# Drivers of larval connectivity variability among coral reefs in Southeast Sulawesi

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*Submitted in accordance with the requirements for the degree of Master of Science by Research*

The University of Leeds, School of Biology

September 2025

I confirm that the work submitted is my own and that appropriate credit has been given where reference has been made to the work of others.

## Acknowledgements

I would firstly like to acknowledge my deepest gratitude for the guidance on this project provided by my supervisor, Dr. Maria Beger. Her help in forming this project idea, shaping it into something tangible, and carrying it through was essential to my completion of this work. Through many struggles with conceptualization, statistical analysis, GIS, and writing, her support helped me create a piece of work I am proud to present here. I would additionally like to thank my co-supervisor Dr. Christopher Hassall, who is largely responsible for my understanding of GIS, and for his constant support throughout the project.

Secondly, I would like to thank everyone in Manton 8.17 who were quick to offer advice and support throughout my time here. I am also deeply grateful to every member of the Beger Lab, who were welcoming, friendly, and supportive. It was especially inspiring to have a chance each week to discuss coral reefs and marine ecology with similarly passionate people.

I would finally like to thank my brother Sam, who saved me countless times when I thought my code would never work. His excitement for statistical analysis, R coding, often tidyverse, and scientific research was infectious, and encouraged me to push through the harder moments of this project. I would lastly like to thank my Mom and Dad, who supported my decision to move 4,000 miles away to study something I adore. And who continue to encourage me every day to do what I love.

## Abstract

Coral reef patches are connected via dispersal of larvae, i.e., larval connectivity, that varies across space and time. Larval connectivity supports gene flow, sustains fisheries, and stabilizes larval supply. Connectivity also enhances the effectiveness of marine reserves by facilitating valuable conservation processes. How larval connectivity responds to environmental factors, excluding oceanographic factors, is largely unknown, with little information available on the influence of external factors on connectivity patterns. I address this knowledge gap by identifying how environmental, climate, and habitat factors drive variability in larval connectivity. I correlate graph-theoretic proxies of larval connectivity with sea surface temperature (SST) and climate variables using Generalized Additive Models (GAM) and recursive partitioning with regression trees to assess each factor's effect on connectivity between 487 reefs in Southeast Sulawesi, Indonesia over a 20-year period. I further simulate how coral reef habitat degradation over that period may change patterns of larval connectivity. There is a significant effect of El Nino, Pacific Decadal Oscillation (PDO), and Sea Surface Temperature (SST) on larval connectivity. SST above 28°C decreased out-degree and in-degree by an average of 0.65 standard deviations and increased self-recruitment by an average of 0.74 standard deviations. This result means that as SST increases above 28°C, there is a decrease in both incoming and outgoing connections between reefs, and more larvae remaining within their source reef. Generalized Additive Model (GAM) analysis of the effect of SST on connectivity metrics shows higher explanation of variance at higher SST. This result supports the existence of an SST threshold at which connectivity for fish species in the region will predictably decline. Spatial analysis using spectral clustering shows a larger effect of reef location (spatial cluster) on connectivity metrics compared to SST. Generally, two out of six clusters have high self-recruitment while the remaining four clusters have high out-degree and in-degree. Habitat degradation decreases cumulative flow of larvae by 73 percent when comparing flow matrices before and after habitat degradation. Additionally, habitat degradation reduces variance of cumulative flow for coral trout and rabbitfish species. Further, these trends are predicted to continue under future habitat degradation values. These results allow us to predict how connectivity will change as SST and habitat degradation increase due to climate change.

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## Abbreviations

Analysis of Variance (ANOVA)

El Nino Southern Oscillation (ENSO)

Generalized Additive Model (GAM)

Generalized Linear Model (GLM)

Likelihood Ratio Test (LRT)

Marine Protected Area (MPA)

National Research and Innovation Agency (BRIN)

Operation Wallacea (Opwall)

Pacific Decadal Oscillation (PDO)

Pelagic Larval Duration (PLD)

Regional Ocean Monitoring System (ROMS)

Sea Surface Temperature (SST)

## Introduction

Coral reef seascapes are composed of seemingly disconnected habitats, fragmented into multiple patches which may or may not be connected via dispersal and migration (Jones et al., 2009). This connectivity is defined as the "demographic linking of local populations through dispersal of individuals among them as larvae, juveniles, or adults" (Sale et al. 2005). Understanding larval connectivity is essential to predicting population dynamics and sustainably managing marine species (Kough et al., 2013). One example is management of marine fisheries, which are a major source of food and livelihood for communities around the globe (Ramesh et al., 2019). Temporal and spatial variability of larval connectivity contributes to such fisheries, but also to conservation benefits of marine reserve networks. For example, more than 10 billion United States Dollars (value in 2010) in annual fisheries catch over a 10-year period resulted from transnational larval connectivity (Ramesh et al., 2019). However, the main role and interplay of the drivers of annual connectivity variability is still unclear.

Since larval connectivity measures a highly variable movement of very small individuals, the most widespread technique for quantifying larval connectivity patterns is the use of biophysical modeling (Swearer et al., 2019). Biophysical models couple oceanographic conditions with physiological and behavioral conditions of larvae to best predict larval movement in marine environments (Swearer et al., 2019). Biophysical modeling has been used to predict larval movement of coral species (Figueiredo et al., 2022; Faryuni et al., 2024; Sciascia et al., 2022), fish species (Gurdek-Bas et al., 2022; Munguia-Vega et al., 2017; Ramesh et al., 2019; Wang et al., 2022), and other invertebrate species (Ayata et al., 2009; Meerhoff et al., 2025). However, there is a high level of uncertainty in these models, due to high variability in behavior and physiology and a lack of empirical data on the interactions of oceanographic currents and larval behavior (Chaput et al., 2022). Some studies have matched outputs from biophysical models with realized larval connectivity at regional scales (Cowen et al., 2006), while other studies have found a lack of predictive accuracy of biophysical models across large geographic and species scales (Toonen et al., 2011). Still, biophysical models remain to date the best technique for estimating large-scale larval connectivity, and it is therefore important to further investigate the accuracy and predictive ability of these models to improve them for future use (Chaput et al., 2022).

Temporal variability in connectivity patterns may result from a range of factors, such as oceanographic currents, reproductive timing, or larvae mortality. These factors may work synergistically or antagonistically to change dispersal (Andrello et al., 2015). Approaches to connectivity studies that incorporate multiple factors will have the best chance to produce accurate predictions of variability in dispersal patterns (Bashevkin et al., 2020). The main known factors influencing connectivity variability include: (1) oceanographic factors, (2) physiological factors, and (3) climate change factors.

Firstly, oceanographic drivers of larval connectivity patterns are largely dependent on oceanic currents. This dependency is due to the inability of most larvae to swim against the current (Munguia-Vega et al., 2017). Oceanic currents can predict spawning time, larval origin, and larval recruitment (Daudén-Bengoa et al., 2024). For example, oceanic circulation during spring and summer are the best predictors of Pacific red snapper (*Lutjanus peru*) dispersal (Munguia-Vega et al., 2017). Additionally, estuarine fish species that spawn in winter in the Iberian Atlantic coast more commonly disperse northward due to prevailing currents from the Iberian Poleward Currents (Cabral et al., 2021). Intra-seasonal variability in ocean currents can create a spatially and temporally heterogeneous pattern of larval recruitment (Feng et al., 2016). Anisotropic connectivity patterns occur in areas with asymmetric currents, where upstream reefs generally supply more larvae downstream and downstream reefs have little to no effect on larval export (Munguia-Vega et al., 2017). This creates a trend in which connectivity values differ when measured in different directions. The influence of oceanic currents on larval connectivity patterns has been further supported by the use of biophysical modeling to estimate larval connectivity patterns (Werner et al., 2007). Results from larval transport modelling that coupled oceanic current information with satellite mapping matched realized dispersal between coral reefs at a regional scale (Werner et al., 2007). Overall, oceanic circulation structures dispersal pathways, therefore structuring connectivity (Catalano et al., 2024).

Secondly, physiological processes of larvae strongly influence dispersal patterns. Such processes include mortality rate at dispersal stage, maximum Pelagic Larval Duration (PLD), and relative duration of pre-competency windows (Treml et al., 2015). High mortality rates mean most surviving larvae settle close to natal populations, effectively decreasing connectivity (Cowen et al., 2000). PLD is the length of time larvae spend in the water column before settlement (Selkoe & Toonen, 2011). PLD is directly related to dispersal as short PLD results in larvae settling closer to natal populations, and long PLD results in larvae dispersing further (Cowen et al., 2006). Increased PLD increases not only the distance, but also the number of connections between patches (Treml et al., 2015). The pre-competency window is the duration of time in which larvae are not physiologically capable of settling (Randall et al., 2024). Longer pre-competency therefore increases geographical distance that individuals travel, effectively increasing connectivity (Cecino & Treml, 2021). These physiological processes are heavily influenced by environmental variations (Bashevkin et al., 2020; Figueiredo et al., 2022). High mortality rates occur due to increases in temperature, as warmer waters accelerate developmental processes, leading to a higher frequency of fatal malformations (Llopiz et al., 2014). Warm temperatures also decrease the length of pre-competency (Randall et al., 2024). Additionally, fluctuations in PLD are attributed to changes in conditions such as temperature, pH, and salinity (Bashevkin et al., 2020). Therefore, with ongoing warming due to climate change, physiological larval processes will change, in turn creating variability in connectivity patterns.

Thirdly, impacts from climate change (e.g., extreme ENSO, increased SST) affect larval connectivity and dispersal. Rising atmospheric temperatures associated with climate change directly or indirectly alter ocean pH, salinity, stratification, circulation, long-term climate cycles, storms, upwelling, ultra-violet radiation, and dissolved $O_2$. These factors directly impact larval development by changing embryo development time, metabolic rates, oxygen consumption, increasing morphological deformities, increasing otolith size, etc. (Llopiz et al., 2014). Long-term climate cycles like El Nino Southern Oscillation (ENSO) are likely to increase in extremity with climate change (Cai et al., 2021). There is a strong correlation between larval connectivity patterns and the Southern Oscillation Index, with greater poleward connectivity during El Nino and weak Southern Oscillation Index, and alternatively weaker poleward connectivity during La Nina (Gurdek-Bas et al., 2022).

Ocean acidification is deleterious to calcifying larval stages, and changes in salinity also influence larval development and behavior (Llopiz et al., 2014). The magnitude and direction of these effects likely vary between species and region and are unknown. Additionally, temperature influences connectivity patterns. Using a biophysical model of coral larvae, elevating temperature by 2°C resulted in a 7% decrease in distance dispersed and an 8% decrease in number of connections between coral reefs in the southern Great Barrier Reef (Figueiredo et al., 2022). Rising Sea Surface Temperature (SST) increases metabolic rates of larvae, decreases PLD, and increases the probability that larvae will settle on natal reefs (Andrello et al., 2015; Bashevkin et al., 2020; Figueiredo et al., 2022). Net weakening in inter-reef connectivity driven by increased larval mortality in early development is a result of rising temperature, which increases rates of cell division, resulting in a higher frequency of errors leading to fatal malformations (Figueiredo et al., 2022). Warmer temperatures further increase the rate of growth and development (Munday et al., 2009). This process shortens PLD, which in turn disrupts connectivity patterns, with larvae settling closer to natal populations. Similarities in the relationships between temperature, distance dispersed, and PLD were found between a diverse group of marine fish and invertebrates, suggesting such an effect can be universally applied (O'Connor et al., 2007). Additionally, there is evidence that the relationship between PLD and temperature is non-linear, with a decline in PLD with rising temperature up to 28-29°C, then PLD stabilizes in some species and increases in others (McLeod et al., 2015). Increased temperature also shifts reproduction and spawning times through disruption of environmental cues, which shifts dispersal timing (Andrello et al., 2015).

