditions, graph theory is used in the spirit of Treml et al. (2008). A graph-theoretic framework is useful for examining marine connectivity because it provides directionality and a spatial context for the connections within a network. Nodes represent the ecoregion in question. Arrows, also known as arcs, connect ecoregions and are used to show the direction of particle transport from one node to another, with the arrow pointing in the direction of particle flow and arrow thickness representing the strength of the connection. Gray arrows represent persistent “strong” connections that are present during all three ENSO conditions; here, this depicts greater than 15% of particles released from source to sink ecoregions. Weak but persistent connections that exist

during all three ENSO conditions are not shown. Colored arrows represent connections that only occur during specific ENSO phases. These arrows are generated directly from summing across the rows of the connectivity matrix (Figure 3.4).

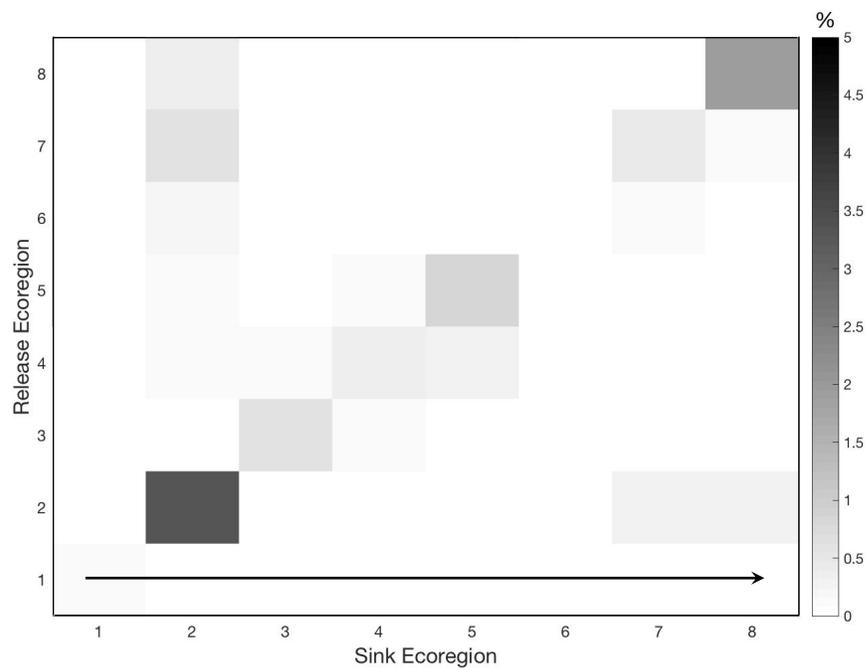


Figure 3.4: Particle Potential Connectivity Matrix as a total percentage of particles released, averaged over April 1962-March 1966 after 20 days.

For the full 43x43 connectivity matrix, the sum across a particular row indicates the total number of particles that were released for a given ecoregion. Each cell in a given row indicates how many particles ended up in a given ecoregion after a set period of time. Cells on the diagonal of the full connectivity matrix represent particle retention—particles

that “settle” in their originating ecoregion.

To convert this connectivity matrix into a graph theory-type plot, the tail of the arrow is placed in the ecoregion in which the particles were released, and the head of the arrow points toward one of the other ecoregions to which particles successfully traveled. The thickness of the arrow is determined by the total percentage of particles that traveled into that ecoregion of the possible 43 ecoregions (e.g. Figure 3.8, below). To depict particle retention, colored rings were used to show the mean particle retention across the three interannual conditions (El Niño, La Niña, and ENSO neutral), the warmer the color, the greater the particle retention. The diameter of the colored rings increases as a function of the standard deviation among the three particle retention values for each ecoregion; the greater the standard deviation, the greater the diameter of the ring.

3.3 Results

Particle retention within the study ecoregions is generally high, with greater particle retention during El Niño conditions than during La Niña conditions. Taiwan experiences significantly greater particle re-

tention during El Niño ($\geq 5\%$) after all dispersal periods: 20-day (+13.2%), 40-day (+16.3%), 60-day (+7.8%), 80-day (+6.2%), and 100-day (+5.6%) dispersal periods. SCS experiences greater particle retention during El Niño after 40- (+9.2%), 60- (+10.3%), 80- (+11.5%), and 100-day (+11.0%) dispersal periods; the Java Sea ecoregion experiences increased particle retention after 60- (+5.8%), 80- (+6.0%), and 100-day (+6.5%) dispersal periods; and the Celebes Sea ecoregion experiences increased particle retention after 20-day (+8.3%) dispersal periods. The Philippines North, Sunda, and Sulu Sea ecoregions do not experience significant changes in particle retention, while Makassar experiences decreased particle retention under El Niño conditions during 100-day particle dispersal periods (-6.4%).

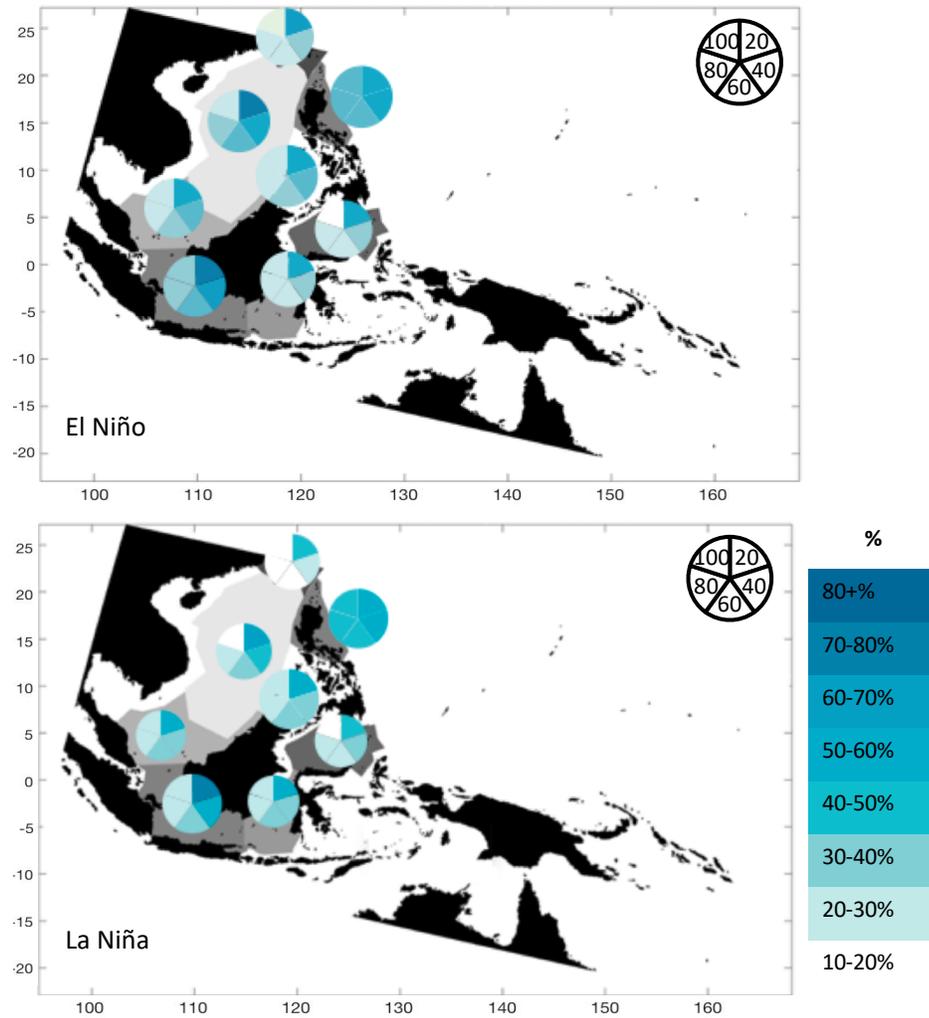


Figure 3.5: Particle retention as a percentage of the total number of particles released per ecoregion. Starting at the first wedge of the pie, pie wedges show particle retention percentage (%) 20, 40, 60, 80, and 100 days after particle release.

The SCS in particular experiences significant increases (≥ 2 ecoregions) in sourciness during La Niña conditions after dispersal periods of 40 (+3 ecoregions), 60 (+3), and 80 (+2) days. Other ecoregions of note include the Sunda ecoregion, which experiences increased sourciness after a 40-day (+3) dispersal period; the Java Sea ecoregion, which experiences increased sourciness after 20- (+2) and 40-day (+3) dispersal periods; and the Makassar ecoregion, which experiences increased sourciness after 20- (+2) and 60-day (+3) dispersal periods. The Taiwan, Celebes Sea, and Sulu Sea ecoregions do not experience significant changes in sourciness during any of the 5 dispersal periods. The Philippines North ecoregion shows the opposite pattern, with significantly decreased sourciness during La Niña conditions after 60- (-3) and 80-day (-5) dispersal periods.

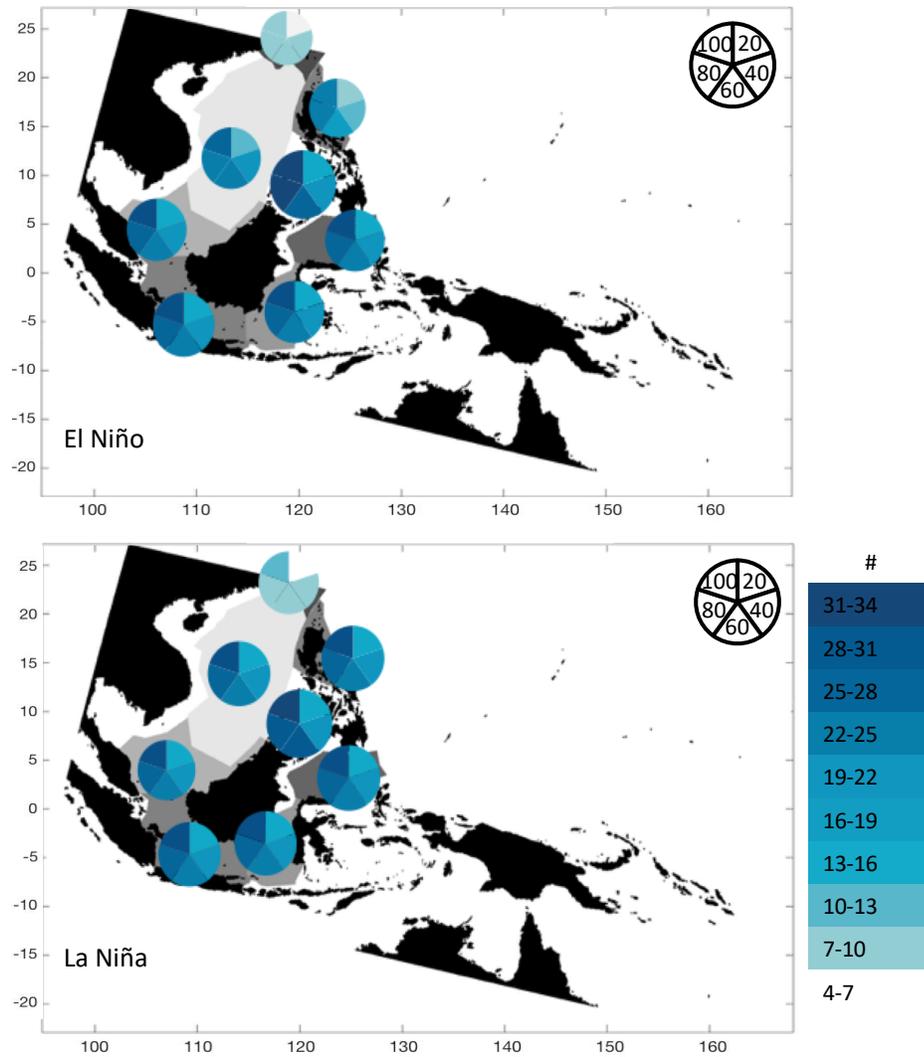


Figure 3.6: Sourciness as a function of the number of ecoregions that the particles from a particular ecoregion travel to. Starting at the first wedge of the pie, pie wedges show # of ecoregions 20, 40, 60, 80, and 100 days after particle release.

During La Niña, the Philippines North ecoregion experiences increased sinkiness after 40- (+4) and 100-day (+4) dispersal periods; the Taiwan ecoregion experiences increased sinkiness after 40-day (+3) dispersal periods; and the SCS ecoregion experiences increased sinkiness after 60-day (+2) dispersal periods. The Sunda and Java Sea ecoregions do not experience any significant changes in sinkiness between El Niño and La Niña conditions. Finally, the Makassar, Celebes Sea and Sulu Sea ecoregions experience significantly decreased sinkiness during La Niña conditions, with Makassar experiencing decreases after 60- (-3), 80- (-4), and 100-day (-6) dispersal periods, the Celebes Sea experiencing decreases after 60- (-2) and 80-day (-3) dispersal periods, and the Sulu Sea experiencing a decrease after an 80-day dispersal period (-2).

