LARVAL CONNECTIVITY AMONG THE CORAL REEFS OF THE ANDAMAN SEA

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B.Sc. – M.Sc. (Integrated) Climate Change Adaptation Faculty of Agriculture Kerala Agricultural University



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2021

DECLARATION

I, Vimuktha Viswanath (2016–20–007) hereby declare that this thesis entitled "Larval connectivity among the coral reefs of the Andaman sea" is a bonafide record of research work done by me during the course of research and the thesis has not previously formed the basis for the award to me of any degree, diploma, associateship, fellowship or other similar title, of any other University or Society.

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Certified that this thesis entitled "Larval Connectivity among the coral reefs of the Andaman Sea" is a record of research work done independently by Miss. Vimuktha Viswanath under my guidance and supervision and that it has not previously formed the basis for the award of any degree, diploma, fellowship or associateship to her.

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CONTENTS

DECLARATION	ii
CERTIFICATE	iii
CERTIFICATE	iv
ACKNOWLEDGEMENT	v
CONTENTS	vii
LIST OF FIGURES	x
LIST OF TABLES	xi
SYMBOLS AND ABBREVIATIONS	xii
CHAPTER 1	1
INTRODUCTION	1
CHAPTER 2	
REVIEW OF LITERATURE	
2.1. CORAL REEF DISTRIBUTION IN ANDAMAN SEA	
2.2. OCEAN CURRENT PATTERN IN ANDAMAN SEA	6
2.3. MARINE CONNECTIVITY	
2.4. IMPACTS OF CLIMATE CHANGE ON MARINE CONNECTIVITY	
2.5. MARINE CONNECTIVITY PARAMETERS	14
2.6. EXISTING CONNECTIVITY MODELS	
CHAPTER 3	
MATERIAL AND METHODS	
3.1 STUDY AREA	
3.2 SPECIES OCCURRENCE DATA	
3.3 SELECTION OF ENVIRONMENTAL PARAMETERS	

3.4 SPECIES DISTRIBUTION MODEL	19
3.5 BIOLOGICAL PARAMETERS	
3.6 RUNNING THE CONNECTIVITY MODEL	
3.7 ESTIMATION OF THE DISPERSIVE POTENTIAL OF THE CORAL DURING IOD POSITIVE AND IOD NEGATIVE YEARS	
3.8 ESTIMATION OF THE PATTERN OF CORAL LARVAL CONNECTIVITY	DURING
DIFFERENT SEASONS	
3.9 SST TREND ANALYSIS	
CHAPTER 4	
RESULTS	
4.1 SPECIES DISTRIBUTION MODEL	
4.1.1 Prediction of the current distribution	
4.1.1.1 Model Evaluation Score	
4.1.1.2. Analysis of variable contributions	
4.1.1.3. Response curves of variables used	
a)Generalized Linear Model (GLM)	
b)Generalized Boosting Model (GBM)	
c)Random Forest (RF)	
d)Classification Tree Analysis (CTA)	
e)Flexible Discriminant Analysis (FDA)	
f)MAXENT.Phillips	
4.1.4 Evaluation Score of Ensemble Model	33
4.2. CONNECTIVITY MATRIX	
4.2.1. Different seasons	
4.2.1.1. Northeast Monsoon	
4.2.1.2. First inter-monsoon	

4.2.1.3. Southwest Monsoon	0
4.2.1.4. Second inter-monsoon	1
4.2.2. Different climatic conditions 4	3
4.2.2.1. Extreme negative IOD year - 2016 4	3
4.2.2.1.1. PHASE 1- First peak phase (May to August 9) 4	3
4.2.2.1.2. PHASE 2- Second peak phase (Stronger than first peak)	4
4.2.2.2 Positive IOD year - 2015	5
4.2.2.2.1. Positive IOD Peak phase (August to November 9) 4	5
4.3. SST TREND ANALYSIS 4	6
CHAPTER 5	9
DISCUSSION	.9
CHAPTER 6	3
SUMMARY	3
CHAPTER 7	4
REFERENCES	4
ABSTRACT7	7

LIST OF FIGURES

Fig. 3.1: Location map of study area 17
Fig. 3.2: Correlation matrix of environmental parameters for the study area
Fig. 4.1: Graph showing Model Evaluation Score of seven models
Fig. 4.2: Variable importance by seven models
Fig. 4.3: The response curves of GLM
Fig. 4.4: The response curves of GBM
Fig. 4.5: The response curves of RF
Fig. 4.6: The response curves of CTA
Fig. 4.7: The response curves of FDA
Fig. 4.8: The response curves of MAXENT.Phillips
Fig. 4.9: Map showing the predicted habitat suitability of P. damicornis in the Andaman Sea in
present condition
Fig. 4.10: Coastal and island reefs in Andaman Sea and their identification name used in
connectivity matrix
Fig. 4.11: Connectivity matrix indicating the probability of Pocillopora damicornis larvae
recruiting to reef site (horizontal axis - destination reef), originating from a reef site (vertical axis -
source reef) for northeast monsoon season
Fig. 4.12: Connectivity matrix of <i>P. damicornis</i> larvae during the first inter-monsoon season 39
Fig. 4.13: Connectivity matrix of <i>P. damicornis</i> larvae during southwest monsoon season41
Fig. 4.14: Connectivity matrix of Pocillopora damicornis larvae during the second inter-monsoon
season
Fig. 4.15: Connectivity matrix of P. damicornis larvae during extreme negative IOD year - during
its first peak phase
Fig. 4.16: Connectivity matrix of P. damicornis during extreme negative IOD year - during the
second peak phase which is stronger than the first peak
Fig. 4.17: Connectivity matrices of <i>P. damicornis</i> larvae during positive IOD phase
Fig. 4.18: Time series map of SST Anomaly in the Andaman Sea for the year 1889 to 2020 47
Fig. 4.19: Time series map of SST in the Andaman Sea from 1889 to 2021 May
Fig. 4.20: The monthly average SST during the year 2017