Reef habitat degradation may also influence variability in connectivity. Reef degradation typically relates to structural reef complexity, with highly degraded reefs being composed of dead coral and rubble and healthy reefs being composed of live coral (Wolfe et al., 2021). Anthropogenic disturbance has historically resulted in increased habitat degradation of reefs (Hughes, 1994). More recently, climate change impacts such as increased SST have led to coral bleaching and loss of live coral cover, influencing ecosystem structure and function (Stuart-Smith et al., 2018). This decline has implications for larval connectivity between coral reefs. Reductions in habitat quality reduce reproductive output, and therefore dispersal (Magris et al., 2016). However, there remains a significant knowledge gap in understanding the role of connectivity in moderating coral reef resilience under future climate regimes (Edmunds et al., 2018). Similarly, little is known about the role of habitat degradation in influencing larval connectivity. While it is unknown whether coral reef degradation acts as a driver of variability in connectivity, investigations of this relationship are crucial due to the global decline in coral cover, and therefore increased abundance of "degraded" reefs (Eddy et al., 2021).

Lastly, connectivity plays a key role in the success of no-take marine reserves (Green et al. 2015). Marine reserves with enhanced connectivity host fish taxa with increased body mass, increasing fecundity and contributing to spillover (Goetze et al., 2021). Well-connected reserves also provide a dampening effect which minimizes temporal fluctuations in larval supply and recruitment (Harrison et al., 2020). This dampening is referred to as the "connectivity portfolio effect" and can be utilized in marine network design to create marine reserves that are well connected and therefore can successfully provide such benefits (Harrison et al., 2020). Environmental drivers may influence connectivity and subsequently the connectivity portfolio effect, but this relationship remains unknown. Therefore, understanding variability in connectivity will allow us to better conserve the effectiveness of marine networks and marine reserves.

Here, I study how environmental factors influence larval connectivity in coral reef ecosystems over a period of 20 years (1993-2012). Specifically, I examine three main hypotheses in Southeast Sulawesi, Indonesia. First, I predict connectivity will decrease over the 20-year period as environmental factors change (SST, ocean acidification, extreme climate cycles, stratification, salinity), disrupting larval processes. Second, I predict that variance in SST, El Nino, and PDO will be a significant predictor of variance in connectivity, as climate cycles and warming water influence the movement and development of larvae. Third, I predict habitat degradation will decrease cumulative larval flow over time as degraded reef habitat is functionally "smaller" and outputs less larvae. These hypotheses aim to understand external drivers of variability in connectivity, which in turn will allow me to infer potential impacts of climate change on coral reef connectivity to inform marine management and marine network design.

## Methodology

### *Study Site*

I focus on connectivity and climate change processes on coral reefs in the Southeast Sulawesi province of Indonesia (Figure 1). This region is at the center of the Coral

Triangle, containing some of the most biodiverse coral reefs in the world (Reaka et al., 2008). The coral reefs of Southeast Sulawesi are threatened by bleaching (Yusuf & Jompa, 2012), pollution and destructive fishing (Edinger et al., 1998), and the Crown of Thorns starfish (*Acanthaster planci*) (Plass-Johnson et al., 2015). These effects on the reef have consequences for fisheries and local livelihoods (Ferse et al., 2014). To help alleviate some of these impacts, Southeast Sulawesi supports various ongoing projects and policies to enhance marine conservation efforts (Watt-Pringle et al., 2024). In 2018, the Indonesian government announced plans to protect 30 million hectares of marine area by 2030, joining together village and fishing communities to codevelop a management plan (Muenzel et al., 2023). The protection of marine areas is accomplished through Marine Protected Areas (MPAs), which focus on conservation and sustainable use of marine biodiversity, with an emphasis on fisheries in Indonesia (Tranter et al., 2022). These efforts aim to successfully manage MPAs, while conserving MPA function to protect and sustainably source marine biodiversity. The larval connectivity data I am using are from 487 coral reef sites, quantifying connectivity from 1993-2012 (Figure 1).

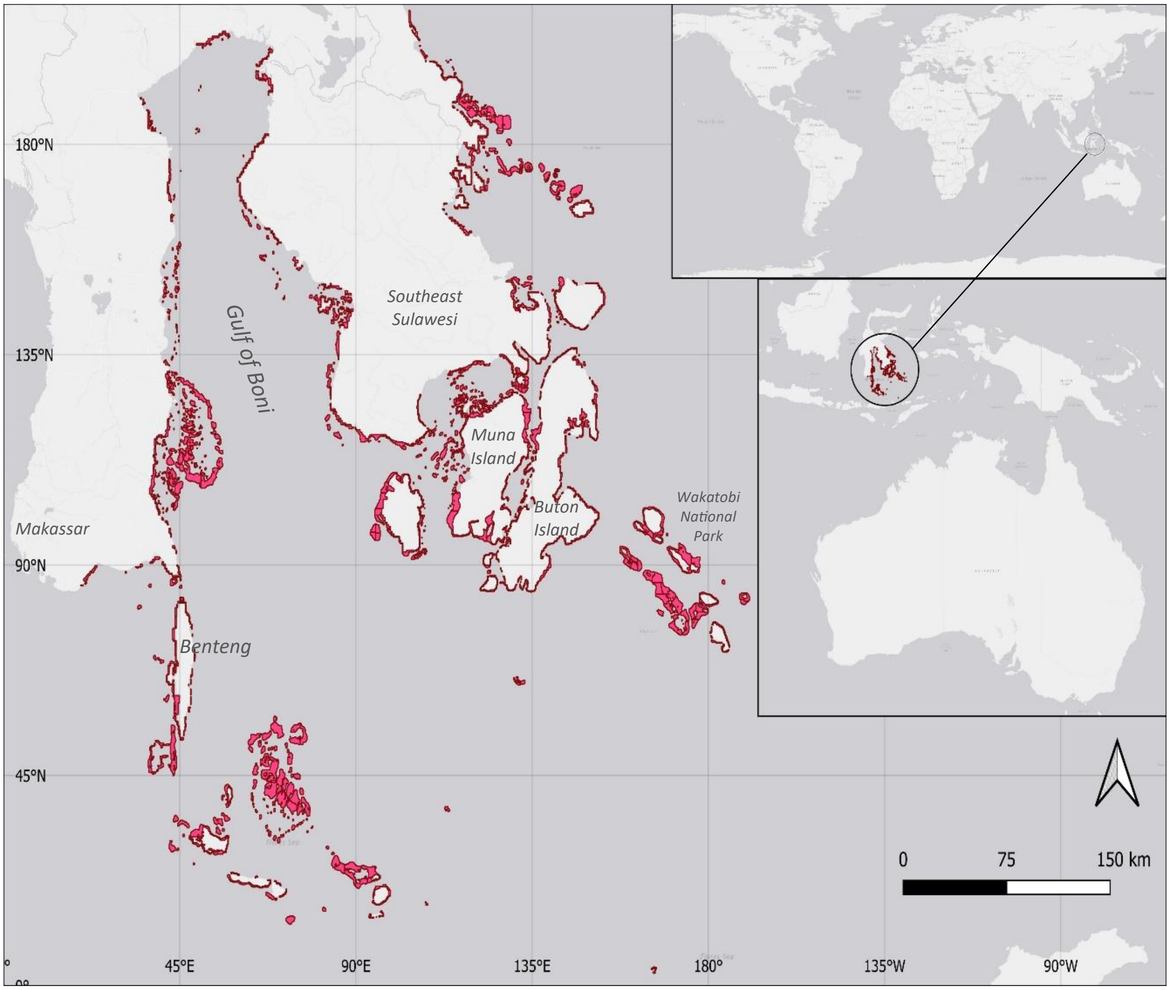


Figure 1. Map of study area in Southeast Sulawesi showing 487 reefs (in pink) used in the biophysical model.

### *Larval Connectivity Model*

Larval connectivity estimates for coral trout (*Plectropomus leopardus*), white-spotted rabbitfish (*Siganus canaliculatus*), malabar snapper (*Lutjanus malabaricus*), and common octopus (*Octopus vulgaris*) were created using a biophysical modeling approach (Treml et al., 2012). The first species, coral trout, have an average pre-competency window of 15 days, a PLD of 19-31 days, and spawn September-November (Doherty et al., 1994; SCRFA, 2019). Secondly, rabbitfish have an average pre-competency of 10 days, a PLD of 17 days, and spawn March-September (Soliman et al., 2010). Thirdly, snapper have an average pre-competency of 25 days, a PLD of 33-40 days, and spawn October-February (Quéré & Leis, 2010). All three species are important to commercial fisheries in the area, while the species octopus was added because they spawn year-round (Lourenço et al., 2012), allowing me to analyze variance based on spawning period and length.

Larval connectivity data were derived from the biophysical model in Treml et al., 2012. The model has three components: 1) a gridded map of the seascape, 2) biological parameters, and 3) data on oceanic currents and velocity. The map extends from 100°E to 170°E and 30°N to 30°S. The biological parameters included in the model are: 1) larval release date and periodicity (months), 2) reproductive output per area (fecundity), 3) maximum Pelagic Larval Duration (PLD) (days), 4) pre-competency period (days), 5) larval swimming and homing behavior during settlement, and 6) larval mortality (survival function). Oceanic currents were modeled from the US Jet Propulsion Laboratory Regional Ocean Monitoring System (ROMS). The ROMS data was forced with the National Center for Environmental Prediction/National Center for Atmospheric Research reanalysis to account for wind, temperature, and solar radiation. This creates an oceanographic model that reflects seasonal and interannual variability.

A 2-D Eulerian model was used, which represents dispersal as a cloud of larvae, as opposed to individual larvae. Each simulation of the model involved releasing a cloud of larvae over a habitat patch and tracking the cloud as it moved through the seascape. The clouds moved through the model using an advection transport algorithm. As a cloud encountered suitable habitat, the quantity of larvae settled was recorded and this process repeated for years 1993-2012 (Treml et al., 2012). The total amount of larvae that settled on each habitat was recorded through time and saved as the dispersal matrix (D). Simulations were run across three years (a strong El Nino, La Nina, and a neutral year) then a weighted average was taken to create the dispersal matrix. The settlement matrix (S) was then calculated by multiplying D by a larval survivorship function and post-settlement mortality parameters. S represents the cumulative number of larvae exchanged between all habitats after larval mortality. The probability matrix (P) rescales S to the probability of larval exchange between habitats. Therefore, the probability matrix represents the proportion of individuals originating from a donor habitat which arrive at a recipient habitat, or the arrival likelihood (Marxan Connect Glossary, 2024). The migration matrix (M) quantifies the proportion of settlers to each destination habitat that came from each source habitat, or the proportion of individuals arriving at a recipient habitat that originated from a donor habitat (Bodmer &

Cavalli-Sforza, 1968; Caswell, 2014). An additional matrix we created was the flow matrix, which is calculated by multiplying P by reef size to account for the effect of differing population sizes on connectivity. Therefore, the flow matrix represents connectivity between habitats based on fecundity and density of species per $km^2$ area of reef. The flow matrix does not account for habitat degradation, meaning the $km^2$ reef size used to calculate fecundity and density of species assumes all habitat is suitable. These matrices are summarized at a yearly resolution, resulting in 20 matrices for the 20 years of the biophysical model.

### *Environmental Data*

To determine the influence of environmental factors on connectivity, I use Sea Surface Temperature (SST), El Niño 3.4 SST Index, and Pacific Decadal Oscillation (PDO) (Table 1). This approach allows me to examine annual and interannual variation of environmental conditions. The SST data combines a 5km resolution European Space Agency Climate Change Initiative SST Analysis daily dataset and a 1km Multi-scale Ultra-high Resolution SST Analysis dataset. The 5km dataset was downscaled to match a 1km resolution (Dixon et al., 2022). The El Niño 3.4 SST Index samples a specific region from 5N-5S and 170W-120W and represents average SST anomalies. Anomalies are defined by SSTs exceeding +/-0.4°C for six months or more (Schneider et al., 2013). PDO data are representative of more long-lived El Niño patterns. PDO is positive when SST is anomalously warm on the Pacific Coast and sea level pressures are below average. Therefore, PDO is negative when SST is anomalously cool on the Pacific Coast and sea level pressures are above average (Newman et al., 2016). I obtained habitat degradation data from two different sources, the National Research and Innovation Agency (BRIN, https://data.brin.go.id/dataverse/crmis) and Operation Wallacea (Opwall, https://www.opwall.com) which each provided percent hard coral cover data. Habitat degradation data was provided from 1997-2024. An average percent cover value was calculated per year and used to multiply into the connectivity matrix.