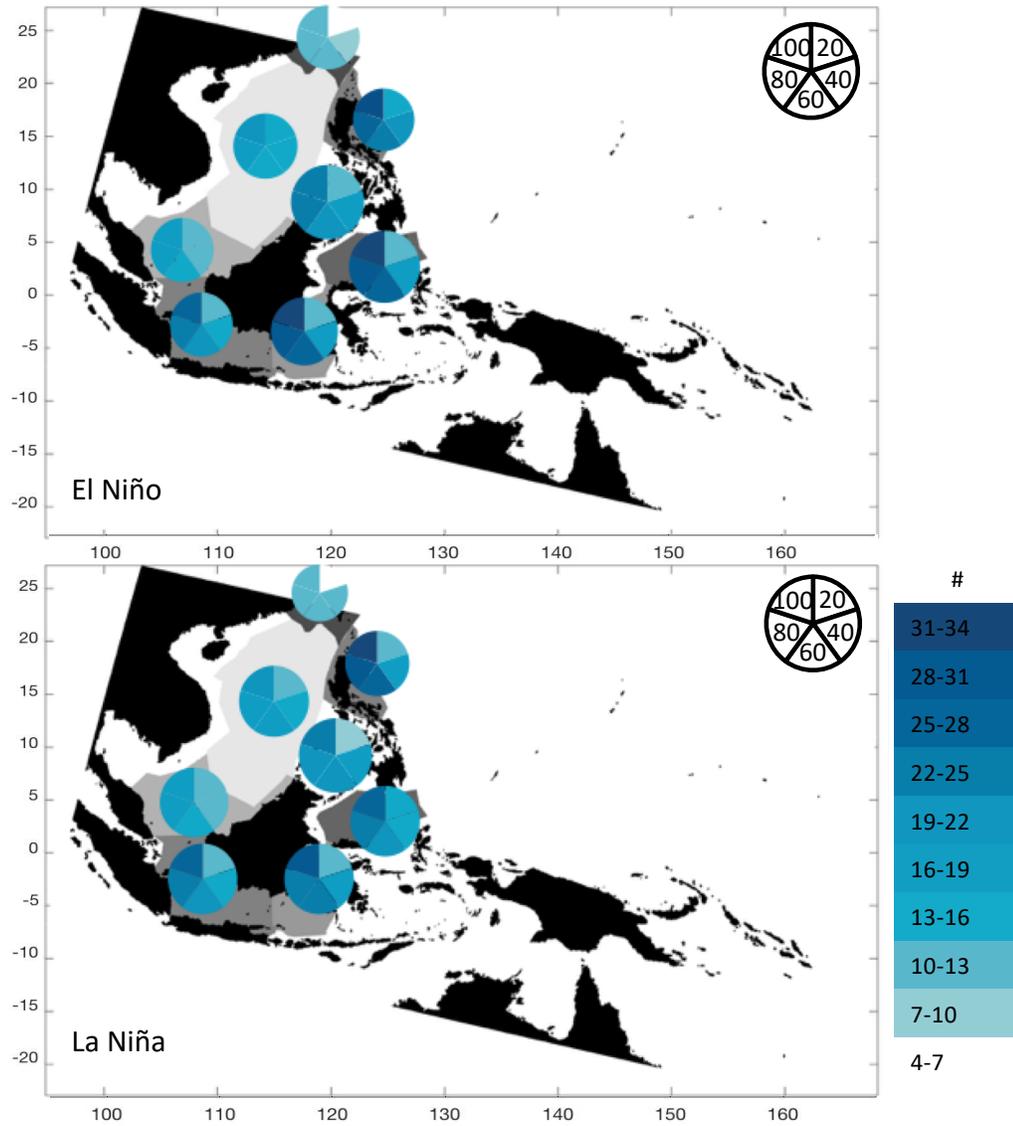


Figure 3.7: Sinkiness as a function of the number of ecoregions that contributed particles to a particular ecoregion. Starting at the first wedge of the pie, pie wedges show # of ecoregions, 20, 40, 60, 80, and 100 days after particle release.

Particle retention generally decreases, and the standard deviation of particle retention generally increases, as particle dispersal period increases. In Figure 3.8, high particle retention is consistent ($\geq 50\%$) after a 20-day dispersal period, with less particle retention for the Makassar, Celebes Sea, and Sulu Sea ecoregions. Dispersal corridors (see Trembl et al., 2012) exist from the northern Philippines to the SCS, and from Taiwan to the SCS. Weak dispersal from the SCS to Taiwan is seen during El Niño conditions only, and weak dispersal from the northern Philippines to the Celebes Sea is seen during ENSO neutral conditions only. These results are qualitatively supported by Thompson et al. (2018) which found that the northern Philippines, Taiwan and the Spratly Islands are all a single subpopulation if the CT is divided into 4 subpopulations after a 30-day PLD. However, in their scenario, the Sulu Sea was also part of this subregion, while in our results, the Sulu Sea is isolated, having no dispersal corridors or weak ENSO-dependent connections. Thompson et al. (2018) also found that western Indonesian reefs were strongly isolated from other regional reefs after a 30-day PLD. Again, these results qualitatively agree with the results in the present study: no dispersal corridors were found from the Sunda and Java Sea ecoregions after a 20-day PLD; only weak pathways exist from Sunda to the Celebes Sea, and from the Java Sea to the SCS ecoregion

during La Niña conditions. Finally, a weak dispersal pathway exists from the the Makassar ecoregion to the Celebes Sea during La Niña conditions and ENSO neutral conditions.

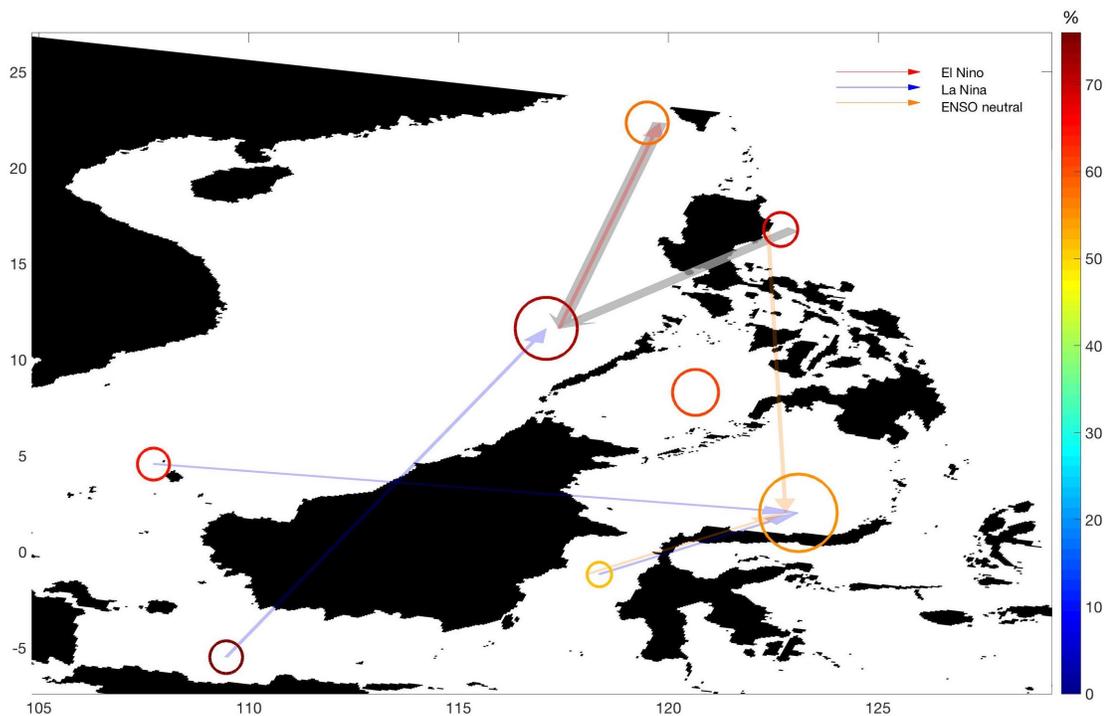


Figure 3.8: Graph theoretic plot of ecoregions along the SCSRF after 20 days. Gray arrows indicate persistent pathways with at least 20% of particles traveling from one ecoregion to another under all three ENSO conditions; colored arrows indicate transport of particles from one ecoregion to another under a specific climate condition. Color of the dots indicates the mean % particle retention and the radius of the dots indicates the standard deviation under the three climate conditions.

After a 60-day dispersal period, particle retention is strongest at the upstream ecoregions: Philippines North, SCS, Sunda, and Java Sea ecoregions and weaker further downstream (Makassar, Celebes Sea, and Sulu Sea ecoregions; Figure 3.9). Dispersal corridors direct flow from the northern Philippines to the SCS, from the SCS to the Sulu Sea,

from the Sunda ecoregion to the SCS, and from Makassar to the Java Sea, while a persistent, bi-directional dispersal pathway connects Sunda and the Java Sea, suggesting that, at moderate PLDs, these ecoregions should instead be considered one ecoregion. Weak dispersal pathways during La Niña conditions connect Taiwan and the northern Philippines to Sunda. During ENSO neutral and La Niña conditions, a weak pathway connects Makassar to the Celebes Sea, and during El Niño and ENSO neutral conditions, pathways exist from the SCS to Makassar and from the northern Philippines to the Celebes Sea. Finally, weak dispersal exists from Taiwan to the northern Philippines during El Niño years only.

Following a 100-day larval dispersal, particle retention is highest within Philippines North, SCS, and Java Sea ecoregions, and lower at the Taiwan, Sunda, Makassar, Celebes Sea, and Sulu Sea ecoregions. Standard deviations were relatively large at Makassar and Sulu Sea ecoregions. Dispersal corridors connect the Makassar ecoregion to the Java Sea ecoregion, and the Java Sea ecoregion to the Sunda ecoregion (Figure 3.10). Weak dispersal during La Niña conditions connect Taiwan to Sunda, and the northern Philippines to Sunda and the Java Sea. During La Niña and ENSO neutral conditions, weak dispersal oc-

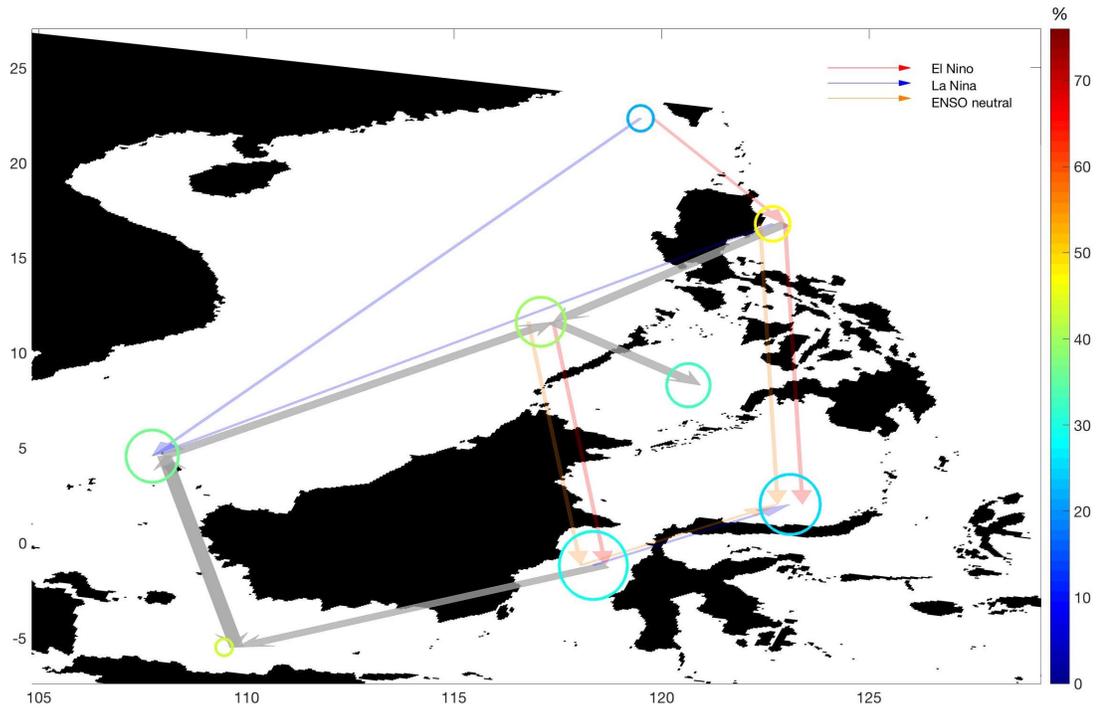


Figure 3.9: Graph theoretic plot of ecoregions along the SCSR after 60 days. Gray arrows indicate persistent pathways with at least 20% of particles traveling from one ecoregion to another under all three ENSO conditions; colored arrows indicate transport of particles from one ecoregion to another under a specific climate condition. Color of the dots indicates the mean % particle retention and the radius of the dots indicates the standard deviation under the three climate conditions.

curs from Makassar to the Celebes Sea, and during El Niño and ENSO neutral conditions, dispersal between the northern Philippines and the Celebes Sea occurs. Finally, dispersal pathways during El Niño conditions alone exist from the Sulu Sea to Taiwan, and from the Celebes Sea to the SCS and northern Philippines.