LIST OF TABLES

Table 4.1: Evaluation score of the Ensemble model

SYMBOLS AND ABBREVIATIONS

ABBREVIATION	EXPANSION
NE monsoon	North East monsoon
SW	South West
BOB	Bay of Bengal
PLD	Pelagic Larval Duration
IPCC	Intergovernmental Panel on Climate Change
CO ₂	Carbon dioxide
O ₂	Oxygen
N ₂	Nitrogen
SST	Sea Surface Temperature
MGET	Marine Geospatial Ecology Tools
MPDATA	Multidimensional Positive Definite Advection Transport Algorithm
EEZ	Exclusive Economic Zone
GBIF	Global Biodiversity Information Facility
BIOMOD	BIOdiversity MODelling
GLM	Generalised Linear Models
GBM	Generalized Boosting Model
СТА	Classification Tree Analysis

SRE	Surface Range Envelop
FDA	Flexible Discriminant Analysis
RF	Random Forest
TSS	True Skill Statistics
ROC	Receiver Operating Characteristic
SDM	Species Distribution Model
GEBCO	General Bathymetric Charts of the Ocean
НҮСОМ	HYbrid Coordinate Ocean Model
NCODA	Navy Coupled Ocean Data Assimilation
IOD	Indian Ocean Dipole
NOAA	National Oceanic and Atmospheric Administration
СОВЕ	Centennial in situ Observation-Based Estimates
GISTEMP	GISS Surface Temperature Analysis
NASA	National Aeronautics and Space Administration
GRADS	Grid Analysis and Display System
рН	Potential of hydrogen
ppt	Parts per thousand
m	Meter
km ²	Kilometer square

°C	Degree Celsius
%	Percentage

INTRODUCTION

CHAPTER 1

INTRODUCTION

Coral reefs, the rainforests or souls of the ocean, are one of the most essential and biologically rich ecosystems (Davidson, 1998). Despite the fact that coral reefs make upforms only 0.2 % of the world's oceans, they are home to 34% of all known marine species (Reaka-Kudla, 2001). They provide essential ecosystem services, such as creating the circumstances for human populations to flourish and prosper in coastal locations near reefs (Allemand et al., 2019). Reefs, on the other hand, are among the most vulnerable ecosystems to climate change, being particularly vulnerable to ocean warming (Heron et al., 2016), ocean acidification (Lam et al., 2019), ocean deoxygenation (Hughes et al., 2020), and other climatic conditions. De'ath et al. (2009) found that, based on an investigation of 328 colonies of massive corals from the Great Barrier Reef, reef growth has been dropping by 14.2% since 1990, after being stable for the past 400 years. According to Hughes et al. (2003), 30% of the reefs have already severely deteriorated, and 60% will be destroyed by 2030. The extensive destruction of coral reef ecosystems, which is getting hastened by climate change, puts the commodities and services that tropical countries derive from reef ecosystems in jeopardy (Cinner et al., 2016). As a result, maintaining a healthy and resilient ecosystem is essential, and it requires the process of connectivity to be maintained (Hock et al., 2017).

Connectivity is the exchange of individuals among marine populations (Cowen and Sponaugle, 2009; Ospina-Alvarez *et al.*, 2020). Since most marine organisms have a pelagic early-life stage in which individuals float away from natal locations transported by ocean currents (Ospina-Alvarez *et al.*, 2020), connectivity is synonymous with larval dispersal (Guizien and Bramanti, 2014). Since adult corals are sessile, connectivity between different patches of reef population is maintained solely by larvae dispersal (Sale 1991, Sale and Kritzer, 2003). Larval behaviour and species life-history characteristics can determine dispersal distance (Shanks, 2009). There is a tangible link between dispersal distance and propagule duration (Shanks *et al.*, 2003). The scale of dispersal and the magnitude of the settlement are known or expected to be influenced by several factors. The factors include water currents that the larvae encounter, the availability of

suitable habitat, and larval biological parameters such as pelagic larval duration (PLD), larval mortality rate, settlement rate, larvae behaviour, and the number of reproductive propagules produced and these factors can be affected by climate change (Cowen, 2002; Munday *et al.*, 2009; Scill *et al.*, 2015).