Table 1. Environmental data sources used in analyses and their citations.

| **Environmental Data Sources** | |
|---|---|
| Sea Surface Temperature (SST) | Dixon et al., 2022 |
| El Nino 3.4 Index | https://psl.noaa.gov/data/timeseries/month/ |
| Pacific Decadal Oscillation (PDO) | https://psl.noaa.gov/data/timeseries/month/DS/PDOUW/ |
| Opwall | https://www.opwall.com/ |
| BRIN | https://data.brin.go.id/dataverse/crmis |

### *Data Analysis*

To create a usable data frame for analysis, I first summarized PDO and El Nino data into mean values per year. These means were generated from the 14 provided values per year for each year within the connectivity model (1993-2012). SST values were clipped from the original raster to only include dates from January 1, 1993 to December 31, 2012. Values were then split by species, and the only dates retained were those within that species' spawning month (inclusive of PLD). SST mean and standard deviation were calculated. These data were then combined into a data frame which included species, year, SST mean, and SST standard deviation for each of the 487 reefs within the connectivity model. Approximately 30 percent of the data was comprised of NA values, so I used an interpolation technique to populate all missing values. I then calculated varying connectivity metrics to add to the data frame. Using the package "igraph" (Csardi & Nepusz, 2006) in RStudio (2024), I calculated out-degree and in-degree for each unique combination of species, year, and reef. I used the package "ConnMatTools" (Kaplan et al., in press) in RStudio (2024) to calculate self-recruitment for each species, year, and reef. These values were then added into the SST data frame. I then used spectral clustering in the "kernlab" (Karatzoglou, Smola, & Hornik, 2024) package in RStudio (2024) to create spatial clusters for each species, year, and reef. Spectral clustering is a graph-based method that caters to complex, non-convex cluster structures (Ng et al., 2001). Creating clusters and using them as a random effect in the models allowed me to account for spatial variation in connectivity patterns. I chose to calculate 6 clusters after performing clustering using between 5-10 cluster groupings and examining the spatial clustering in QGIS to ensure groupings were generally aligned with geographic proximity. I then calculated a mean matrix for each of the four model species and performed spectral clustering with 6 centers on these mean matrices to obtain a cluster grouping across all years for each species. These data were then added to the data frame. The final result was a data frame that included cluster group, out-degree, in-degree, self-recruitment, mean El Nino, mean PDO, and mean SST for each unique combination of reef, species, and year (n=38960).

To determine how connectivity changed over the 20-year period, I used cumulative flow and three graph-theoretic metrics (out-degree, in-degree, and self-recruitment) as a proxy for connectivity. Cumulative flow is the sum of all values within one flow matrix, resulting in a single value for each year. Out-degree is the number of connections originating from each reef (Minor & Urban, 2007). This metric can be a useful tool in determining source reefs. In-degree is the number of connections coming into each reef, useful in determining sink populations. Self-recruitment is the proportion of individuals arriving at each reef from that reef (Minor & Urban, 2007), which quantifies the local retention. These metrics are dimensionless, all representing a number or proportion of connections or larvae. To compare all four metrics, I averaged out-degree, in-degree, and self-recruitment per year, per species, to obtain one value for each species within each year. I then performed a Generalized Linear Model (GLM) (McCullagh, 2019) to test my hypothesis that connectivity would decrease over time. A GLM was performed for each connectivity metric for each species. Lastly, to summarize the variance seen in cumulative flow between species, I calculated the standard deviation for each species and then performed a Levene's test (Levene, 1960) to determine statistical significance of the variance.

To determine how variability in climate factors affects variability in connectivity, I used a recursive partitioning analysis with a regression tree. This analysis is useful in identifying patterns in large, complex datasets. The analysis works by repeatedly splitting the data into homogenous groups using an explanatory variable (De'ath & Fabricius, 2000). In this case, the regression tree "splits" the connectivity data based on two predictor variables: 1) SST, and 2) cluster. I used these results to separate my data based on the highest SST split in the regression tree (e.g., octopus out-degree values were split by values when SST mean ≥ 29 and values when SST mean < 29). I performed an independent effect size analysis between connectivity metrics of the split data using Cohen's *d* (Davies et al., 2024). Cohen's *d* measures the difference between the means of two groups using standard deviation (e.g. $d = 0.5$, the means of group 1 and 2 vary by half a standard deviation) (Cohen, 1992). Generally, values between 0.2-0.5 are considered a small effect, 0.5-0.8 is medium, and above 0.8 is a large effect (Blanar et al., 2009). This allowed me to quantify the effect of SST on out-degree, in-degree, and self-recruitment for each species when SST was above or below a certain threshold and between cluster groupings. I created a forest plot using an SST threshold of 29°C to visualize Cohen's *d* values with a 95% confidence interval. I then performed a generalized additive model (GAM) (Hastie & Tibshirani, 1986) on the data to further visualize the effect of the threshold SST on out-degree, in-degree, and self-recruitment with year as a fixed effect and cluster as a random effect. I additionally performed GAMs for El Nino 3.4 and PDO values across the whole dataset to examine the effect of these metrics on connectivity. This looked at the effect of mean El Nino 3.4 and PDO values (i.e. the mean El Nino 3.4 and PDO value across space for each year) across the 20-year period on out-degree, in-degree, and self-recruitment for each species. The GAMs were run across the entire dataset (all reefs across all years) and had year as a fixed effect and cluster as a random effect. Model fits were evaluated via adjusted R-squared.

To account for spatial variance in connectivity patterns, I included cluster as a random effect in each GAM analyzing El Nino 3.4 and PDO with out-degree, in-degree, and self-recruitment. I additionally repeated all GAMs without cluster as a random effect and performed a Likelihood Ratio Test (LRT) (Lewis et al., 2011) to examine the significance of the random effect of cluster. I then used cluster as a predictor variable in the recursive partitioning analysis. I repeated the Cohen's *d* effect size analysis using the highest cluster split in the recursive partitioning model to determine the effect of cluster on connectivity (e.g., octopus out-degree values were split by values within clusters 1, 4, and 6 and values within clusters 2, 3, and 5). I created a forest plot using each cluster split for each connectivity metric and species to visualize the Cohen's *d* values with a 95% confidence interval.

To quantify to what degree habitat degradation is reducing connectivity, I used coral cover as a proxy for reef habitat condition (Vercammen et al., 2019). I first summarized coral cover data from the two sources to determine average percent coral cover for each year in the dataset (1997-2024 with missing years 1993-1996, 2000, 2002, and 2004). I then performed a GLM to predict coral cover values for missing years within my connectivity data range (1993-2012) using the known percent cover values and the data provider (Opwall and BRIN) as a random effect. Years in which there were both Opwall and BRIN data the percent coral cover value was the average of the two values (years 2006-2010). Since data were not from the exact locations of the 487 model reefs, I determined average percent coral cover temporally (average percent cover value in that year) rather than spatially for model years. I multiplied percent cover values into the flow matrices for all years and species (1 value for each year and across all species), simulating model results if each reef were smaller and therefore output less larvae. This approach created flow matrices that account for habitat loss due to habitat degradation. I then calculated the sum of each matrix to obtain a cumulative flow value. I then compared cumulative flow before and after habitat degradation using an Analysis of Variance (ANOVA). I used these results to calculate the relative difference in flow to obtain a percentage decrease value for each species and then calculated the average percent decrease in flow across all four species. Additionally, I performed a Levene's test to determine the statistical significance of the variance between cumulative flow before and after degradation for each species. I then used the percent coral cover values from non-model years (2013-2020, 2023, and 2024) and multiplied each value into all 20 flow matrices for each species. I calculated the sum of each flow matrix for each species. I took the mean of the cumulative flow values for each year (mean cumulative flow values being from percent coral cover values 2013-2020, 2023, and 2024 multiplied into model year flow matrices from 1993-2012) to obtain a "predicted" cumulative flow value with standard error for years 2013-2020, 2023, and 2024.

## Results

### *1. How is connectivity changing across the 20-year period?*

All connectivity metrics had non-linear trends across time (Figure 2). GLM results showed non-significant decreases in cumulative flow (p = 0.140), out-degree (p = 0.846), and in-degree (p = 0.846) across time. There was a significant increase in self-recruitment across time (p = 0.042).Minimum and maximum values varied across metrics, species, and year with no visible trend. There was a significant difference in variance of cumulative flow between species. The standard deviations of flow for octopus (σ = 0.003) and snapper (σ = 0.001) were lower than coral trout (σ = 0.300) and rabbitfish (σ = 0.032). Levene's test further supported these results, showing a significant difference in variance between the four species (p < 0.001).

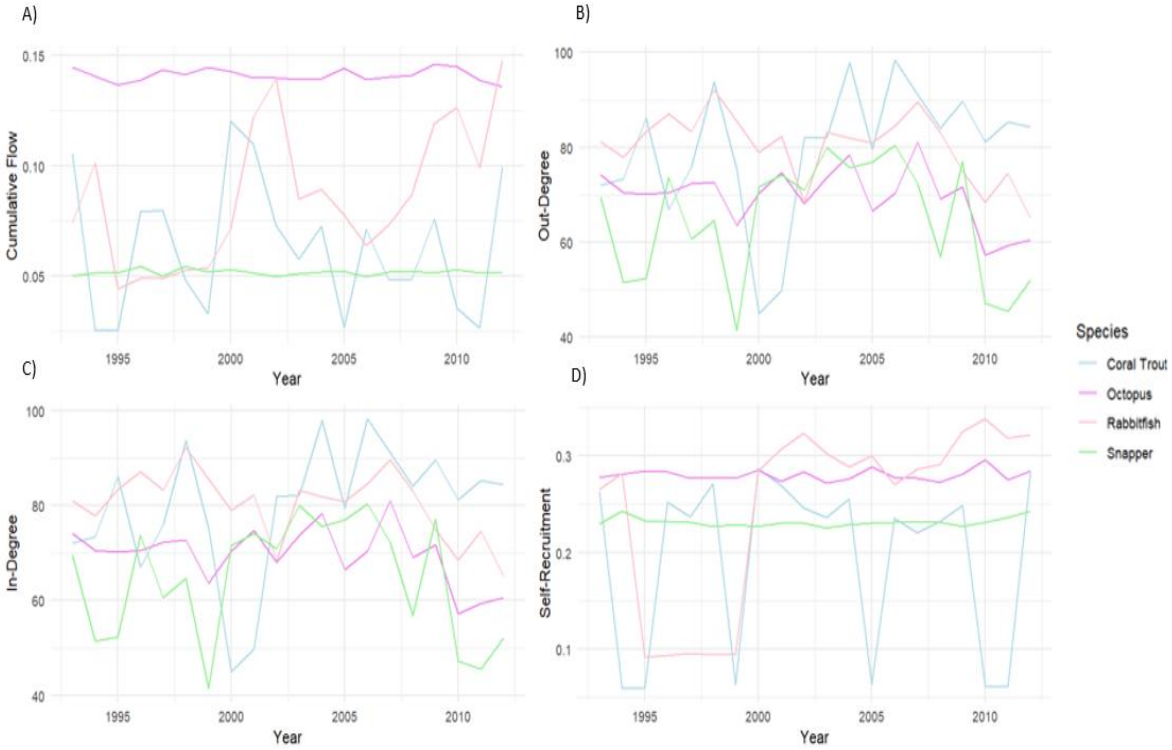
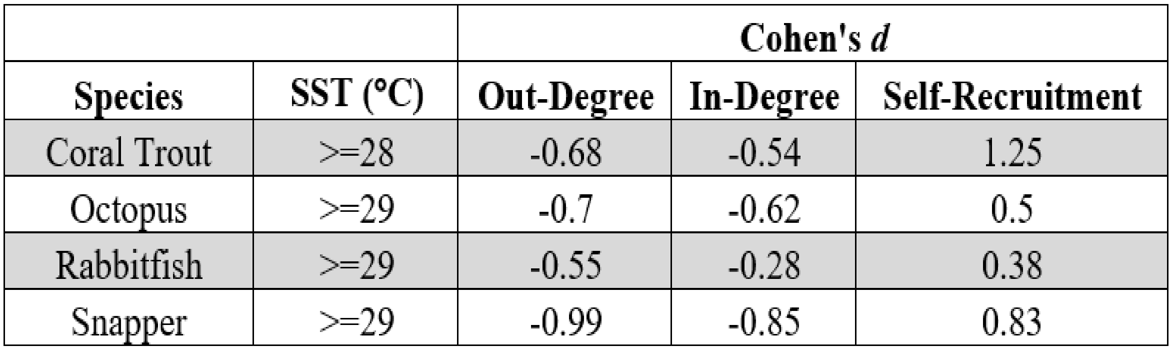


Figure 2. Changes in connectivity over the 20-year model period (1993-2012). Metrics are A) cumulative flow, B) out-degree, C) in-degree, and D) self-recruitment. Each colored line represents a different species.