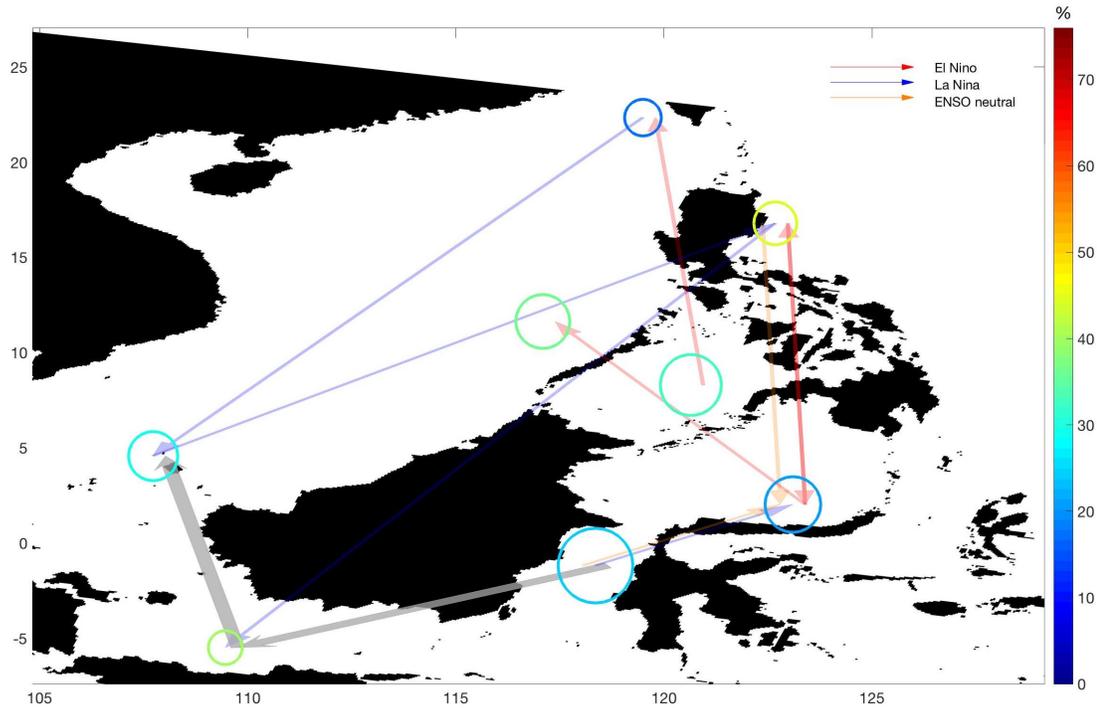


Figure 3.10: Graph theoretic plot of ecoregions along the SCSRF after 100 days. Gray arrows indicate persistent pathways with at least 20% of particles traveling from one ecoregion to another under all three ENSO conditions; colored arrows indicate transport of particles from one ecoregion to another under a specific climate condition. Color of the dots indicates the mean % particle retention and the radius of the dots indicates the standard deviation under the three climate conditions.

3.4 Discussion

By using a mixed-layer, passive particle model in our research, we omit many processes that would impact larval distribution in more realistic scenarios. Despite this, our results demonstrate the inherent complexity of attempting to characterize a suite of circulatory scenarios for the mixed layer that are ecologically relevant to the dynamic CT. Generally, there is much spatial heterogeneity in regional connectivity that experiences changes as a result of interannual climate phenomenon; in-

creased levels of model complexity will not remove this climate influence on connectivity but may perhaps obscure it. As the most biodiverse ecoregion in the world, considering the role that circulation plays on the transport of new recruits as well as its influence on genetic diversity of populations is crucial to making informed management decisions such as the location, number and duration of MPAs.

Consideration when designing an MPA should be given to resilience of local populations to climate change, protecting those populations that serve as refugia. In coral reefs ecosystems, the effects of climate change conditions including thermal stress and coral bleaching should be considered. Elevated temperatures induce higher rates of mortality and may produce a several-fold increase in local retention, increasing the genetic isolatedness of reefs that were previously well-connected (e.g., Cumbo et al., 2013; Figueiredo et al., 2014; Nozawa and Harrison, 2007). Thus, those reefs that were particularly strong sinks may experience a decrease in stock following extreme disturbances and have slower recovery. Conversely, those reefs that are already fairly isolated may actually demonstrate quicker than normal recovery times with decreased PLD. To account for this, MPAs should be selected which incorporate a variety of historical temperature regimes.

While many management decisions go into defining a single MPA, Gaines et al. (2010) proposed the idea of a network of MPAs which can have additive or multiplicative effects on biological and ecological parameters such as biomass. Previous studies have shown that if one assumes that an MPA is closed (does not have organisms migrating in from outside the MPAs), then for the MPAs to be self-sustaining, it must be larger than the mean dispersal distance of the species in question (Botsford et al., 2001; Lockwood et al., 2002). But, if a network of MPAs is implemented, then the total area of the network need only be 1/2 to 1/3 of the area needed for a single MPA in order to promote self-sufficiency and sustainability of the protected species (Botsford et al., 2001). And, as suggested by Crowder et al. (2000), it seems logical to protect those regions which are the strongest upstream sources, thereby contributing the most to other locations while harvesting from strong downstream sinks.

In creating networks, MPAs need to be placed along dispersal corridors (e.g. Malhi et al., 2008; Wilson and Willis, 1975) as has been implemented terrestrially in Gondwana and elsewhere (e.g. Klausmeyer and Shaw, 2009), linking protected areas to one another and providing

multiple protected habitats for nomadic species (Gaston et al., 2008) and potentially reducing inbreeding in populations. In the terrestrial environment, these corridors are designed to connect protected areas and are typically static in nature, as barriers to dispersal in the terrestrial environment are also usually static (Carr et al., 2003). However, the relative openness of MPAs, compared to their terrestrial counterparts, needs to be accounted for, as both larvae and adults of many pelagic and sessile species can readily move outside MPA domains. To strengthen networks of MPAs along the SCSRF, MPAs should be implemented protecting dispersal corridors for larvae with short PLDs from the northern Philippines and Taiwan to the South China Sea and Spratly Islands; for larvae with moderate PLDs from the northern Philippines to the SCS, from the SCS to the Sulu Sea, from the Sunda ecoregion to the SCS, and from Makassar to the Java Sea; and for larvae with long PLDs from Makassar to the Java Sea, and the Java Sea ecoregion to the Sunda ecoregion. In marine ecosystems, barriers to dispersal in the physical environment are mobile, being controlled by factors like current location and migration, zones of upwelling and downwelling, thermal fronts, and eddies which would require corridors to be defined in the context of these currents and for the corridors to be able to migrate with the currents they are designed to protect, adding

an additional, dynamic layer of protection to networks of MPAs (Carr et al., 2003; Game et al., 2009).

In the context of our study region, one suggestion might be to devise a network of relatively small MPAs particularly in the SCS (which, unsurprisingly, has relatively high sourciness even after a 20-day PLD), and the Sulu Sea and Java Sea ecoregions (which also have relatively high sourciness after 60-, 80-, and 100-day PLDs; Figure 3.6). Since these ecoregions in particular were able to disperse at least some particles to a majority of ecoregions, they would be particularly valuable from a conservation standpoint because of their capacity for widespread reseedling of reefs that have experienced deleterious events. As reefs experience increased bleaching and thermal stress under La Niña conditions (Kleypas et al., 2015), the SCS ecoregion in particular might be influential in repopulating sink ecoregions, since it experiences increased sourciness during La Niña after 40-, 60-, and 80-day PLDs and would, thus, be a strong candidate for establishment of a network of MPAs as the variability in PLDs represented would encompass a variety of species. The Sunda and Java Sea ecoregions, which also experience increased sourciness under La Niña conditions, would also be candidates for MPAs under this criteria.

Although preserving strong source regions is conservationally important to survival of the species in question, preserving strong sink regions may be important to preserving species richness and genetic diversity (Almany et al., 2009). Areas which are particularly biodiverse or are important to endemic species should also be included in MPAs, in addition to strong source regions (e.g., Green et al., 2009). And, since strong sinks may recover more slowly following disturbances, reefs in these regions are particularly vulnerable and may benefit from the establishment of MPAs.

In the present work, the northern Philippines is especially sinky; as such, it might be a good region in which to look for particularly biodiverse reefs that would be good candidates for MPAs seeking to preserve species richness (Figure 3.7). Coral reefs in the western equatorial Pacific generally experience increased bleaching and thermal stress under La Niña. The Makassar, Sulu Sea and Celebes Sea ecoregions would also benefit from the establishment of MPAs since they experience decreased sinkiness at longer PLDs during stressful conditions; thus, populations with long PLDs would receive particles from fewer ecoregions, potentially decreasing the evolutionary diversity and ther-

mal tolerance of these downstream regions (Figure 3.7). Ecoregions such as the northern Philippines, SCS and Taiwan may actually be more resilient to changing climate since they experience increased sinkiness under La Niña conditions over moderate to long PLDs.

Additionally, isolated regions that may have unique assemblages and populations should also be included in MPA design (Almany et al., 2009), as these locations may contribute to maintaining the allelic richness of a particular species. Previous work by Pinsky et al. (2012) suggested that populations which are greater than twice the standard deviation of larval dispersal distance from their neighbors can be considered isolated. In regions such as these which are susceptible to the founder effect and genetic drift, these populations are likely to be less resilient to episodic events and climate change; to ensure the survival of these regions, large geographic portions should be protected (Almany et al., 2009; Freedland et al., 2011).

A recent Mediterranean study found that islands experienced a significant decrease in heterozygosity compared to coastal zones, possibly as a result of non-random mating, isolation, small population size, or fishing pressures (Perez-Ruzafa et al., 2006). Thus, islands with the most

self-sustained persistence (self-seeding) would potentially benefit most from MPA protection in ensuring their survival. In the present study, the northern Philippines experience elevated particle retention over 80- and 100-day PLDs, relative to other ecoregions in the study, while the SCS and Java Sea ecoregions experience increased particle retention during 20-day PLDs. Thus, species of interest with long PLDs in the northern Philippines should be considered when formulating MPAs, while those with short PLDs (<20 days) should be considered when formulating MPAs for the South China and Java Seas. Reefs in locations like the Makassar ecoregion, which experience increased particle retention under La Niña conditions, which border islands, and which are not resilient to such stresses may be particularly vulnerable and benefit most from the protection of MPAs.

The combined effects of ocean warming and decreased levels of dissolved oxygen in the water column should also be considered, as these will induce a poleward migration, as well as a surfaceward shift within the water column, of species (Deutsch et al., 2015). However, coral migration poleward due to climate change will be self-limiting due to the need for corals to have high levels of irradiance in order to photosynthesize properly (Muir et al., 2015). In more poleward latitudes,

particularly during winter months, corals may not be able to obtain the necessary amount of solar energy to self-sustain. These findings, combined with those of the present study, suggest the need for migratory MPAs.

Generally, pathways from Taiwan and the northern Philippines to the SCS ecoregion are robust under a 20-day PLD (Figure 3.8); and persistent pathways from the Sunda Sea and the northern Philippines to the SCS ecoregion, from the SCS to the Sulu Sea, from Makassar to the Java Sea, and from the Java Sea to the Sunda Sea are evident after a 60-day PLD (Figure 3.9). The connections from Makassar to Java and from Java to the Sunda Sea persist after a 100-day PLD (Figure 3.10). Because of the robustness of these connections, they are less likely to be affected by changing climate.

Conversely, under La Niña conditions, pathways from the Sunda Sea to the Celebes Sea and from the Java Sea to the South China Sea are evident after a 20-day PLD, from Taiwan and the northern Philippines to the Sunda Sea after a 60-day and 100-day PLD, and a pathway from the northern Philippines to the Java Sea after a 100-day PLD. Likewise, some weak connections are only evident during ENSO neutral

conditions: pathways from the northern Philippines to the Celebes Sea and from the SCS to Taiwan are evident after a 20-day PLD, and a connection from the northern Philippines to the Celebes Sea after a 100-day PLD. Finally, during El Niño, a weak connection from Taiwan to the northern Philippines exists after a 60-day PLD, and weak pathways from the Celebes Sea to the northern Philippines and the SCS and from the Sulu Sea to Taiwan exist after a 100-day PLD. These pathways are only present under certain conditions for species with specific larval life histories, and thus, may benefit from temporary MPAs that can help facilitate the persistence of these pathways under specific climate conditions.

Through the combined use of state-of-the-art ocean circulation and Individual-based models (IBMs), as well as *in situ* and laboratory measurements, we can hope to begin to quantify the potential migratory pathways of ecologically and economically relevant species like corals. In addition, IBMs with finer resolution and with realized connectivity, which allows for the examination of the effects of environmental conditions such as SST on potential connectivity, need to continue to be developed. Finally, ongoing efforts examining the past and future effects of climate change at the local level need to continue to help inform

management decisions regarding more strategic placement of MPAs.

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Chapter 4

Static Marine Protected Areas: An Effective Management Tool in a Changing Climate? The Coral Triangle –A Case Study

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Abstract

Anthropogenic impacts threaten coral reefs worldwide and need to be curtailed through effective implementation of ecosystem-based management tools like marine protected areas (MPAs). The Coral Triangle (CT), the epicenter of marine biodiversity, is particularly vulnerable, with only a small percentage of its reefs located in MPAs and listed as

being effectively managed. The present study uses horizontal velocity fields from the Coral Triangle implementation of the Regional Ocean Modeling System (CT-ROMS) to calculate trajectories for passive particles released in coral reef locations within ten ecoregions along the Indonesian Throughflow (ITF). Average particle retention, sources and sinks during three five-year periods from the 1960s, 1980s and 2000s are evaluated for each of these ten ecoregions after 20-, 40-, 60-, 80- and 100-day pelagic larval durations (PLDs). Because of the region's complex ocean dynamics, no single narrative explains the decadal and secular variability in particle retention and regional sources and sinks along the ITF. However, these results can be used to select localized areas of study. Overall, our research suggests the need for dynamic MPAs, which could include temporary, migratory or zoned MPAs, in the context of changing climate and its impacts on larval transport. Such implementations may provide increased compliance from local stakeholders, prove more cost-effective, and more effectively meet longterm conservation goals than current, static MPAs.

4.1 Introduction

Human impacts pose a significant threat to the ocean's ecosystems including coral reefs which provide essential nursery grounds for various fish species and other valuable ecosystem services (Nagelkerken et al., 2000). Anthropogenic impacts, which include overfishing, tourism activity, pollution, excess nutrients in river runoff, and anthropogenically-driven ocean acidification and global warming, need to be curtailed. While management efforts can support individual fisheries through temporary or permanent closure, ecosystem-based management decisions such as the implementation of marine protected areas (MPAs) can help protect fragile and vital ecosystems as a whole.

MPAs can result in effective increases in biomass, biodiversity and size of individuals within their bounds (e.g. Lester et al., 2009; Claudet et al., 2008; D'Aloia et al., 2017). Gaines et al. (2010) first proposed the idea of a network of MPAs, which can have additive or multiplicative effects on biomass when compared to each isolated MPA. And, a network of MPAs need enclose only $1/3$ to $1/2$ of the area required by a single MPA to ensure sustainability and self-sufficiency of the target species (Botsford et al., 2001). However, conservation efforts and fish-

ing efforts are often seen as being at odds with one another (Gaines et al., 2010), the inherent argument being that the bigger the reserve, the better, from a conservation perspective. But Gaines et al. (2010) argue that carefully designed networks of moderately-sized ($\sim 10\text{km}$) MPAs can increase fishery yields and profits, and that such a network may even be critical to optimizing harvest. Indeed, empirical studies have shown that increased catch per unit effort/area is generated in zones surrounding reserves (e.g. orangespine surgeonfish, Tupper, 2007; European spiny lobster, Goñi et al., 2010). In addition, when devising a network of MPAs, the location of the MPAs can be selected to maximize stakeholder profits, since the network as a whole may achieve the desired results with a variety of placement configurations (Game et al., 2008).

To further improve the seeming disparity between the perceived goals of conservation and fisheries, rotating MPAs, analogous to temporary closures (e.g. haddock, Murawski et al., 2000) or rotating harvest closures (e.g. northwest Atlantic sea scallop, Hart, 2003) of specific fisheries, could be implemented, rather than MPAs that are permanently closed and in a fixed location. This strategy would help assuage fishermen's reluctance to permanently close desirable fishing locations (Mc-

Clanahan et al., 2006). Game et al. (2009) speculate that, once the populations within an MPA have been allowed to recover, little additional benefit may be gained by continuing to maintain this MPA. Instead, if this MPA was rotated to a different, degraded population, then this population could begin to recover under its newly protected status, thus ensuring better overall fitness of the ecosystem; Game et al. also found that, when 10-30% of reefs were protected (the percentage range of reefs historically constrained), rotating MPAs over a subset of the total number of reefs significantly improved herbivore biomass when compared to rotating MPAs over all reefs or over static MPAs (2009). The authors point out, however, that this idea of a rotational MPAs has its drawbacks: designating new protected areas and communicating these changes to shareholders could prove expensive.

Effectively forming and enforcing even static MPAs can be a challenge. In the case of coral reefs, 95% of the reefs in SE Asia were listed as threatened in 2011, with more than 60% of reefs worldwide under immediate threat from local sources, and 55% of reefs affected by overfishing practices (Burke et al., 2011). In an attempt to address this problem, 27% of reefs worldwide are located inside MPAs; however, only 6% of reefs were effectively protected from overfishing, while another

13% of MPAs partially succeeded in protecting their reefs from over-fishing (Burke et al., 2011). These problems are particularly relevant for the Coral Triangle (CT, Figure 1.1), whose MPAs are overseen by the Coral Triangle Initiative (CTI), comprised of Indonesia, Malaysia, Philippines, Timor Leste, Papua New Guinea, and the Solomon Islands (Berdej et al., 2015). While 17.8% of coral reefs within the CT are within MPAs (a figure which the CTI hopes will reach 20% by 2020), only 1% of these reefs are considered to be effectively managed (White et al., 2014).

These reefs are vital to the survival of the many peoples of the CT who rely on them for survival. In 2009, commercial fisheries were providing 3 billion USD to the six CT countries (Hoegh-Guldberg et al., 2009). Better management and enforcement of MPAs is necessary to insure the continuation of these delicate and complex ecosystems. This can only be accomplished by uniting conservation and shareholder interests through effective communication and zoning within MPAs to allow shareholders to continue to make a living in a sustainable way. While rotational or temporary MPAs may be more expensive, they may also prove ultimately more effective because the resources within a given MPA will not be permanently restricted to local activities that

may be necessary for shareholders to survive.

While MPAs are often equated with a no-take marine reserve, MPAs could also be managed zonally or by restricting certain fishing equipment, activities, or taking certain species within their boundaries to promote compliance. Good management of key fishing stocks is necessary to prevent phase shifts (Hughes et al., 2007). For example, Bellwood et al. (2004) concluded that bioeroding, grazing and scraping herbivores should all be protected to promote reef health as they allow substrate recruitment, manage macroalgal growth and reduce algal turf. Overfishing key herbivores places reefs at risk for increased difficulty recovering from bleaching events, with the potential for a phase shift to an algal-dominated reef (Hughes et al., 2003) and a descent down the “slippery slope to slime” (Pandofi et al., 2005). While effectively managing fish stocks and restricting damaging practices such as reef detonation are an essential part of conservation efforts, MPAs are necessary but not sufficient for successful conservation efforts (Allison et al., 1998). In addition to direct, anthropogenic factors such as overfishing and destructive fishing practices, conservation efforts must also attempt to mitigate the effects of changing climate.

Currently, the combined impacts of anthropogenic factors and changing climate are threatening 75% of coral reefs worldwide, and 50% of the world's coral reefs are expected to disappear by 2050 (Burke et al., 2011; Hoegh-Guldberg, 2007). Adult corals are particularly susceptible to changing climate through coral bleaching (Donner et al., 2005), reduced skeletal integrity (Crook et al., 2013) and decreased calcification rates (De'ath et al., 2009) from ocean acidification, and shifts in coral larval transport due to changes in ocean circulation (Chapter 3). Because coral larvae are essentially passive particles, they are subject to the whims of ocean currents. And, coral larvae are also affected by changing SSTs through increased respiration (e.g. Cumbo et al., 2013), and decreased settlement (e.g. Randall and Szmant, 2009), survival (e.g. Graham et al., 2008) and pre-competency period (e.g. Heyward and Negri, 2010). Together, these climate effects impact all life stages of corals, and, because corals are the main reef-building organism, threaten the entire ecosystem.

In order to appropriately formulate networks of MPAs or dynamic MPAs to effectively protect coral reefs, connectivity studies are necessary to understanding how individuals communicate larvae and genetics downstream. Generally, information on larvae *in situ* is sparse; rather,

knowledge of larval transport and life stages comes from a combination of genetics, model-based connectivity studies and laboratory studies. Model-based connectivity studies provide an idea of how circulation distributes larvae. In a CT study by Kleypas et al. (2016), better connected reefs should be less susceptible to thermal stress due to increased genetic diversity, and source reefs with thermally resistant genetic phenotypes, such as those along the southern coasts of Sumatra and Java, should in turn increase heat tolerance of downstream reefs and should be protected through the implementation of MPAs. Reefs downstream from thermally resistant individuals, such as reefs along the ITF should then be more ecologically fit, having received larvae from these adapted reefs (Kleypas et al., 2015). In addition, it is also important to provide protection to thermally sensitive reefs since these reefs are particularly vulnerable to phase shifts (Kleypas et al., 2015). Finally, Done (2001) recommends protecting reefs which could act as refugia, insuring the overall survival of the clade.

Recent work has also examined the effects of ENSO on larval trajectories in the CT. Thompson et al. (2018) found an overall slight decrease in source and sink strength during El Niño conditions in the CT for short pelagic larval durations (PLD; 10 and 30 days). The present

work (Chapter 3) provides evidence supporting various conservation and management plans for ecoregions throughout the CT depending on ENSO phase and PLD (from 20 to 100 days). These include protecting particularly sinky locations (particles from many different ecoregions are arriving in these ecoregions) such as Makassar, the Celebes Sea and northern Philippines ecoregions to further ecosystem biodiversity and/or genetic diversity management goals; protecting sourcey (ecoregions that distribute particles to many different ecoregions) ecoregions such as the South China Sea, Sulu Sea and Java Sea as they contribute larvae to other parts of the CT and may help downstream reefs recover from bleaching events; and protecting isolated reefs such as those in the northern Philippines, Java Sea and South China Sea which are particularly retentive as they are susceptible to bleaching and poor recovery.

The goal of the present study is to assess how changing climate has impacted potential connectivity (the movement of passive particles from a source location to a sink/destination) over the past half century for various organisms with pelagic larvae by examining particle trajectories along the ITF from three five-year windows over the 1960-2007 period with a variety of PLDs (20 days to 100 days). The remainder of this paper examines ecoregion connectivity as a function of

particle retention, sources and sinks within 10 ecoregions along the ITF. Section 4.2 briefly describes the models and modeling strategy used in the study and the computation of connectivity and graph theory statistics. Section 4.3 depicts particle retention, source and sink results for the ten ITF ecoregions, while Section 4.4 seeks to place these results both in a terrestrial and marine management context and discusses how these results can be used to inform management decisions in the future.

4.2 Methods

The present study uses the CT implementation of the Regional Ocean Modeling System (CT-ROMS ; Castruccio et al., 2013) as described in Chapter 2 which provides the necessary daily average velocity fields to run TRACMASS, an offline particle trajectory model (Doos et al., 2013) and which has been previously used with CT-ROMS (Kleypas et al., 2016; Thompson et al., 2018). To examine how secular changes in circulation over the study period have impacted particle trajectories, connectivity patterns during the 1960s, 1980s and 2000s are examined using volume transport time series from CT-ROMS over three five-year periods to generate particle trajectories in TRACMASS: April 1962-March 1966, October 1982-September 1986, and September 1997-

August 2001. These time periods are selected as being particularly variable in volume transport at 30 key passages in the CT as described in Chapter 2. We decided to keep the present study simple, modeling our larvae as passive particles, because this allows for community-wide assessment of the effects of climate change over the past half century.