*2. How do changes in climate change factors (i.e. SST, El Nino, PDO) affect connectivity?*

The effect of SST on out-degree, in-degree, and self-recruitment varied widely by species. For coral trout, when SST is greater than or equal to 28°C, there is a medium negative effect on out-degree (Cohen's *d* = -0.68) and in-degree (*d* = -0.54), and a large positive effect on self-recruitment (*d* = 1.25) when SST is greater than or equal to 29°C. For octopus, when SST is greater than or equal to 29°C, there is a medium negative effect on out-degree (*d* = -0.70) and in-degree (*d* = -0.62) and a medium positive effect on self-recruitment (*d* = 0.50). For rabbitfish, when SST is greater than or equal to 29°C, there is a medium negative effect on out-degree (*d* = -0.55), a small negative effect on in-degree (*d* = -0.28), and a small positive effect on self-recruitment (*d* = 0.38). For snapper, when SST is greater than or equal to 29°C, there is a large negative effect on out-degree (*d* = -0.99) and in-degree (*d* = -0.85), and a large positive effect on self-recruitment (*d* = 0.83) (Table 2). These results are further summarized into a forest plot using an SST threshold of 29°C with 95% confidence intervals (Figure 3).

Table 2. Cohen's *d* values comparing the effect of SST on three connectivity metrics (out-degree, in-degree, self-recruitment) for each species. Values between 0.2-0.5 are considered a small effect, 0.5-0.8 is medium, and above 0.8 is a large effect (Blanar et al., 2009).



| | | **Cohen's *d*** | | |
|---|---|---|---|---|
| **Species** | **SST (°C)** | **Out-Degree** | **In-Degree** | **Self-Recruitment** |
| Coral Trout | >=28 | -0.68 | -0.54 | 1.25 |
| Octopus | >=29 | -0.7 | -0.62 | 0.5 |
| Rabbitfish | >=29 | -0.55 | -0.28 | 0.38 |
| Snapper | >=29 | -0.99 | -0.85 | 0.83 |

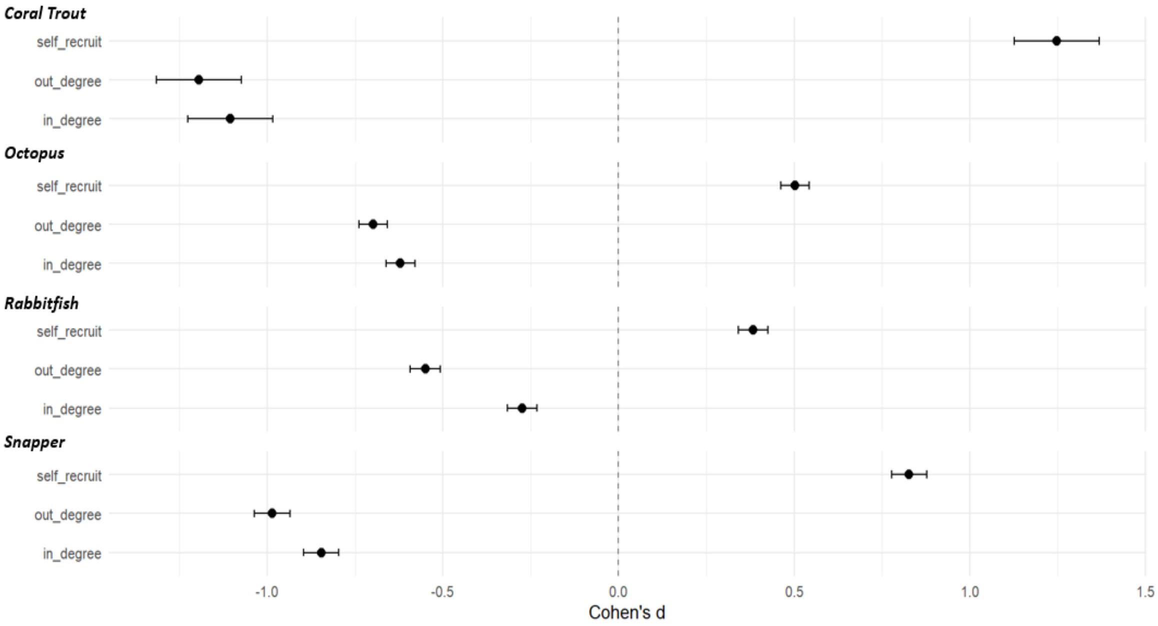


Figure 3. Forest plot of Cohen's *d* values with 95% confidence intervals for each of the three connectivity metrics (out-degree, in-degree, and self-recruitment) separated by species (coral trout, octopus, rabbitfish, and snapper). Cohen's *d* compared connectivity values at SST < 29°C to values at SST ≥ 29°C. The dashed line in the middle represents zero effect.

When comparing GAM model results between SST groupings (e.g. coral trout data split into SST mean values ≥ 28 and SST mean values < 28), the model results fit better at higher SST. For example, for coral trout, out-degree at values when SST ≥ 28°C had an $R^2$ value of 0.397 compared to values when SST < 28°C with an $R^2$ of only 0.146. This trend is seen in all connectivity metrics for coral trout (Figure 4), octopus (Figure 5), rabbitfish (Figure 6), and snapper (Figure 7). GAM results were significant for all models ($p < 0.001$) while the $R^2$ values differed between each model (Table 3).

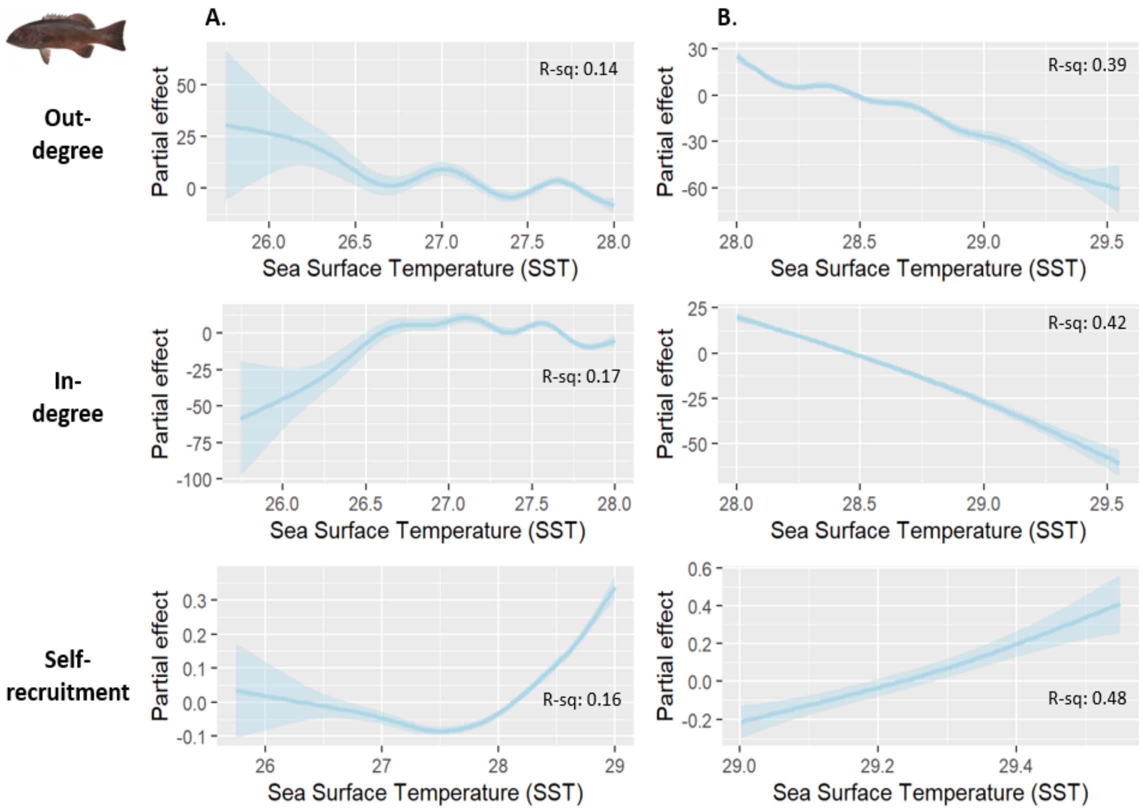


Figure 4. GAM results analyzing three connectivity metrics (out-degree, in-degree, and self-recruitment) against mean SST for values A. below 28°C (for out-degree and in-degree) 29°C (for self-recruitment) and B. greater than or equal to 28°C (for out-degree and in-degree) and 29°C (for self-recruitment) for coral trout.

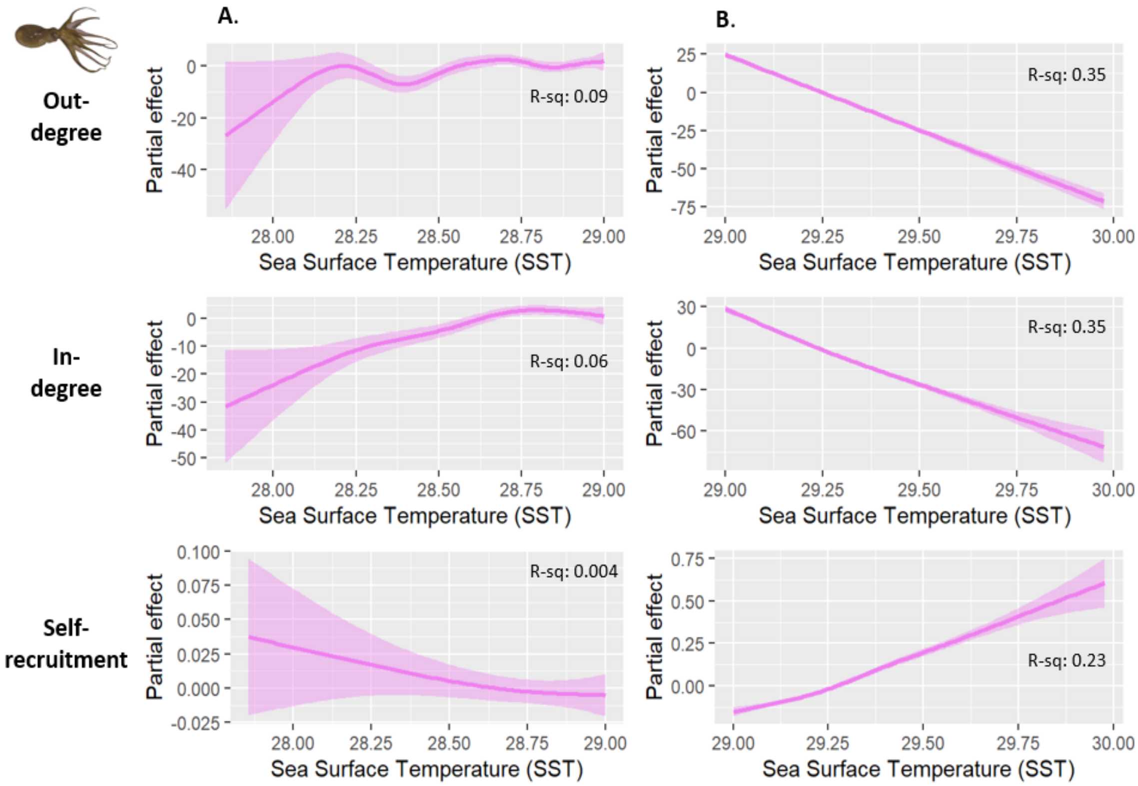


Figure 5. GAM results analyzing three connectivity metrics (out-degree, in-degree, and self-recruitment) against mean SST for values A. below 29°C and B. greater than or equal to 29°C for octopus.