Briefly, particles are released year-round from the forty-three ecoregions described in Veron et al. (2009). Of these forty-three ecoregions, particle retention (the percentage of retained particles in a given ecoregion), sourciness (how many ecoregions a particular ecoregion contributes particles to) and sinkiness (how many ecoregions contribute particles to a particular ecoregion) are calculated for ten ecoregions which lie along the ITF (Figure 4.1) and are thought to be sensitive to secular changes in circulation over the study period based on results in Chapter 2. In that study, passages where significant secular trends were observed included Molucca Strait, Celebes Sea, Halmahera Sea, Lifamatola Strait, Makassar Strait, Lombok Strait, Ombai Strait and Timor Strait. Based on this work, ten ecoregions along the ITF are selected to examine secular changes in connectivity metrics: Celebes Sea, Makassar, Lesser Sunda Islands, Banda Sea and Moluccas, Arafura Sea North, Arafura Sea, Timor Sea, Ashmore Reef, Scott Reef and

Kimberly Coast ecoregions (Figure 4.1).

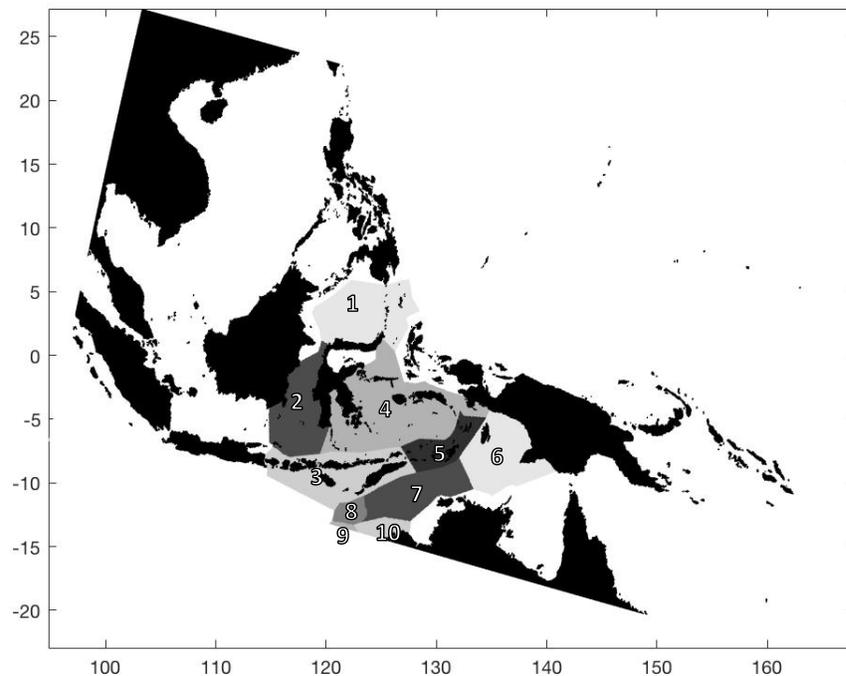


Figure 4.1: Ten ecoregions along the ITF: 1. Celebes Sea, 2. Makassar, 3. Lesser Sunda Islands, 4. Banda Sea and Moluccas, 5. Arafura Sea, North, 6. Arafura Sea, 7. Timor Sea, 8. Ashmore Reef, 9. Scott Reef, 10. Kimberly Coast, from Veron et al., 2009.

Forty surface-following passive particles are released for each CT-ROMS grid cell in which some coral cover was present (Thompson et al., 2014), and the number of particles released is consistent with previous studies examining larval connectivity in the CT (e.g. Thompson et al., 2014; Dorman et al., 2016; Kleypas et al., 2016). Particles are released year round following the lunar cycle; additional details regarding release strategy can be found in Chapter 3. Particles are followed for 20,

40, 60, 80 and 100 days to allow for a range of species with pelagic larval life stages to be considered (e.g. Harii et al., 2002; Richmond, 1988; Riginos and Victor, 2001). While many larvae settle within very short time periods (often less than 24 hours), genetic and modeling studies have both demonstrated the ability for settlement and successful metamorphosis to occur after much longer time periods, up to 100 days or more (Wood et al., 2014; Richmond, 1987; Graham et al., 2008; Graham et al., 2013).

Potential connectivity is computed for all the particles released from the forty-three study ecoregions, while sourciness, sinkiness and particle retention are computed for the ten ecoregions along the ITF. Sourciness, sinkiness and particle retention for each ecoregion are depicted as pies, with the pie divided into 20-, 40-, 60-, 80-, and 100-day wedges, based on figures and code by Defne et al. (2016).

4.3 Results

Particle retention is generally high, with significantly greater particle retention ($\geq 10\%$) during the 1980s than during the 1960s or 2000s. Makassar, Arafura Sea, North and Arafura Sea ecoregions have in-

creased particle retention during the 1980s after short to moderate PLDs: Makassar experiences a +11% increase after a 40-day PLD compared to the 2000s; Arafura Sea, North experiences a 14% increase after a 20-day PLD and a 12% increase after a 40-PLD compared to the 1960s; and Arafura Sea ecoregion experiences a 10% increase after 20- and 40-day PLDs compared to the 2000s. Kimberly Coast ecoregion experiences increased particle retention after moderate to long PLDs: an 18% increase after a 40-day PLD, an 11% increase after a 60-day PLD and a 12% increase after a 100-day PLD compared to the 2000s, while a 14% increase was seen after a 60-day PLD compared to the 1960s. Finally, the Lesser Sunda Islands ecoregion experiences increased particle retention during the 1980s during all PLD conditions: a 10% increase after 40-day and 60-day PLDs compared to the 2000s and 1960s respectively, an 11% increase after an 80-day PLD compared to the 1960s, and a 10% increase after a 100-day PLD compared to the 2000s.

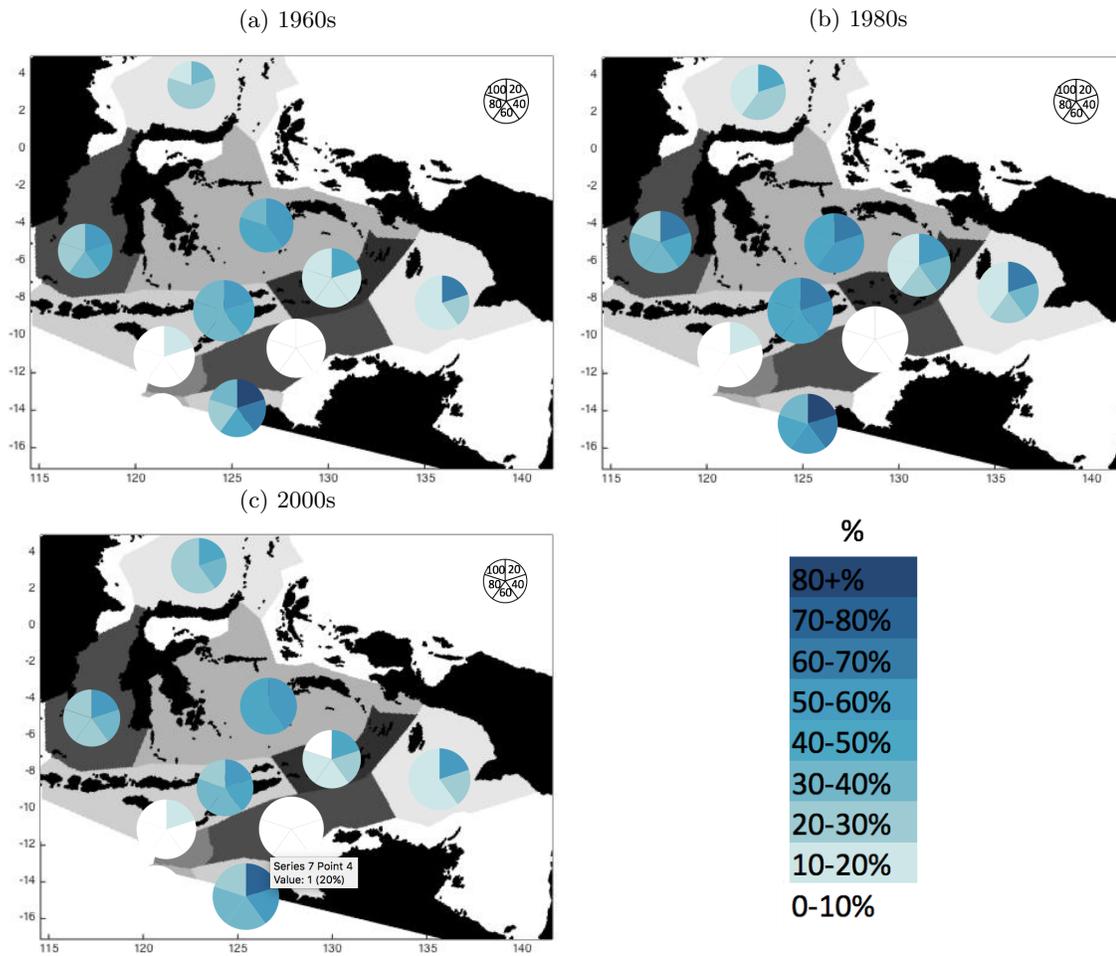


Figure 4.2: Particle retention as a percentage of the total number of particles released per ecoregion. Starting at the first wedge of the pie, pie wedges show particle retention %, 20, 40, 60, 80, and 100 days after particle release.

Generally, the upper ITF experiences the greatest increase in sourciness (≥ 3 ecoregions) during the 2000s, while the lower ITF experiences the greatest increases in sourciness during the 1960s, particularly at longer PLDs. The Celebes Sea experiences increased (+3 ecoregions) sourciness during the 2000s after an 80-day PLD, compared to the 1960s, as does Makassar ecoregion. Additionally, Makassar experiences

an increased sourciness (+3) during the 2000s after a 100-day PLD, compared to the 1980s. The Lesser Sunda Islands and Arafura Sea, North experience increased sourciness (+4) during the 1980s compared to the 2000s for a 100-day PLD, and the Arafura Sea also experiences an increased sourciness of +4 for an 80-day PLD, but during the 1980s compared to the 1960s. Arafura Sea, North also experiences increased sourciness of +3 ecoregions after PLDs of 20, 60 and 80 days, but the increased sourciness is seen during different decades: the increased sourciness after a 20-day PLD is during the 2000s compared to the 1980s; after a 60-day PLD, during the 1960s compared to the 1980s; and after an 80-day PLD, during the 1960s compared to the 2000s. Finally, Arafura Sea experiences an increased sourciness of +3 after a 40-day PLD during the 2000s, compared to the 1980s.

Along the lower part of the ITF, the Timor Sea experiences significantly increased sourciness (+3) during the 1960s, compared to the 2000s for PLDs of 60 and 100 days. Ashmore Reef contributes particles to 4 more ecoregions during the 1960s, compared to the 1980s after a 60-day PLD. Scott Reef contributes to an additional 4 ecoregions during the 1960s compared to the 1980s after a 100-day PLD. Lastly, the Kimberly Coast experiences increased sourciness (+3) during the 1960s

compared to the 2000s after a 60-day PLD; but, the Kimberly Coast experiences increased sourciness of +3 during both the 1960s and the 1980s compared to the 2000s after an 80-day PLD and an increased sourciness of +4 during the 1960s and 1980s compared to the 2000s after a 100-day PLD.

Typically, increased sinkiness (≥ 3 ecoregions) in the ITF ecoregions is experienced during the 2000s, with only one ecoregion, Makassar, experiencing increased sinkiness during the 1980s. The Celebes Sea receives particles from an additional 3 ecoregions after 40, 80 and 100-day PLDs: increased sinkiness during the 2000s compared to the 1960s after 40 and 80 days, and increased sinkiness after 100 days during the 2000s compared to the 1960s and the 1980s. Makassar experiences increased sinkiness (+3) during the 1960s and 1980s compared to the 2000s after a 60-day PLD, but an increased sinkiness (+3) during the 2000s compared to the 1980s after an 80-day PLD, and, it also experiences increased sinkiness (+3) during the 2000s and 1960s compared to the 1980s after a 100-day PLD. The Lesser Sunda Islands ecoregion experiences quite large increases in sinkiness during the 2000s compared to the 1980s for moderate to long PLDs: an additional 6 ecoregions after 60 days, 4 ecoregions after 80 days, and 7 ecoregions after 100 days.

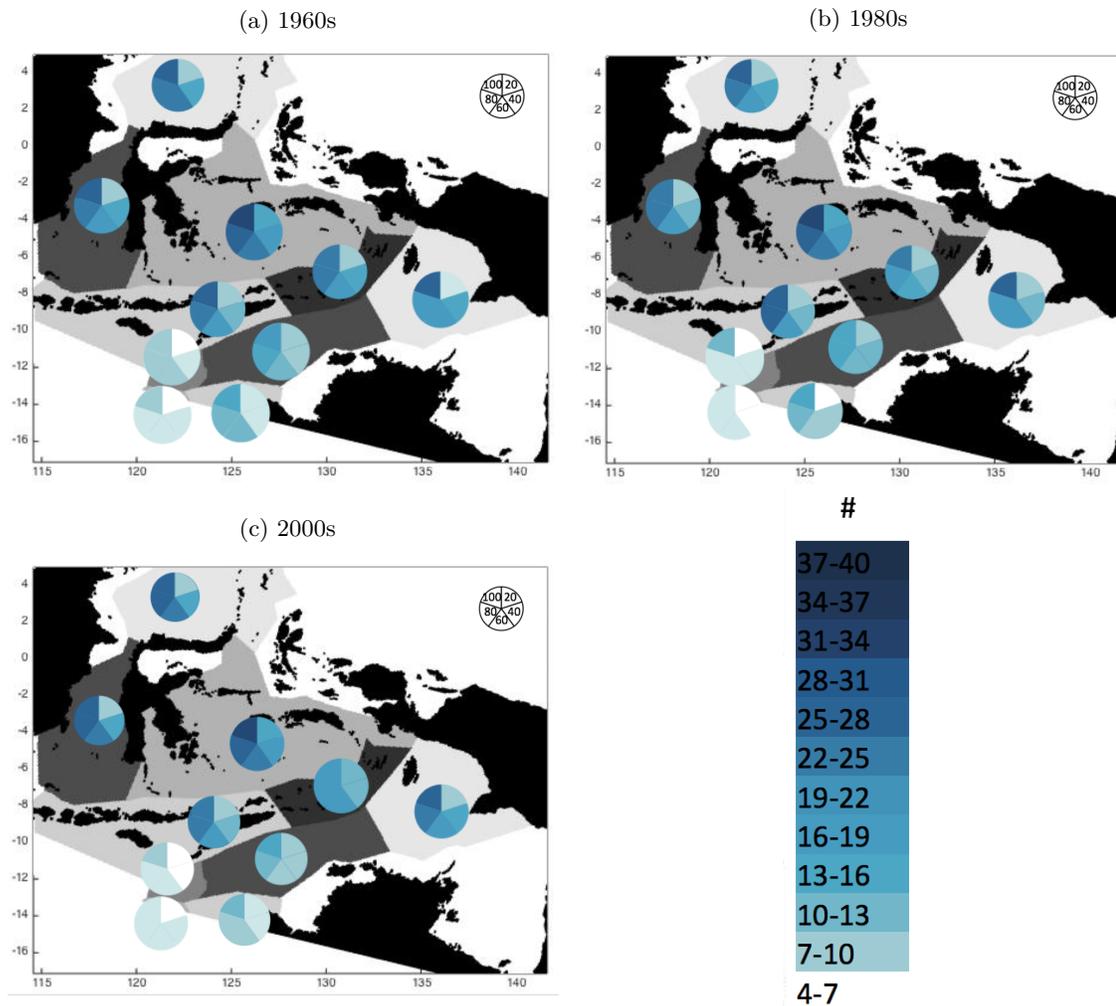


Figure 4.3: Sourciness as a function of the number of ecoregions that contributed particles to a particular ecoregion. Starting at the first wedge of the pie, pie wedges show # of ecoregions, 20, 40, 60, 80, and 100 days after particle release.

The Band Sea and Moluccas ecoregion receives particles from an additional 3 ecoregions during the 2000s after 80- and 100-day PLDs, compared to the 1980s, and 1960s and 1980s, respectively. Arafura Sea, North experiences increased sinkiness (+3) during the 1960s compared to the 1980s after 40-day and 100-day PLDs but experiences increased

sinkiness during the 2000s compared to the 1960s and 1980s after an 80-day PLD. Finally, the Arafura Sea ecoregion experiences significant increases in sinkiness during all PLDs: after a 20-day PLD, increased sinkiness (+3) is experienced during the 2000s and 1960s compared to the 1980s; after a 40-day PLD, increased sinkiness (+4) is experienced during the 1960s compared to the 1980s; after a 60-day PLD, increased sinkiness (+5) is experienced during the 1960s compared to the 1980s; after an 80-day PLD, increased sinkiness (+3) is experienced during the 1960s and the 2000s compared to the 1980s; and increased sinkiness (+3) is experienced during the 2000s compared to the 1960s and 1980s after a 100-day PLD.

The Timor Sea, Ashmore Reef, Scott Reef and Kimberly Coast ecoregions all experience increased sinkiness during the 2000s compared to the 1980s for moderate to long PLDs, except for the Timor Sea ecoregion after a 60-day PLD when particles are received from an additional 6 ecoregions during the 1960s compared to the 1980s. The Timor Sea also experiences an increased sinkiness of +4 ecoregions after both 80- and 100-day PLDs. The Ashmore Reef ecoregion experiences increased sinkiness after 60- (+6), 80- (+5), and 100-day (+6) PLDs. Likewise, Scott Reef ecoregion also experiences significant increases in sinkiness

after 60- (+7), 80- (+5), and 100-day (+7) PLDs. The Kimberly Coast ecoregion receives particles from an additional 4 ecoregions after an 80-day PLD, and from an additional 6 ecoregions after a 100-day PLD.

Generally, the connectivity of the 10 ecoregions along the ITF is complex, and no one, comprehensive explanation for why the resulting connectivity patterns are present could be determined. That is, there was no apparent secular change in connectivity, such as was seen in volume transport through ITF passages in Chapter 2. The 1980s did appear “different,” with particle retention generally being higher, and sourciness and sinkiness being lower during the 1980s. One explanation for this could be that 1982/1983 El Niño, which was included in the 5-year velocity values used to force TRACMASS, could have had a significant enough impact on particle trajectories as to make the 1980s appear “different” from the 1960s and 2000s.

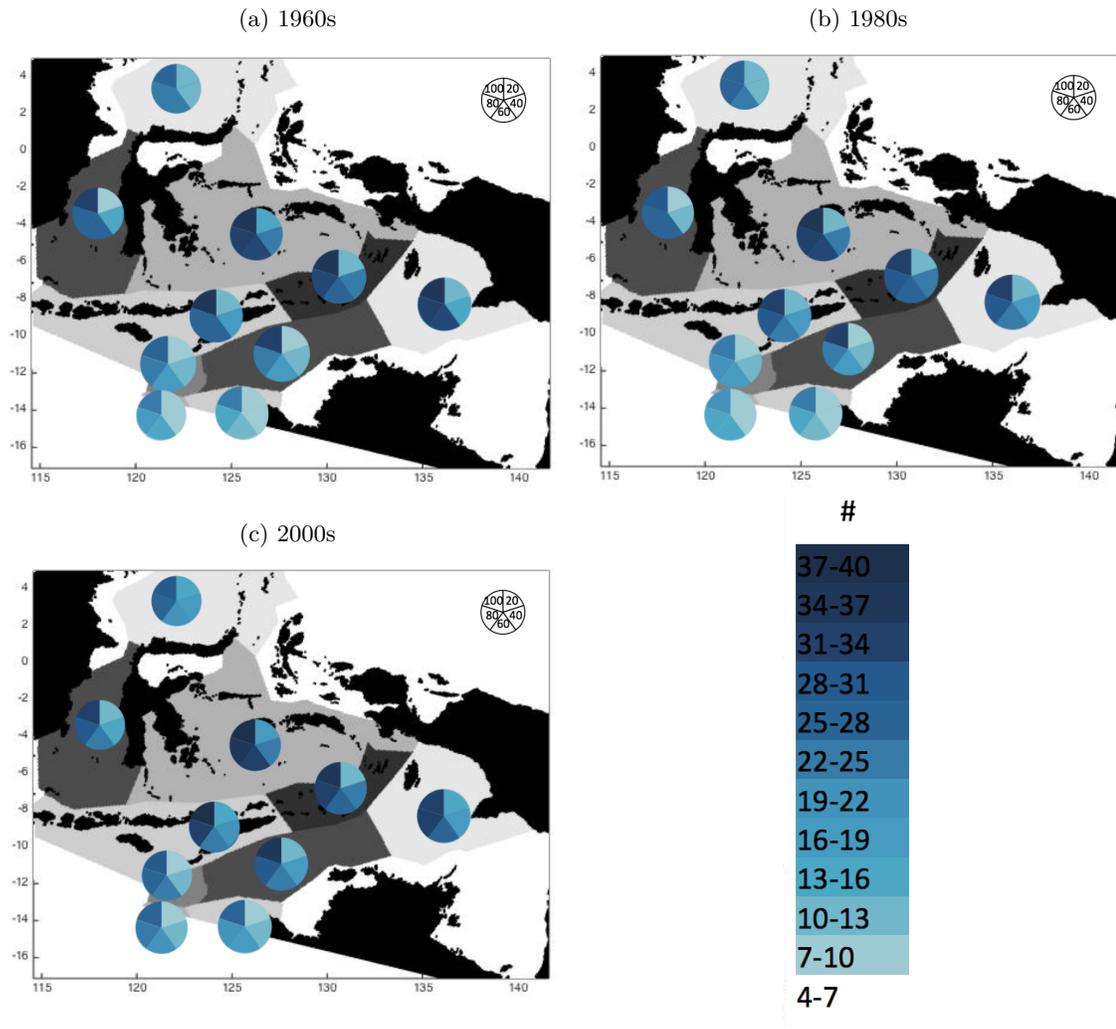


Figure 4.4: Sinkiness as a function of the number of ecoregions that contributed particles to a particular ecoregion. Starting at the first wedge of the pie, pie wedges show # of ecoregions, 20, 40, 60, 80, and 100 days after particle release.

4.4 Discussion

Overall, the decadal variability of our results suggests the need for dynamic MPAs, due to the variable nature of larval transport and retention, even at a coarse, ecoregion level. We propose that such MPAs will prove more effective conservationally and economically. The changes

seen here from one ecoregion to another or from one decade to another can be significant, particularly for organisms with long PLDs: multiple ecoregions experience a 16% increase in the number of ecoregions contributing particles under certain conditions, while other ecoregions experience upwards of a 20% increase in particle retention during other conditions.

Our results also demonstrate the importance of PLD in determining region-scale connectivity, encompassing a number of marine species with a wide range of early-stage life histories. Because all connections were included in determining the strength of a source or sink, changes in sourciness and sinkiness seen in the present study include rare connections, which could result in larvae from thermally resistant reefs, for example, reaching usually isolated reefs, introducing genetic differentiation and facilitating adaptation, diminishing the possibility of a genetic bottleneck. Long PLDs highlight the significance of rare, evolutionarily significant connectivity levels (Supplementary Material from Trembl et al., 2012).

While these findings are on a broad, ecoregion-based scale, they illustrate how static MPAs may not be able to achieve their goals, partially

because the ecosystems that they are trying to protect have altered, perhaps significantly, since the foundation of these MPAs. Because of the coarse resolution of these results, we recommend that our findings be used to guide finer-scale modeling efforts which can then inform management decisions regarding the dynamic nature of MPAs at the local level. The need for dynamic MPAs in the CT is also suggested by previous work by Thompson et al. (2018) which found that potential connectivity varied greatly among years, with the standard deviation of potential connectivity among years greater than the mean at many of the study sites. And, a similar study by Munroe et al. (2012) found large temporal changes in genetic sources and sinks of the mid-Atlantic *Crassostrea virginica* metapopulation between the differing regimes of the 1970s and 2000s. Because of the small spatial scale of many MPAs, MPAs will need to be relocated, potentially often, as even small changes in currents could have significant impacts for local connectivity.

Qualitatively, our findings are corroborated by previous research. A 2014 modeling paper found that 50% of connections occurred between 50 and 100 kilometers, but occasional connections on the order of 1000s of kilometers were observed (Wood et al., 2014); these results are on the same order of magnitude as our particles were dispersed. With lar-

vae traveling up to 1000s of kilometers, they are able to link entire ocean basins through sequential stepping stones, after a 120-day PLD (Wood et al., 2014); another CT modeling study found that 95% of coral larvae “settled” within 147 kilometers of their release site after a 13-day PLD with rare connections made at greater distances (Tremblay et al., 2012). These findings of larval transports over 100s to 1000s of kilometers are also consistent with genetic studies (e.g. Van Oppen et al., 2011; Glynn and Ault, 2000). Furthermore, similar large ranges of self-seeding were observed in Wood et al. (2014) and Thompson et al. (2018) as in the present study, with 15-100% self-seeding observed in Wood et al. and with average self-seeding of 5-11% but as high as 57-99% after 10- and 30-day PLDs in Thompson et al., while 0.5-84% self-seeding is observed in the present study.