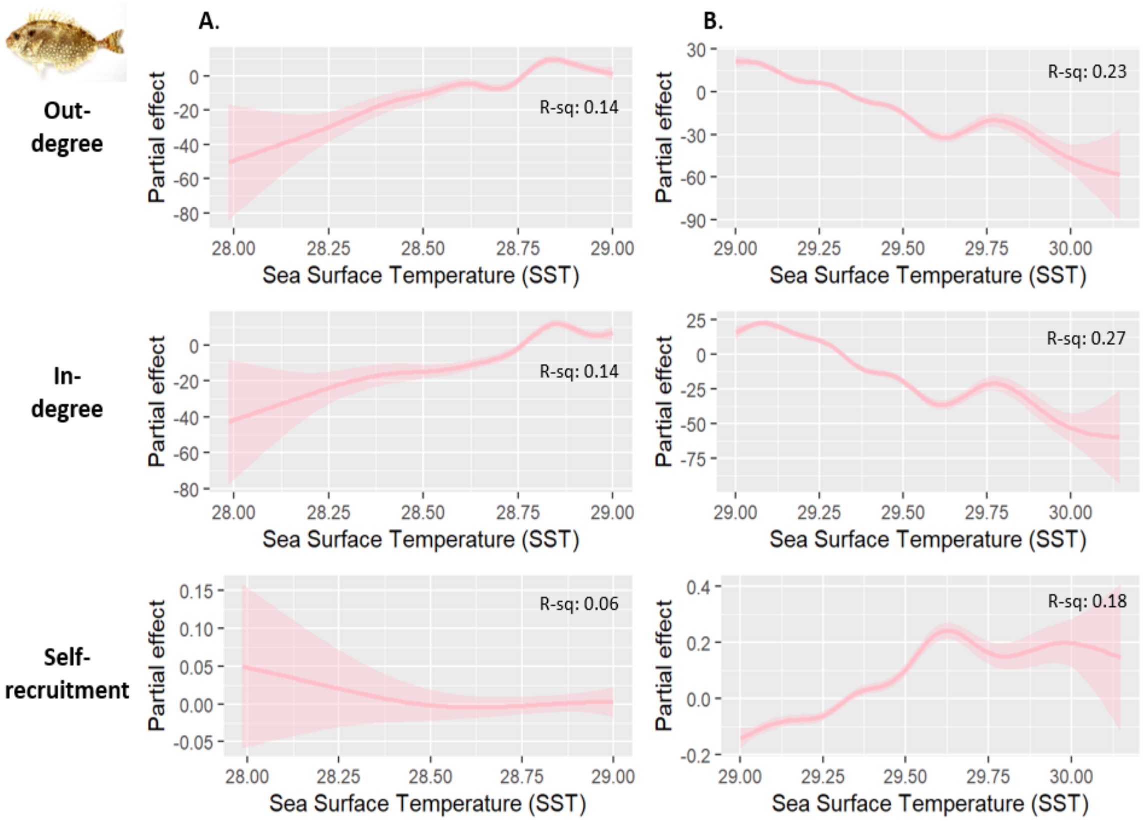


Figure 6. GAM results analyzing three connectivity metrics (out-degree, in-degree, and self-recruitment) against mean SST for values A. below 29°C and B. greater than or equal to 29°C for rabbitfish.

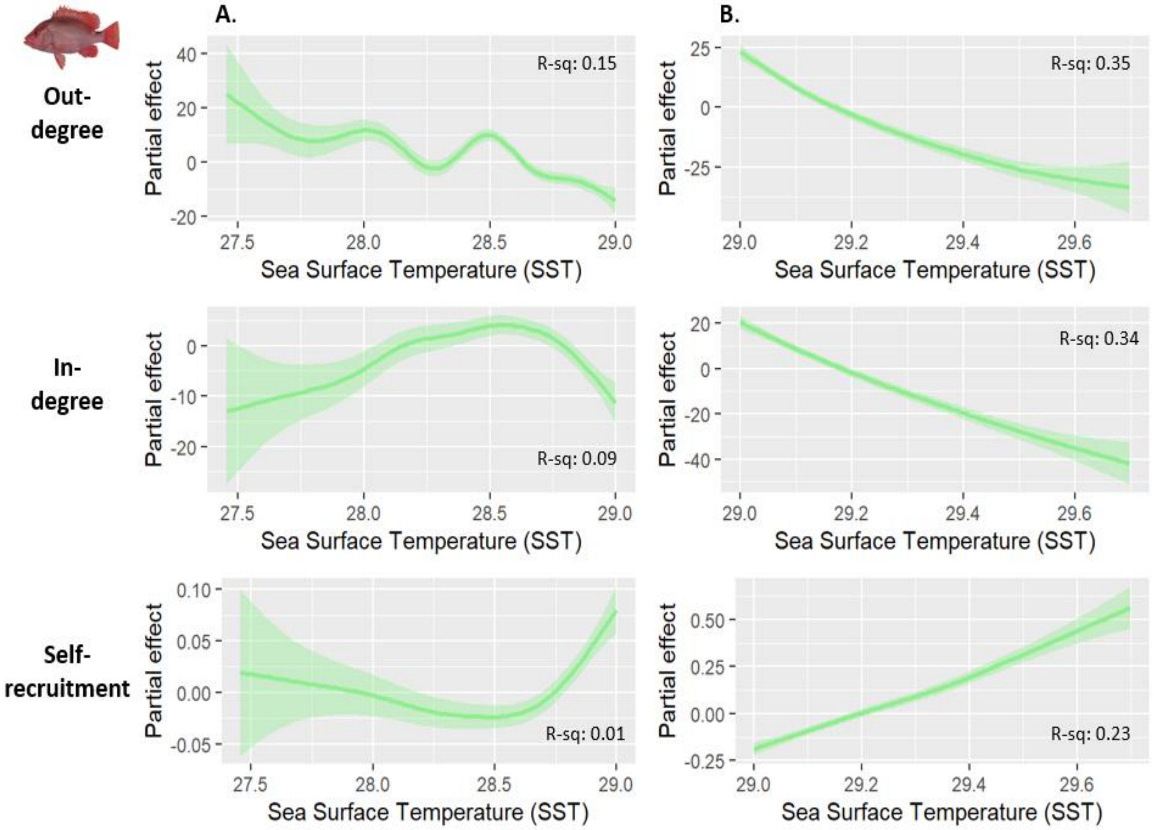


Figure 7. GAM results analyzing three connectivity metrics (out-degree, in-degree, and self-recruitment) against mean SST for values A. below 29°C and B. greater than or equal to 29°C for snapper.

I performed a GAM for El Nino 3.4 and PDO to assess the relationship between mean El Nino 3.4 and PDO and connectivity metrics out-degree, in-degree, and self-recruitment between species. GAM results showed significance across all metrics and species ($p < 0.001$). The adjusted $R^2$ value was highest for out-degree, followed by in-degree and self-recruitment for all species across El Nino and PDO models. Adjusted $R^2$ was on average 0.59 across species between El Nino and PDO on out-degree, $R^2$=0.52 on in-degree, and $R^2$=0.25 on self-recruitment (Table 3). The significance of year as a fixed effect was $p < 0.001$ for El Nino and PDO across all metrics for coral trout and rabbitfish, and for out-degree and in-degree for octopus and snapper. Year as a fixed effect was not significant for El Nino and self-recruitment for octopus (p=0.808), and snapper (p=0.853), and PDO and self-recruitment for octopus (p=0.764) and snapper (p=0.897).

Table 3. GAM results from El Nino 3.4, PDO, and split SST values by the three connectivity metrics. GAMs were split between species and connectivity metric, resulting in three models for each species. Results are represented by the mean adjusted R2 value across the four species for each connectivity metric and predictor variable.

| **Species** | **Connectivity Metric** | **El Nino R2** | **PDO R2** | **SST (<29) R2** | **SST (≥29) R2** |
|---|---|---|---|---|---|
| **Coral Trout** | Out-degree | 0.16 | 0.16 | 0.14 | 0.39 |
| | In-degree | 0.19 | 0.18 | 0.17 | 0.42 |
| | Self-recruit | 0.10 | 0.10 | 0.16 | 0.48 |
| **Octopus** | Out-degree | 0.14 | 0.14 | 0.09 | 0.35 |
| | In-degree | 0.10 | 0.09 | 0.06 | 0.35 |
| | Self-recruit | 0.05 | 0.05 | 0.004 | 0.23 |
| **Rabbitfish** | Out-degree | 0.08 | 0.07 | 0.14 | 0.23 |
| | In-degree | 0.07 | 0.07 | 0.14 | 0.27 |
| | Self-recruit | 0.09 | 0.09 | 0.06 | 0.18 |
| **Snapper** | Out-degree | 0.14 | 0.14 | 0.15 | 0.35 |
| | In-degree | 0.12 | 0.11 | 0.09 | 0.34 |
| | Self-recruit | 0.01 | 0.01 | 0.01 | 0.23 |

The effect of spatial clusters was significant for both El Nino and PDO GAMs across all species and metric ($p < 0.001$) and when comparing models with and without cluster as a random effect using an LRT ($p < 0.001$). There was a large effect ($d > 0.8$) of cluster on all connectivity metrics for all species (Table 4). For coral trout, there was a decrease in out-degree and in-degree for reefs in cluster 4, and an increase in self-recruitment (Figure 8). For octopus, there was a decrease in out-degree and in-degree for reefs in clusters 1, 4, and 6, and an increase in self-recruitment (Figure 9). For rabbitfish, there was a decrease in out-degree and in-degree for reefs in cluster 6, and an increase in self-recruitment (Figure 10). For snapper, there was a decrease in out-degree and in-degree for reefs in cluster 6, and an increase in self-recruitment (Figure 11). These are the effects compared to connectivity metric values in the other clusters (e.g., an increase in self-recruitment for reefs in cluster 6 compared to self-recruitment for reefs in clusters 1, 2, 3, 4, and 5) (Figure 12). This effect varies slightly between metric within each species, with only the shared cluster groups being retained here.