In addition to our findings showing variability in larval transport at a decadal scale, previous research has demonstrated changes in ecosystems due to long-term climate change such as poleward range shifts of organisms in both marine and terrestrial environments (e.g. Rose, 2005; Loarie et al., 2009; Sorte et al., 2010; Pinsky et al., 2013), earlier spring phenology in marine environments (Thackeray et al., 2010) as well as earlier spring temperatures (Supplementary Material from Bur-

rows et al., 2011), increased self-seeding and significantly decreased larval duration with increasing SSTs (e.g. Sponaugle et al., 2006; Kendall et al., 2013), increased individual growth rates (e.g. Drinkwater, 2005), reduced intra- and interspecific competition (e.g. Choi et al., 2004) and decreased body size, biomass and physiological condition of marine organisms (e.g. Choi et al., 2004). Similar climate-related impacts can be seen in the terrestrial environment, including the loss of habitat and migration routes for various species (e.g. Bolger et al., 2008). These findings all suggest that climate is driving the distribution of marine and terrestrial species and their environs at large spatial scales and that such change need to be accounted for in MPA design.

As the effects of changing climate on marine species distributions becomes better understood, studies are more frequently calling for the implementation of additional MPAs to counteract climate change effects (e.g. decreased larval dispersal; McLeod et al., 2009; Hannah et al., 2007) and the release of old MPAs that are no longer achieving their desired outcomes. A 2014 paper called for the release of redundant terrestrial protected areas in management decisions, concluding that releasing these areas in the light of changing climate would result in gains in effectiveness and efficiency for resource management, par-

ticularly when monetary support is a limiting factor (Alagador et al., 2014). Conversely, multiple papers have suggested that the obstacles to implementing dynamic MPAs such as enforcement and cost are not inconsequential and that the removal of specific MPAs could damage the overall health of the MPA network (e.g. Game et al., 2009; Magris et al., 2015). However, a similar, dynamic approach has been successfully used in fisheries management; for example, the longline southern bluefin tuna fishery in Australia has updated fisheries boundaries on a biweekly basis since 2003, creating a migratory MPA of sorts (Hobday et al., 2010).

A 2004 study concluded that, in order to meet the World Parks Congress target of a global MPAs network covering 20-30% of the world's oceans, 5-19 billion USD would need to be spent annually (Balmford et al., 2004). Furthermore, the study concluded that this cost of a global MPA network was less than the international expenses incurred by subsidizing the fishing industry (world trade fish and fishery exports were valued at 148 billion USD in 2014; of the United Nations., 2016). And, such a network of MPAs would generate many jobs, possibly as many as 1 million, would increase revenue through improving the tourism industry and other ecosystem services (ocean revenues from

marine and coastal tourism were valued at 161 billion USD in 2014), and would improve the condition of nursery habitats for important fisheries (Balmford et al., 2004; of the United Nations., 2010; of the United Nations., 2016). This, then, suggests that if such an extensive MPA network is feasible on a global scale, then the ability to implement dynamic MPAs should also be within reach.

By releasing areas that underperform and no longer meet long-term goals, financially-limited conservation budgets will be able to optimize their use of resources. Setting periodic assessments of each MPA up front, deciding whether or not each MPA is meeting its long-term goals, and examining each MPA in the context of the most recent ecological, climate variability, and population dynamics studies on a case-by-case basis is necessary for the successful implementation of a dynamic MPA network (Alagador et al., 2014). This will allow for the placement of new MPAs, the migration of old ones whose bounds could be shifted to still effect management goals, and the removal of ineffective MPAs from the management domain. Finally, MPAs which have, in the past, met community needs by being periodically open to fishing (being dynamic) were still apparently able to facilitate conservation of reef fish stock because the local community was compliant with self-imposed

regulations (McClanahan et al., 2006). Thus, utilizing a dynamic MPA design framework with zonation or periodic closures or migratory MPAs will not only be more cost-effective but will also elicit better compliance from local stakeholders, and, ultimately, establish MPAs which are able to more effectively meet their target conservation goals long-term.

Some priorities for future work should include selecting local-scale regions of interest for study using biophysical models with improved spatial and temporal resolution, incorporating vertical swimming and other behaviors for specific species of interest into these models, as well as adding realized connectivity such as temperature-induced mortality. In addition, studies which can forecast larval connectivity and examine individual movement, taking into account *in situ* information as is reasonable, need to become more commonplace so that more success stories like the southern bluefin tuna fishery in Australia can occur and dynamic and migratory MPAs can be effectively implemented to maximize conservation efforts as well as stakeholder profits.

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Chapter 5

The Coral Triangle: Its Ecology, Management and Socioeconomics

5.1 An Overview of the Coral Triangle

The epicenter of the world's biodiversity the Coral Triangle (CT; Figure 1.1) contains >76% of the world's shallow-water reef-building coral species and 35% of reef fish species as well as 834 species of conservation concern, but covers only 1.6% of the world's oceans (Veron et al., 2009; Hoegh-Guldberg et al., 2009; Green et al., 2011; Asaad et al., 2018). The CT is also home to the world's largest mangrove forest; of the mangrove forests worldwide, an estimated 35% have been lost in the past two decades, with current annual deforestation rates estimated at 1-2% (Valiela et al., 2001; Alongi, 2008). In addition, the CT has a population of approximately 373 million people with an estimated 8% de-

pending on fishing and aquaculture for their livelihoods and 130 million people depending on fish resources, while its reefs provide annual benefits of \$10 billion USD (Cruz-Trinidad et al., 2014; Bank, 2014a; Bank, 2014b). However, regional reefs have been severely exploited through unsustainable fishing pressures and illegal fishing practices. To attempt to mitigate these pressures, 1972 marine protected areas (MPAs) exist within the CT, encompassing 17.8% of the region's coral reefs (White et al., 2014). The MPAs of the CT are overseen by the Coral Triangle Initiative, comprised of Indonesia, Malaysia, Philippines, Timor Leste, Papua New Guinea, and the Solomon Islands (Berdej et al., 2015). Unfortunately, only 2% of the MPAs protecting reefs of the CT are considered to be fully protective (Burke et al., 2011).

5.1.1 Indonesia

The world's largest archipelago, Indonesia includes 5.8 million square kilometers of marine territory; of the reefs in Southeast Asia including those of Indonesia, 95% of these reefs are threatened by local disturbances including overfishing and destructive fishing practices (Nuridin and Grydehoj, 2014; Burke et al., 2011). Possessing high biodiversity, the Indonesian Raja Ampat Archipelago is home to over 100 endemic reef fish species (the highest in the CT; Asaad et al., 2018) with the rich-

est reef fish diversity worldwide (Chou, 2000) and 574 species of coral (Veron et al., 2009). In addition, both the Raja Ampat Archipelago and the Banda Sea possess high habitat diversity, providing homes for many endangered and endemic species (Asaad et al., 2018). The northern tip of Sulawesi, and Ambon and Kei Islands have also been identified as areas of significant biodiversity, possessing >4000 marine species (Asaad et al., 2018). As of 2011, Indonesia possesses 153 MPAs covering 17 million hectares but much of this area is protected in name only due to the region's complex social and political dynamics (Carter et al., 2010). Indonesian reefs are valued at approximately 94 million USD based on their carbon storage value alone (Chou, 2000), with a majority of these reefs threatened by destructive fishing practices (Hoegh-Guldberg et al., 2009). It is estimated that destructive fishing practices including overfishing and blast fishing, as well as sedimentation, could cost Indonesia 2.6 billion USD by 2022 (Chou et al., 2002).

5.1.2 Papua New Guinea

In contrast to Indonesian reefs, most of the reefs in Papua New Guinea are in very good condition with some of the highest fish and coral diversity worldwide, routinely possessing >40% coral cover and showing little anthropogenic-induced damage (Maniwavie et al., 2000). One

reason for this low human impact is that subsistence and artisanal fisheries predominate reef fish harvest and are thought to be sustainable, although invertebrate fisheries such as the sea cucumber fishery are being subjected to substantial overfishing (Maniwavie et al., 2000). Other growing threats to regional reefs include increases in urbanization and population growth, logging, sedimentation, bleaching and reef harvesting; however, the greatest threat to Papua New Guinean reefs is global warming (Miller and Sweatman, 2004). Unlike other countries of the CT, Papua New Guinea has few MPAs, protected coverage only representing 0.1% of territorial waters (Miller and Sweatman, 2004).

5.2 Sustainable harvesting and aquaculture

An important source of revenue, the worldwide ornamental fish industry is worth between 800 million and 30 billion USD, with global exports worth 372 million USD as of 2011 and with a 14% annual growth rate (Ladisa et al., 2017; Reynoso et al., 2012; Stevens et al., 2017). The annual global catch for the marine ornamental fish trade alone is estimated to be between 14 and 30 million fish (Wood, 2001). As of 2011, the ornamental marine fish trade was valued at 28-44 million USD (Reynoso et al., 2012). However, of this multi-million dollar industry,

less than 10% of marine species are cultured, placing a heavy burden on the coral reefs (Ladisa et al., 2017). In addition to the 30 million fish, upwards of 1.5 million live stony corals and millions of kilograms of live rock are harvested yearly from reefs worldwide (see Tissot et al., 2010 for review; Cato and Brown, 2003). However, coral reefs provide many valuable ecosystem services and, according to one estimate, have been valued at over 350000 USD per hectare per year in 2007 (de Groot et al., 2012). These valuable ecosystems must be protected through MPAs and other management practices.

The U.S. is the major importer of marine ornamental species, importing 64% of worldwide coral imports; of the total U.S. imports, 44% come from the Philippines and another 27% come from Indonesia (Tissot et al., 2010). And, at least 85% of ornamental marine fish imported into the US come from the CT (Ladisa et al., 2017). Of the numerous species being traded annually, 85% of the individuals traded account for 92% of the global marine aquarium trade belong to 8 families of those collected; the remaining 15% of the individuals collected come from an additional 31 families (Bruckner, 2005). It is these species that aquaculture efforts should be focused upon. In its capacity as the primary consumer of marine ornamentals, the US can use its place

in the worldwide marine ornamental market, driving more sustainable harvesting practices and a move towards an aquaculture-predominated industry.

One notable example of US companies driving more sustainable marine ornamental practices is Petco's pledge to move towards 100% maricultured species in its stores; they are already supplying 100% aquacultured live rock and coral species (Petco, 2018). In many cases, wild-caught individuals have been harvested in environmentally unfriendly and unsustainable ways, including cyanide capture, dredging, and reef detonation. In the ornamental fish trade, mortality rates are high, requiring capture of excess numbers of individuals to make quotas, making harvests even more unsustainable (Ladisa et al., 2017). And, fishermen are having to travel further and place themselves in increasing risk to meet these quotas (Glaser et al., 2015).

As of the 2014 Food and Agriculture Organization assessment, the global aquaculture industry was worth 144.4 billion USD, having grown an estimated 5.8% in 2013 with the production of aquacultured food fish more than doubling from 2000 to 2012 (of the United Nations, 2014), and its place in marine ornamental trade is growing. For example, giant

clams, which were first cultured in the 1980s, have since flourished as an aquaculture product, with over 75000 aquacultured clams being exported from the Pacific in 2007 (Ladisa et al., 2017). Likewise, villages in the Solomon Islands have been mariculturing for two decades, and Indonesia is now mariculturing the majority of its *Acropora* spp. and is a coral mariculture leader in the global market (Rhyne et al., 2014). Indonesia has also become a major producer of maricultured seahorses, particularly *Hippocampus barbouri* and *Hippocampus histrix* (Williams et al., 2014).

5.2.1 Indonesia: A case study

Indonesia is one of the world's top suppliers of the marine ornamental trade, with 91% of live corals being exported from Indonesia in 2008 (Jones, 2008). The country faces complex societal issues and dwindling stocks in regard to its fishing industry. Islanders of the Spermondes acknowledge that fishing has been poor since the 1960s, unsurprising given that an estimated 30000-40000 marine fish were available on a daily basis in the Paotere market of the Spermondes alone (Williams et al., 2014). One of the more well-known casualties of this over-harvesting is the Banggai cardinalfish (*Pterapogon kaudneri*), a species endemic to Sulawesi, and which has had its populations decimated from over-

harvesting for the marine aquarium trade since the 1990s (Vagelli and Erdmann, 2002). Fortunately, the species is now one which can be easily aquacultured, even by the home aquarist, alleviating fishing pressures on wild populations. As desirable fish like the Banggai cardinal become rarer through over-harvesting, fishermen must travel further, dive deeper (often using air compressors) which can result in permanent paralysis and death, and risk becoming crippled from unsafe fishing practices. The economic downturn in the 1990s has placed additional strain on Indonesian fisheries, as individuals who were once employed by other industries, have turned to fishing and other jobs which exploit coral reefs to make a living (Chou, 2000).

In addition, the *punggawa-sawi* (patron-client) relationship, which exists in Sulawesi and elsewhere, further complicates matters, as fishermen (clients) have little ability to change their livelihood strategies (Ferse et al., 2002). The *sawi* (fishermen) do not own their own boats or equipment and are indebted to their patrons; a form of indentured servitude, it can be difficult for *sawi* to pay off *punggawas* and gain financial independence (Nurdin and Grydehoj, 2014). The *punggawa* are middlemen who move along the products to both local and international markets, but they are also responsible for protecting their *sawi* from fi-

nancial troubles due to market instability, getting their sawi out of jail if caught participating in illegal fishing practices and participating in their sawi's family ceremonies (Ferrol-Schulte et al., 2014; Glaser et al., 2015). Punggawas may dictate where fishing occurs, which species are collected and what gear is used (Ferrol-Schulte et al., 2014; Ferse et al., 2002; Glaser et al., 2015); they also have sway with government officials, paying off anyone who might prosecute illegal fishing behaviors (Glaser et al., 2015). Punggawas perpetuate the use of illegal fishing methods through the gear and methods that they select; a prevalent belief among punggawas is that illegal fishing practices like bombing and cyanide fishing are not, in fact, harmful to the marine environment, insuring that these practices continue (Nurdin and Grydehoj, 2014; Glaser et al., 2015). Those who do see destructive fishing practices like bombing reefs as detrimental, both to their own health and the health of the reef, still maintain these practices because they are more profitable and efficient—a necessity for the impoverished fisherman (Nurdin and Grydehoj, 2014). Furthermore, the Islamic culture of the islanders permeates their work, as they believe that their destiny is God-given, which they cannot influence, so trying to change this future would be futile and unrewarding (Glaser et al., 2015). Because of the impact that the culture has on the fishing industry, it is vital

that discussions of MPA implementation, shifts to aquaculture-based production and other management strategies take scenarios like these into account so that positive change can actually be effected.

In contrast to the dependency that sawi typically have on their *pung-gawa*, individuals who participate in aquaculture own their own supplies and sell their products directly to the exporter, providing a more stable income (Williams et al., 2014). For example, families who aquaculture seahorses in Indonesia can make roughly seven times what the male heads of household would be expected to make otherwise (350 USD versus 50 USD per month; Williams et al., 2014). Other areas of emerging mariculture for local individuals in Indonesia include raising corals and giant clams in broodstock habitats, growing out species such as clownfish (*Amphiprion* spp.) for government hatching, and mariculturing other desirable species such as blue tangs (*Paracanthurus hepatus*), spiny lobsters (*Panulirus homarus*) and moray eels (Williams et al., 2014; Mañez and Paragay, 2013; Jones, 2010). Due to the size of the fishing industry in Indonesia, it is unlikely that mariculture would act as a replacement industry; it could, however, provide some much-needed relief to this particularly vulnerable ecosystem (Glaser et al., 2015; Ferse et al., 2002; Williams et al., 2014).

5.3 The case for dynamic MPAs

Currently, the most common implementation of MPAs is as static, no-take reserves. However, while having large, no-take, static reserves is the chief goal for many in the conservation community, according to a 2006 paper, <0.1% of coral reefs worldwide are within poach-free, no-take MPAs (Mora et al., 2006). The ability of MPAs to meet conservation goals has had mixed success (e.g. Cinner et al., 2018; Selig and Bruno, 2010). It has been argued that the inability for some MPAs to meet conservation objectives may be due to small MPA size (e.g. Krueck et al. (2018) estimates 100-kilometer reserves are needed to fully protect most species) as well as poor compliance and enforcement (e.g. McClanahan et al., 2006) and migration of species out of MPAs (e.g. Moilanen et al., 2014). It is possible that these perceived failures of MPAs may cause decreased motivation to continue to manage them. This, in conjunction with the public perception that coral reefs are facing inevitable decline has the potential to have detrimental effects on conservation efforts into the future (Mumby et al., 2017). However, areas where MPAs are not meeting their conservation goals should be used as resources to understand how to improve MPA efficacy into the

future. In those areas where MPAs are meeting limited success, different management strategies could be implemented, including zonation, gear restriction, temporary closures, and migration of MPAs, to create a dynamic management strategy. Such strategies have the potential for increased compliance with local populations while also being able to address migration of mobile species and shifting habitats in the context of changing climate. In particular, conservation efforts need to consider future food security needs of local populations and attempt to develop management plans that take food security into consideration to try to elicit better compliance (Rice and Garcia, 2011).

One management strategy for creating effective MPAs is through the implementation of “multi-zoned” MPAs (e.g. Salomon et al., 2002; Grantham et al., 2013) or MPAs with reduced restrictions (e.g. Hobday, 2011). Salomon et al. (2002) suggests that an MPA with a core no-take zone, surrounded by a buffer zone will result in the greatest organism biomass increase, while reducing social conflict. A more recent paper contends that the implementation of such a buffer zone is ineffective, as these zones lack effective management and legal protection and, instead, produces an edge effect (Gaston et al., 2008). However, over the last 25 years, the Great Barrier Reef Marine Park has been

effectively managed through a multi-use zoning approach, which allows for effective management of the area as a whole, rather than as isolated MPAs surrounded by unregulated waters (Day, 2002).

The concept of dynamically managed reserves was first introduced by Gunning et al. (1996) which allows for the release and replacement of parts of the reserve, or movement of the reserve itself over time by updating reserve boundaries on a weekly basis, allowing for the reserve to follow dynamic boundaries of interest, such as thermal fronts and upwelling zones (Game et al., 2009; Hooker et al., 2011; Moilanen et al., 2014). Dynamic reserves can also include management strategies such as temporary reserves that provide temporary or periodic protection or reserves which protect certain parts of migratory routes such as breeding or feeding grounds or corridors between these grounds. These strategies have been implemented in both the terrestrial (see Moilanen et al., 2014 for a terrestrial overview) and marine environments (e.g. see Game et al., 2009; Hooker et al., 2011; and Moilanen et al., 2014 for overviews). Releasing areas of reserves which are not meeting reserve goals frees up resources to protect new reserve areas, optimizing the use of available resources, as does selecting reserve locations such that they encompass distributions of multiple species of interest. Re-

search in both terrestrial and marine environments indicates that the key to success for migratory protected areas is to ensure that viable areas for reserve placement are available for use when it comes time to relocate the reserve so that the rate of recovery of the new reserve outpaces the decline of the released reserve (Rayfield et al., 2008; Game et al., 2009). In addition, technological advances can be used to enforce MPA boundaries, track protected species and dynamic processes in real time and notify those using surrounding waters where dynamic MPA boundaries are at any given time, as well as make predictions about species distributions using models which can then be updated with observations (Game et al., 2009; Hooker et al., 2011; Hobday et al., 2010).

Although dynamic MPAs run the risk of compromising conservation efforts because of their temporally variable nature, they could experience increased compliance as in the case of the tuna fishery in Australia (Hobday et al., 2010), as the interests of fishermen and other stakeholders are being incorporated into MPA design, providing increased food security to local populaces (Hooker et al., 2011). In Papua New Guinea, management success was directly linked to high levels of compliance; locals were actually aware of and accepting of management decisions, likely because these management decisions integrated local community

culture and tradition and benefited the community since locals were able to periodically fish managed areas (Miller and Sweatman, 2004). In fact, 97% of Papua New Guinea's land and adjacent waters are owned and managed under customary tenure by local clans or tribes (Green et al., 2011). If local communities and governments are more involved in the management process including enforcement of their own resources in a community-based model, then it is hopeful that compliance will improve (Green et al., 2011). Indeed, McClanahan et al. (2006) found that 3 of the 4 sites in their study with the greatest increase in biomass were traditionally managed areas with periodic rather than permanent reef closures. And, in Indonesia, islanders have themselves created Island Exclusion Zones, which are informally managed local waters that only local fisherman are allowed to fish; these also have certain rules to protect them including banning of bombing, trawling, cyanide fishing, throwing garbage into the water, and one Island Exclusion Zone in Saugi has even implemented primitive "multi-zoned" areas where various fishing activities can occur (Glaser et al., 2015).

It is hopeful that the combined efforts of more effectively managed MPAs and a more conservation-driven aquarium trade which encourages sustainable harvesting practices and mariculture can help protect

coral reefs from human exploitation. Increased mariculture efforts have provided an additional source of revenue to coastal communities, while sustainable harvest of animals from coral reefs can occur in MPAs which are “multi-zoned” for a number of uses, thereby supporting local livelihoods and ecosystems (Rhyne et al., 2014). Together with incorporation of local communities in resource management, these strategies can hopefully mitigate the challenges facing coral reef conservation in the CT.

Chapter 6

Concluding Remarks

CT-ROMS is used to study the circulation of the Coral Triangle and its impact on larval transport in a hindcast simulation from 1958-2007. Model validation shows that CT-ROMS is able to capture the ENSO and IOD signals in its SSHa and SSTa output.

Model output is then used to characterize the interannual, annual and intra-annual variability of the volume transport from 30 key passages throughout the CT using power spectral densities. Seasonal frequencies typically explain a majority of the spectral content of the volume transport of straits along the SCSTF, while interannual frequencies account for the majority of volume transport spectral content at passages along the ITF. The mean and trend for the volume transport of these 30 passages is also described. Generally, significant changes

in volume transport are found along the ITF. To then assess the relative contributes of the interannual processes ENSO, PDO and IOD on the volume transport through the CT, linear regression models are constructed, using these three time series as explanatory variables to attempt to reconstruct the volume transport time series of 30 passages. The linear regression models were able to reconstruct a significant portion of the volume transport at 13 of the 30 study passages; these 13 passages generally lie along the SCSTF.

Surface velocity fields from CT-ROMS are used by the offline particle tracking code TRACMASS to generate particle trajectories with 20-, 40-, 60-, 80-, and 100-day PLDs. This range of PLDs allows us to investigate the role of PLD on particle destination. Particle retention, sourciness and sinkiness are examined for 8 ecoregions along the SCSRF. Particle retention is generally high, with greater particle retention during El Niño conditions, compared to La Niña conditions. Particle retention also decreases and the standard deviation of particle retention increases with increasing PLD. Variability in sourciness and sinkiness as a function of ENSO phase and dispersal corridors between ecoregions along the SCSRF are also described. While there is not a unifying explanation for the patterns seen in ecoregional particle

retention, sourciness and sinkiness along the SCSRF, this is unsurprising given the inherent complexity of the region. Because this research tracks particles at the surface, analysis of shorter-frequency processes should also be investigated to determine if the most prominent players in the CT are actually the large climate signals like ENSO or if more regional effects such as monsoons and their impacts on surface winds are more important to particle (and larval) circulation. Our results do suggest the need for well-formulated networks of MPAs to protect the coral reefs of the CT. Furthermore, recommendations for future, more localized work can be made from these results, depending on the desired management strategy (e.g. protection of refugia, areas of high biodiversity, etc.). Other avenues for future research include the development of various IBMs for regionally relevant species to allow the incorporation of behaviors such as swimming, as well as the development of three-dimensional circulation models, particularly along the ITF.

Decadal changes in particle retention, sourciness and sinkiness are also investigated along the ITF. In general, particle retention is higher during the 1980s than during the 1960s or 2000s. Sourciness is higher for the upper ITF during the 2000s and higher for the lower ITF dur-

ing the 1960s. Increased sinkiness is also generally experienced during the 2000s along the ITF. Because of the change seen in particle retention, sourciness and sinkiness during various decades and ENSO phases along both the ITF and SCSRF, we recommend that dynamic MPAs be implemented to help preserve regional coral reefs. Dynamic MPA management strategies could include temporary, migratory, zoned, and gear-restricted MPAs.

Dynamic MPAs are also, arguably, a better management strategy because they provide a better opportunity to improve user compliance. In the developing world, many fishers and others who depend on the coral reefs of the CT for survival are more concerned about feeding their families this week than on whether or not reefs will still exist 50 or 100 years from now. Some evidence even suggests that certain regional cultures have trouble conceptualizing events that far into the future. Furthermore, the complex socioeconomic structure in many of the island nations, for example the patron-client or *punggawa-sawi* relationship in Indonesia, drives fishing practices which are antithetical to MPA regulations and conservation efforts. Without understanding these societal norms and making regulations which allow fishers to continue to generate revenue, effective MPA enforcement will continue to

be a concern. By developing dynamic MPAs which focus on integrating local perceptions into decision-making processes and by providing alternative revenue streams (e.g. sustainable aquaculture), it is hopeful that MPAs can become more effective, achieving their conservation goals both now and into the future.

6.1 Online Supplemental Figures

A complete set of supplemental figures will be made web-accessible. These supplemental figures will include, but may not be limited to, the following: transport time series and power spectral densities at a super-set of the 30 study passages; pie charts showing connectivity between ecoregions at various pelagic larval durations; and particle retention, sourciness, and sinkiness figures for the 43 study ecoregions. Please contact the author Sarah Lietzke (sl2937@cornell.edu) for further information.

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