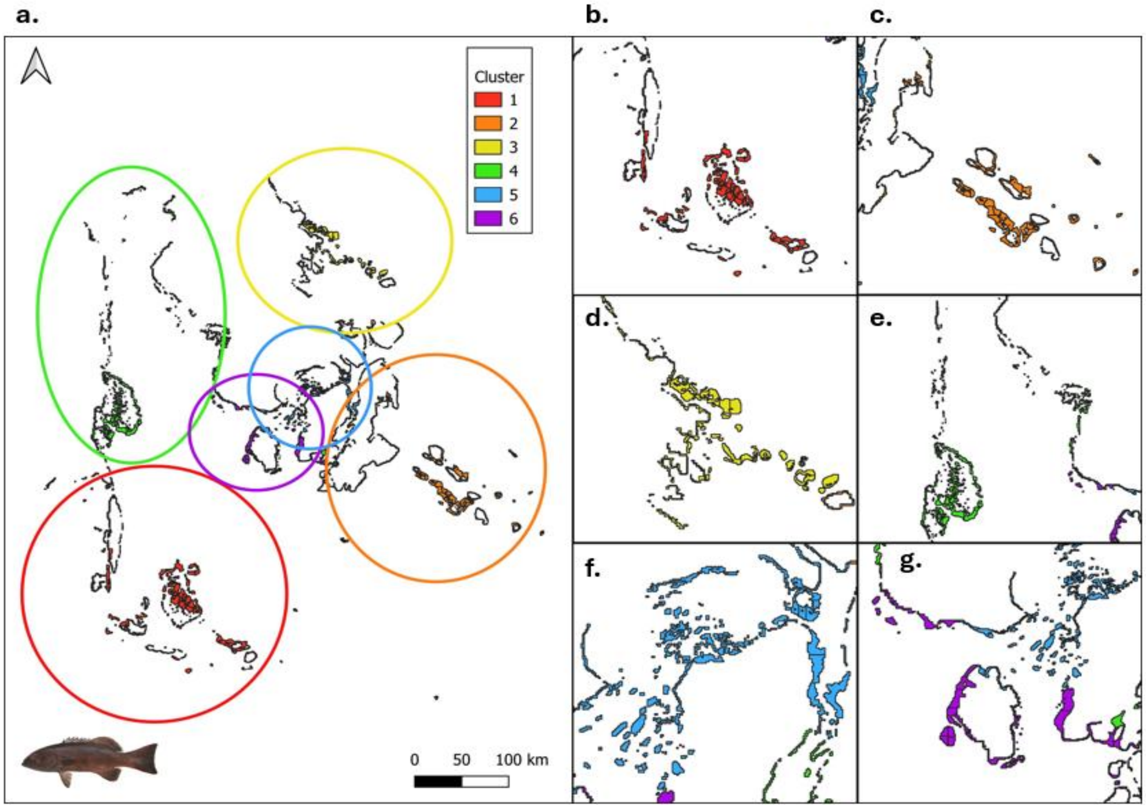


Figure 8. Spectral clustering grouping for coral trout. Each color represents a different cluster group (1-6). Panel: a) all 487 model reefs and their cluster groupings, reefs are colored by cluster and colored circles are used to represent the general area of each cluster group, b) cluster 1, c) cluster 2, d) cluster 3, e) cluster 4, f) cluster 5, and g) cluster 6.

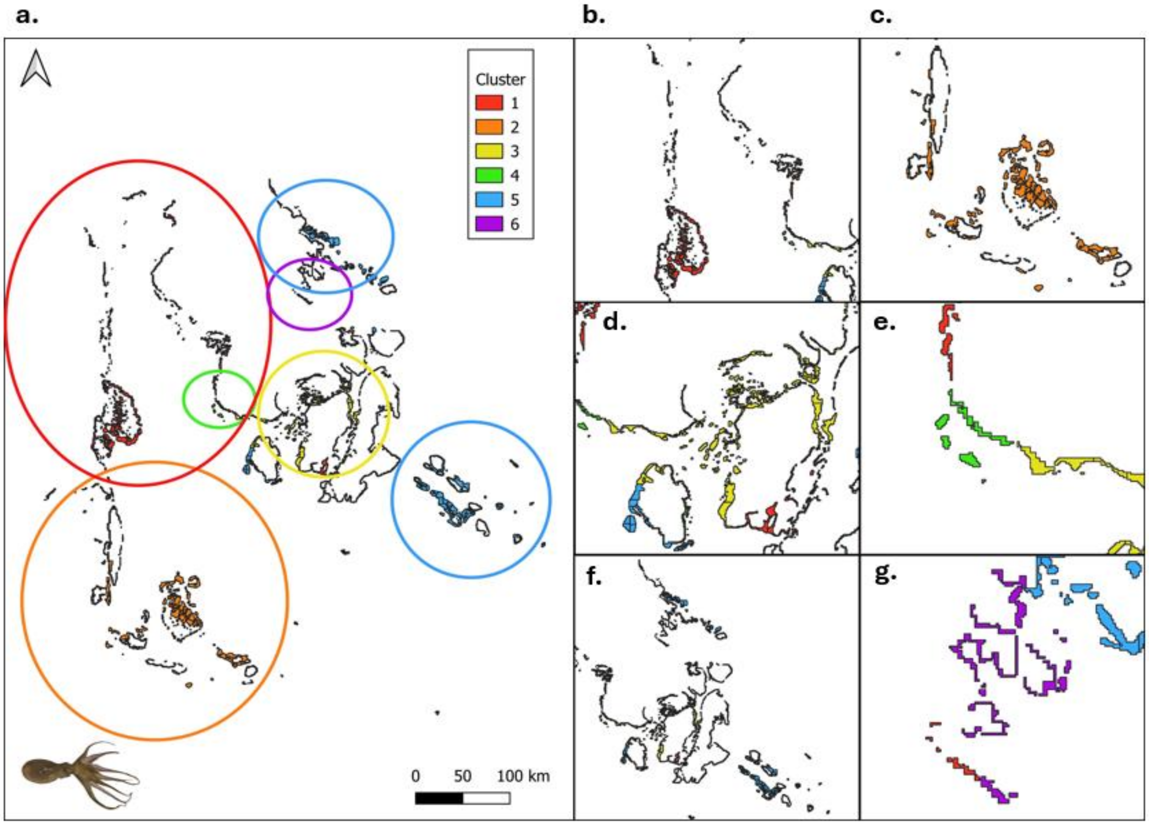


Figure 9. Spectral clustering grouping for octopus. Each color represents a different cluster group (1-6). Panel: a) all 487 model reefs and their cluster groupings, reefs are colored by cluster and colored circles are used to represent the general area of each cluster group, b) cluster 1, c) cluster 2, d) cluster 3, e) cluster 4, f) cluster 5, and g) cluster 6.

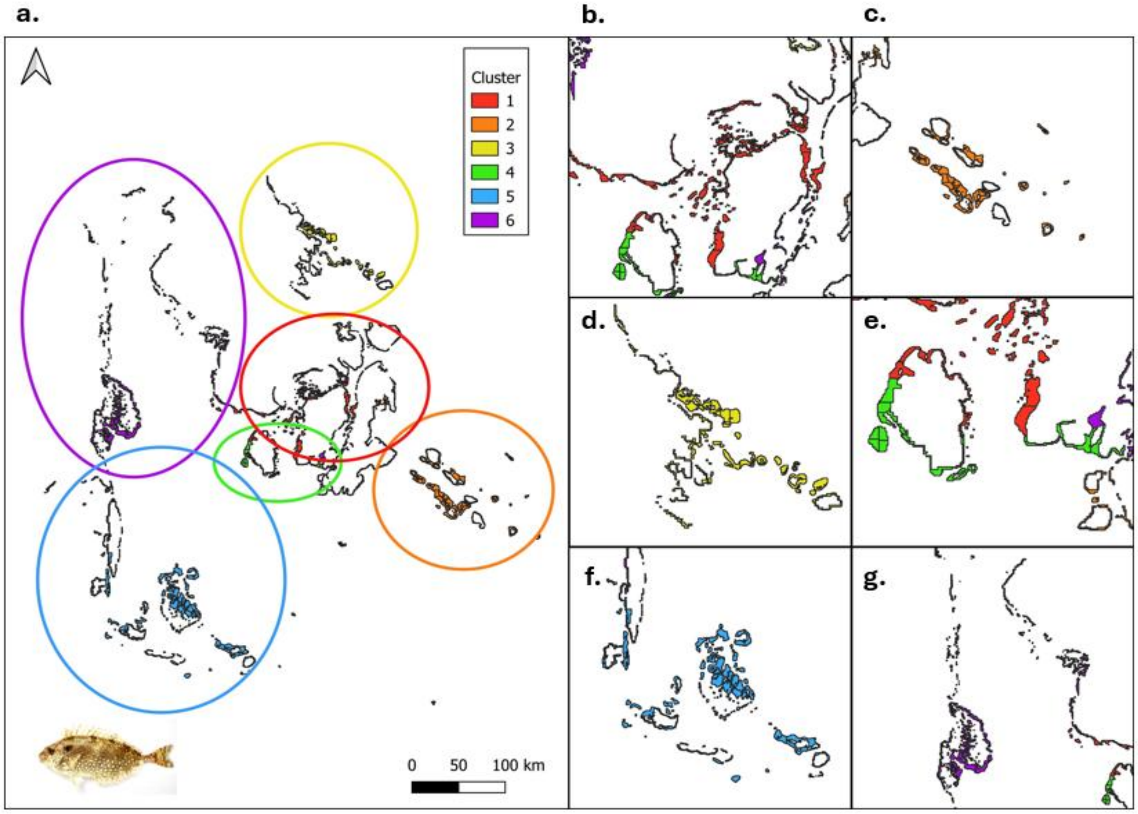


Figure 10. Spectral clustering grouping for rabbitfish. Each color represents a different cluster group (1-6). Panel: a) all 487 model reefs and their cluster groupings, reefs are colored by cluster and colored circles are used to represent the general area of each cluster group, b) cluster 1, c) cluster 2, d) cluster 3, e) cluster 4, f) cluster 5, and g) cluster 6.

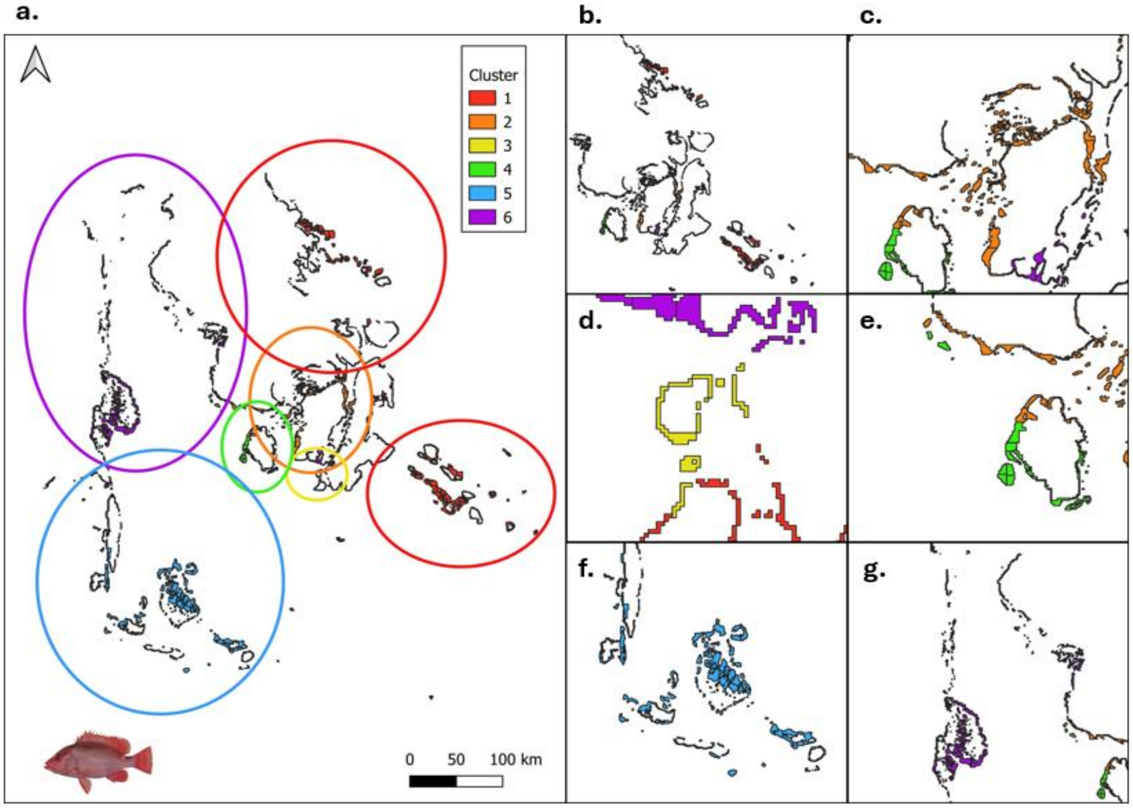


Figure 11. Spectral clustering grouping for snapper. Each color represents a different cluster group (1-6). Panel: a) all 487 model reefs and their cluster groupings, reefs are colored by cluster and colored circles are used to represent the general area of each cluster group, b) cluster 1, c) cluster 2, d) cluster 3, e) cluster 4, f) cluster 5, and g) cluster 6.

Table 4. Cohen's *d* values comparing the effect of cluster on three connectivity metrics (out-degree, in-degree, self-recruitment) for each species. Values between 0.2-0.5 are considered a small effect, 0.5-0.8 is medium, and above 0.8 is a large effect (Blanar et al., 2009).

| Cohen's d | | | | | | |
|---|---|---|---|---|---|---|
| **Species** | **Cluster (out-degree)** | **Out-degree d** | **Cluster (in-degree)** | **In-degree d** | **Cluster (self-recruitment)** | **Self-recruitment d** |
| Coral trout | 3, 4 | -1.75 | 1, 4 | -1.45 | 1, 2, 3, 5, 6 | -0.98 |
| Octopus | 1, 4, 6 | -2.30 | 1, 2, 4, 6 | -1.64 | 2, 3, 5 | -1.37 |
| Rabbitfish | 3, 6 | -2.32 | 6 | -2.59 | 1, 2, 3, 4, 5 | -0.83 |
| Snapper | 6 | -2.31 | 3, 4, 5, 6 | -1.62 | 1, 2, 3, 4, 5 | -1.19 |

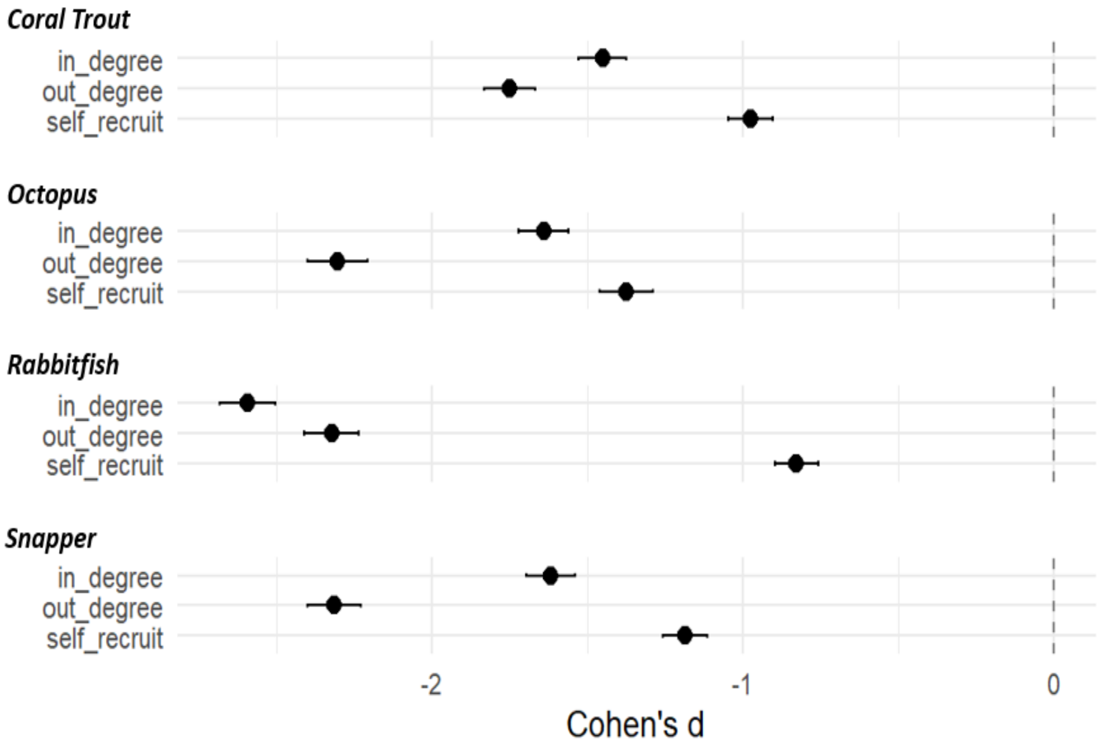


Figure 12. Forest plot of Cohen's *d* values with 95% confidence intervals for each of the three connectivity metrics (out-degree, in-degree, and self-recruitment) separated by species (coral trout, octopus, rabbitfish, and snapper). Cohen's *d* compared connectivity values from different cluster groupings (Table 4). The dashed line on the far right represents zero effect.

*3. How does habitat degradation affect connectivity?*

There was a significant effect of the data source on percent coral cover values in the GLM, confirmed by an LRT between the model with data source as a random effect and a reduced model without it ($p < 0.001$). There was a significant difference for all species between cumulative flow before and after habitat degradation (Figure 13). ANOVA results showed significance for all species ($p < 0.001$). Cumulative flow decreased by an average of 73 percent for all species after habitat degradation. Coral cover values were on average 26.6 percent between the years 1993-2012 (relative to total reef composition) (Figure 14). Levene's test shows a significant difference in the variance of cumulative flow for coral trout ($p < 0.001$), rabbitfish ($p < 0.01$), octopus ($p < 0.05$), and snapper ($p < 0.05$). Overall, all species experienced a decrease in cumulative flow and variance of flow. Additionally, this trend is predicted to continue beyond the year 2012 with cumulative flow remaining at significantly lower values when habitat degradation is included in the calculation (Figure 13).

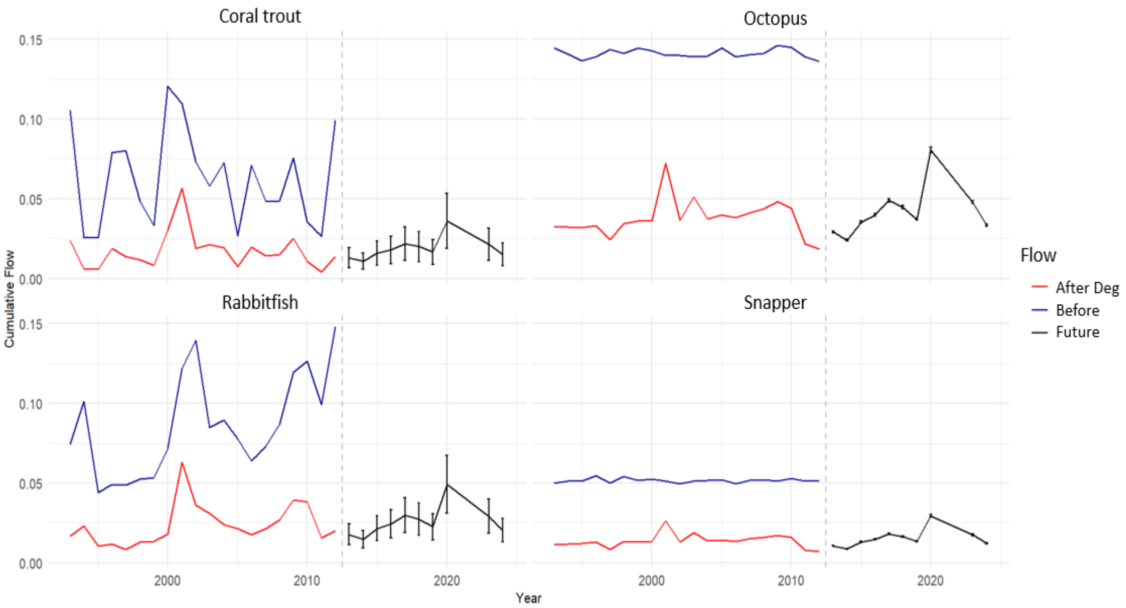


Figure 13. Changes in cumulative flow over the 20-year model period (1993-2012) compared before coral reef habitat degradation (blue line) and after habitat degradation (red line) for each species: A) coral trout, B) octopus, C) rabbitfish, and D) snapper. The grey dashed line represents the first year in which there is no connectivity model data (2013). The black line is “predicted” cumulative flow values using the mean of the 20 flow matrices to get standard error. Cumulative flow predictions were made with percent coral cover values from years 2013-2020, 2023, and 2024.

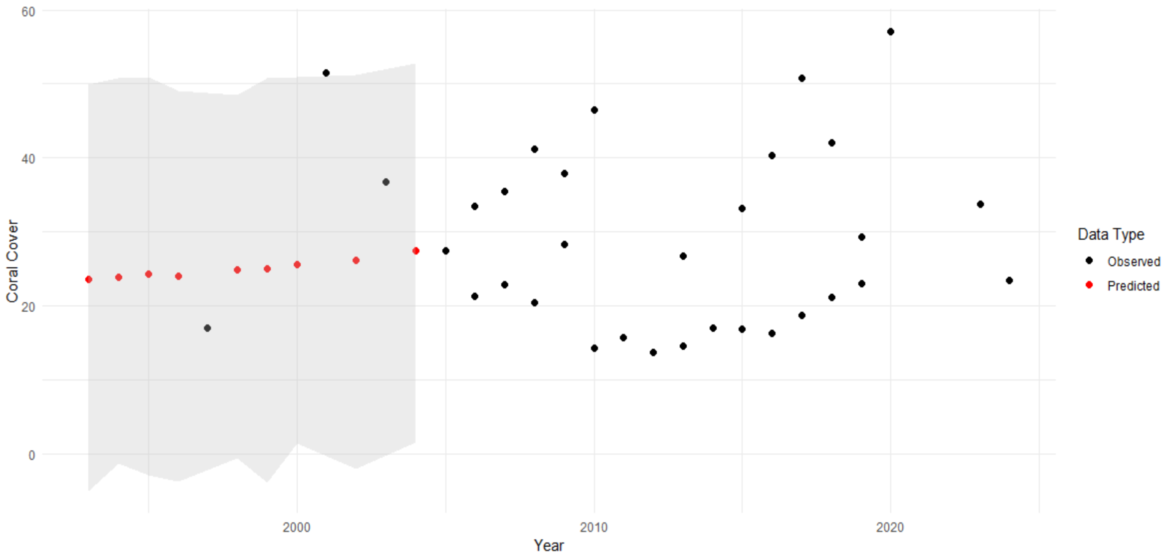


Figure 14. Average percent coral cover values from predicted and observed years. Predicted values are represented by red dots and observed values by black dots. Values for years 1993-1996, 2000, 2002, and 2004 were generated from a GLM using existing percent coral cover values with data source as a random effect. The grey shading represents a 95% confidence interval for predicted values. Percent cover was on average 26.6 percent across the 20-year period.

It is important to note that multiple testing was done to describe the relationships between SST, El Nino, PDO, and connectivity. With multiple testing, the likelihood of a type I error increases, meaning statistically significant results may not reflect true relationships between variables. I did not make any adjustments in my analysis to account for this error, therefore replication and extension of this analysis is necessary to confirm significant findings.

## Discussion

My objective was to determine the effects of external drivers on larval connectivity. My results show that variability in connectivity metrics can be explained by variance in the environmental factors SST, El Nino, and PDO. GAM analysis shows the significance of El Nino and PDO climate patterns in explaining variance of out-degree, in-degree, and self-recruitment. With more extreme ENSO events as a result of climate change, connectivity will decrease. Effect size analysis shows that when SST reaches 28°C or above, there are large effects on out-degree, in-degree, and self-recruitment dependent on species.

Generally, with increasing SST there is a decrease in inter-reef connectivity and an increase in local retention of larvae. Additionally, recursive partitioning, effect size analysis, and compared GAM analysis supports the existence of an SST threshold of 28-29°C at which connectivity will predictably drop for fish species in the region. Spatial analysis showed that spatial clustering of reefs has a larger effect on connectivity metrics compared to SST thresholds. Additionally, models were better fit with cluster as a random effect. Habitat degradation decreases cumulative flow and variance in cumulative flow across species, with similar trends expected in future years. With increasing habitat degradation due to climate change, the effects of increased SST on connectivity may be exacerbated.

These results align with previous work that show correlations between El Nino Southern Oscillation and larval connectivity patterns (Gurdek-Bas et al., 2022), and a decrease in distance dispersed and number of connections caused by an increase in SST (Figueiredo et al., 2022). Effect size analysis shows that when SST reaches 28°C or above, there are large effects on out-degree, in-degree, and self-recruitment dependent on species (Table 2). The effect of temperature was further exaggerated for these two metrics for coral trout when creating the forest plot using 29°C for all values (Figure 3). All species experience a negative effect of SST on out-degree and in-degree, and a positive effect of SST on self-recruitment. This result suggests that increasing SST reduces the number of incoming and outgoing connections and increases the number of larvae returning to their natal population. When modeling larval dispersal under future climate conditions (including increased SST), there was predicted suppression of long-distance dispersal, a decrease in average distance dispersed, and an increase in self-recruitment (Lett et al., 2010). Though distance dispersed was not specifically measured in my analysis, I did observe increases in self-recruitment with increasing SST and decreases in inter-reef connectivity, which may capture a decrease in distance dispersed. Decreased inter-reef connectivity and increased self-recruitment may be due to high mortality rates in warmer water, decreasing pre-competency length, and fluctuations inPLD from changes in temperature, pH, and salinity that all result in larvae settling closer to natal populations (Andrello et al., 2015; Bashevkin et al., 2020; Cecino & Treml, 2021; Cowen et al., 2000; Cowen et al., 2006; Treml et al., 2015). Overall, reefs are becoming more isolated and inter-reef connectivity is decreasing (Figueiredo et al., 2022; Lett et al., 2010).

I observed the strongest effect of increased SST on connectivity in snapper (*Lutjanus malabaricus*) which have the shortest spawning period of the four species (October-December) (Muenzel et al., 2023). The weakest effect was in rabbitfish (*Siganus canaliculatus*) which only spawn March-October (Muenzel et al., 2023). The differential effect of high SST on species could be a result of varying spawning periods or seasons, with species spawning in warmer months (rabbitfish) being less affected by high SST. Spawning periodicity strongly influences the number and persistence of connections between reefs, with more frequent spawning improving connectivity (Kough & Paris, 2015). Though there was less variance in connectivity for octopus (year-round spawners), there were no trends to suggest improved connectivity of octopus compared to the other three species with shorter spawning periods. Increased temperature shifts reproduction and spawning times through disruption of environmental cues (Andrello et al., 2015), which may also relate to the differential impact based on spawning periods.

PLD was included in the spawning period length when clipping SST values to spawning period (spawning period = spawning months + length of PLD), with rabbitfish having the shortest PLD (19 days) compared to the other species (Muenzel et al., 2023). PLD is directly related to dispersal, as species with long PLD will have larvae that settle further from natal populations, increasing connectivity (Cowen et al., 2006; Treml et al., 2015). It is possible that the effect of SST on species might change when looking at temperature during each species' PLD rather than spawning period, though studies suggest decreasing sensitivity of larval dispersal to PLD once PLD is greater than 10 days (Sciascia et al., 2022), which is true for all four species in this analysis. Additionally, there is increasing evidence that the relationship between PLD and temperature is non-linear, with PLD increasing in some species after temperatures reach 28-29°C (McLeod et al., 2015), which means temperature and PLD may not work synergistically to decrease connectivity.

Connectivity did not significantly decrease over time when measuring cumulative flow, out-degree, and in-degree, but did have a significant increase in self-recruitment ($p = 0.042$) across all species (Figure 2). The significant increase in self-recruitment reflects the expected decrease in inter-reef connectivity with global warming (Figueiredo et al., 2022; Lett et al., 2010). The significant increase in self-recruitment across time with no significant decrease in out-degree or in-degree may be due to differing "sensitivities" of each metric. Self-recruitment may be more affected by changes in external variables compared to metrics like out-degree and in-degree (Meerhoff et al., 2025; Wolanski et al., 2024). Additionally, variance in cumulative flow was statistically significant between species (Figure 2) with the standard deviations of octopus ($\sigma = 0.003$) and snapper ($\sigma = 0.001$) being lower than coral trout ($\sigma = 0.300$) and rabbitfish ($\sigma = 0.032$). The differences in variance may be due to spawning periods, as octopus spawn year-round, but are most likely random as snapper species (also with low standard deviation) have the shortest spawning period.

Additionally, connectivity metrics were better predicted by GAMs at higher SST compared to lower SST (Figure 4, 5, 6, 7). This is evidence of an SST threshold at which connectivity is better predicted or driven by SST. This will increase accuracy of connectivity predictions when SST reaches that threshold. GAM results supported the recursive partitioning and effect size analysis, with a decrease in out-degree and in-degree with increasing SST, and an increase in self-recruitment. Variance in the models also aligned with the differential effect based on species. Rabbitfish for example, with the weakest Cohen's *d* effect size, had the lowest adjusted $R^2$ value in the GAM analysis. This result further supports a threshold value of SST at which connectivity will predictably drop for fish species in Southeast Sulawesi. A thermal threshold value increasing prediction accuracy was also seen when evaluating Hotspot and Degree-Heating Week ability to predict coral bleaching in the South China Sea (Liu et al., 2024). The temperature metrics Hotspot and Degree-Heating Week measure degree-difference from an average rather than a fixed temperature, so it is unknown whether the threshold is similar. There are also critical values which determine thermal niches for juvenile and adult fish, which may influence dispersal and connectivity if these same niches apply to larvae (Llopiz et al., 2014).

Though there was a compelling predictive ability of the El Nino 3.4 and PDO parameters, variation in these parameters may be dampened due to the small sample size (n=20) I was constrained to by data availability (Table 3). Effects of ENSO factors on connectivity may be better examined through more localized oceanic current variability rather than global temperature trends. Correlations between ENSO and connectivity may also be better explained by more fine-scale ENSO effects such as changes in stratification or salinity (Bashevkin et al., 2020). El Nino events shift current patterns, which directly influence larval dispersal, resulting in correlations showing an increase in connectivity during El Nino events (Novi et al., 2025). These correlations are often described directionally, as El Nino events influence the direction of currents, therefore increasing connectivity exclusively in one direction (Lian et al., 2025). The decrease observed in out-degree and in-degree with increasing El Nino and PDO might not accurately predict the realized influence of ENSO factors on connectivity due to dampened variation, small sample size, and the measurement of El Nino and PDO being described by SST anomalies, not oceanic currents.

Spatial analysis supported the importance of spatial variation in predicting connectivity patterns. Cohen's *d* effect size analysis results were higher on average when comparing connectivity metrics between clusters (Table 4, Figure 12) than comparing connectivity metrics between the SST threshold (Table 2, Figure 3). Additionally, GAMs were better fit when spatial clusters were used as a random effect in the model. When including cluster as a random effect, cluster was significant across all GAMs for every metric (out-degree, in-degree, self-recruitment), predictor variable (El Nino, PDO, SST), and species. Similar studies have found significant differences in larval dispersal between spatial groupings of reefs (Thomas et al., 2014). Additionally, cluster groupings are influenced by oceanic currents and are therefore inherently linked to larvae dispersal and movement (Wang et al., 2022). In my analysis, clusters 4 and 6 have high self-recruitment and low inter-reef connectivity, and clusters 1, 2, 3, and 5 have low self-recruitment and high inter-reef connectivity when compared to each other (Table 4). These differential patterns in connectivity based on spatial groupings are often not reflected in spatial conservation planning such as Marine Protected Areas (MPAs) (Thomas et al., 2014). Therefore, this information could be useful in spatial conservation planning, possibly prioritizing protection of reef clusters 1, 2, 3, and 5 to promote gene flow and species diversity (Kough et al., 2013).

Habitat degradation had a significant effect on cumulative flow for all species. When degradation was added into the connectivity matrix, cumulative flow decreased by an average of 73 percent for all four species (Figure 13). The habitat degradation value was on average 0.266 between 1993-2012, or 26.6 percent coral cover (Figure 14). This means coral reefs in the Southeast Sulawesi region are on average composed of only 26.6 percent hard coral cover. This is likely due to increased coral bleaching (Yusuf & Jompa, 2012), pollution, and destructive fishing (Edinger et al., 1998). The decrease seen in cumulative flow is a result of this habitat degradation, as coral reefs will host less fish, of smaller size, outputting less larvae when habitat is limited (Magris et al., 2016). Additionally, habitat degradation significantly decreased the variance in cumulative flow for species coral trout ($p < 0.001$), rabbitfish ($p < 0.01$), octopus ($p < 0.05$), and snapper ($p < 0.05$). These trends are expected to continue in future years (Figure 13). It is unknown whether habitat degradation impacts the effect of SST on connectivity metrics such as out-degree, in-degree, and self-recruitment. If implemented into the original connectivity model, it is possible that we would see similar decreases in those connectivity metrics. The original connectivity model uses reef area detected by satellites to scale reproductive outputs. In my habitat degradation analysis, I use coral cover as a proxy for habitat degradation to scale reproductive outputs (i.e., multiplication of percent cover into flow matrices). Therefore, the flow after habitat degradation (red line, Figure 13) can be interpreted as a correction of the original model. Including habitat degradation in these models is therefore important to reduce the risk of overestimation of connectivity, and subsequently conservation priorities (Vercammen et al., 2019).

Certain species are more resilient to high SST (Trégarot et al., 2024). My results suggest that species that spawn in warmer months are less affected by high SST. Though this is a preliminary finding, considering I only analyzed four different species, it suggests a possibility that species which spawn in cold months and those with short spawning periods may be at higher risk of decreased connectivity when SST reaches 28-29°C. This finding could provide insight into future species compositions of reefs (Ceccarelli et al., 2023; Cruz et al., 2024). If SST continues to increase, there may be a higher proportion of species that spawn in warm months on the reefs with species which spawn in cold months becoming rarer. These findings highlight the importance of species-specific research to inform coral reef conservation efforts (Hughes et al., 2023).

Larval connectivity variability can be explained by SST at a threshold of 28-29°C. At this threshold, connectivity declines due to a decrease in outgoing and incoming connections between reefs and increasing self-recruitment. With increasing SST due to climate change, coral reefs will experience a decline in inter-reef connectivity, and an increase in local retention of larvae (Figueiredo et al., 2022). This loss of larval exchange between reefs may have detrimental effects on gene flow and diversity of marine animal populations (Kough et al., 2013). Declining connectivity will also affect marine fisheries, changing diversity, abundance, and size of species within the reef (Ramesh et al., 2019). Increasing SST is also associated with reef degradation due to coral bleaching (Stuart-Smith et al., 2018). This habitat degradation decreases total cumulative flow, possibly leading to a further decline in connectivity. With increasing SST and habitat degradation due to climate change, we can expect a decline in connectivity between coral reefs.

These findings are an important consideration for spatial conservation planning of coral reefs. Larval connectivity plays a key role in the success of marine reserves (Green et al. 2015), increasing fecundity and spillover (Goetze et al., 2021). Well-connected marine reserves also experience a dampening effect on temporal fluctuations in larval supply (Harrison et al., 2020). Understanding how connectivity may change under future climate conditions is therefore important to understanding the success of marine conservation planning. Marine reserves in Southeast Sulawesi, specifically Wakatobi National Park (Figure 1), are not found to overlap with coral reefs that rank high in incoming and outgoing connections (in-degree and out-degree) (Faryuni et al., 2024). As out-degree and in-degree are expected to decrease with increasing SST, determining which reefs rank high in connectivity metrics will be vital information for determining the placement of marine reserves. This analysis suggests those are reefs in clusters 1, 2, 3, and 5 across all species (Figure 8, 9, 10, 11). Therefore, using connectivity models that predict connectivity under future climate conditions (high SST, high habitat degradation) may best inform spatial conservation planning. This strategy will allow for the protection of inter-reef connectivity, fisheries supply, and stable larval supply under future climates conditions (Goetze et al., 2021; Harrison et al., 2020).

## Conclusions

Future studies should focus on the additive effects of high SST and degraded reef habitats on larval connectivity between coral reefs. Biophysical modeling of larval connectivity that can predict connectivity at high SST and high habitat degradation will best predict future connectivity patterns. Additionally, modelling should be performed with a wider range of marine species to accurately infer broader impacts. Connectivity is also useful in determining clusters of well-connected reefs (Ani et al., 2024). Studies that further examine the differential effects of SST on connectivity between reef clusters may be useful in conservation planning, prioritizing resilient reef clusters to be protected in marine reserves (Pata & Yñiguez, 2021). My results suggest a critical SST value at which connectivity will begin to decline between coral reefs in Southeast Sulawesi. This allows us to more accurately predict species compositions and connectivity patterns under future climate conditions.

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