The assessment of coral reef connectivity utilizes a variety of approaches. Baums *et al.* (2006) found a direct link between effective dispersal distances based on oceanographic and life history features and gene flow in a marine organism for the first time. Elemental fingerprinting was developed to track the dispersal of marine larvae (DiBacco & Levin, 2000). Tripp *et al.* (2020) found that larval otolith chemistry helps to assess regional production and connectivity. Torres *et al.* (2018) employed a biophysical model that included ocean currents and larval biology for determining the coral reef connectivity pattern. Because empirical methods are costly and require extensive sampling, biophysical modelling provides the opportunity to investigate coral reef connectivity by tracking a large number of virtual larvae over a wide range of spatiotemporal scales and under a variety of disturbance situations (Lequeux *et al.*, 2018).

The primary focus of this research is on the Andaman Sea, which is a part of the Asian monsoon system, and southwest winds dominate the region in the summer and northeast winds in the winter (Liu *et al.*, 2018). Because of the monsoons, the sea surface temperature (SST) and surface current distributions in the Andaman Sea vary periodically (Rizal *et al.*, 2012). Since larval biology and currents predominantly influence dispersal (Leis, 2002), the connectivity pattern in the Andaman Sea will be affected. The purpose of this study is to present a model-based assessment of coral larval connectivity patterns among the Andaman Sea reef ecosystems over different seasons and climatic conditions. Here, a biophysical modelling approach is used (Treml & Halpin, 2012), and larval dispersal between the reefs of the Andaman Sea is estimated using the methods in the Marine Geospatial Ecology Tools software package (Treml & Halpin, 2012). The results from this study can help in providing the foundation for marine spatial planning in the study area.

REVIEW OF LITERATURE

CHAPTER 2

REVIEW OF LITERATURE

2.1. CORAL REEF DISTRIBUTION IN ANDAMAN SEA

2.1.1. Andaman and Nicobar Islands - India

Andaman and Nicobar archipelago, located at the juncture of the Bay of Bengal and Andaman Sea (Majumdar et al., 2019), comprises a chain of 572 islands stretching from Myanmar (Burma) in the North to Sumatra in the South (6°-14°N and 92°-94°E) and is heavily inhabited by fringing reefs (Marimuthu et al., 2013). Islands which are north of 10° N latitude belong to the Andaman group of Islands, and those South of 10°N latitude belong to the Nicobar group of Islands. It is one of the coral-rich environments of the Indian coastal region. The Andaman group occupies a reef area of 968.44 sq km, while the Nicobar Islands cover 53.02 sq km of coral reefs (Bahuguna et al., 2013). The Andaman and Nicobar islands cover 8,293 km² and have a 1,962 km shoreline, accounting for approximately 30% of the Indian Exclusive Economic Zone (Turner et al., 2001). Estimating reef flats of Indian reefs by remote sensing has revealed that the extent of the area of the reef flats in Andaman and Nicobar Islands is 813.2 km² (Pillai, 2010). Coral reefs of the fringing kind stretch intermittently for 350 kilometres along the western coast of the Andaman Islands, and the eastern side has narrow fringing reefs in certain places (Bahuguna et al., 2013). There is a 320 km long barrier reef with a 4-meter-deep lagoon on the western side of the South and Middle Andaman Islands (Saxena et al., 2008). About 173 species of corals belonging to 59 genera have been recorded from Andaman and Nicobar Islands (Roy et al., 2005). Because the Andaman and Nicobar reefs are closer to Indonesia and Southeast Asia, their reef richness is akin to that of the Indonesian and Southeast Asian centre of biodiversity than that of Indian reefs (Bahuguna et al., 2013). The common coral genera contributing to the reef formation in these islands are Acropora, Montipora, Pocillpora, Porites, Gonopra, Favia, Echinopora, Fungia, Milleporina, Hliopora etc (Saxena et al., 2008). Pocillopora damicornis, Pociliopora elegans,

Stylophora mordax of the family Pocilloporidae are found abundant in both Andaman and Nicobar Islands (Reddiah, 1997).

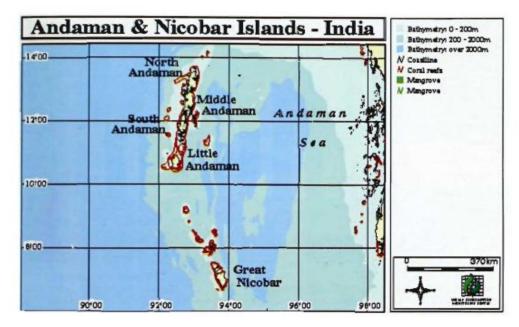


Fig. 2.1. Distribution of corals reefs of Andaman & Nicobar Islands (Adapted from Turner *et al.*, 2001)

2.1.2. Reefs of Myanmar

Along Myanmar's most southern coastline, the Mergui Archipelago (Myeik Archipelago) and neighbouring Moscos Islands are a biologically rich and diversified seascape abounding with unique, endangered, and threatened flora and wildlife (Howard, 2018). Coral reefs are well developed around the islands of the Myeik Archipelago and the Burma Banks of the Tanintharyi Coast (Holmes, 2014). The Myeik Archipelago (formerly Mergui Archipelago) is situated in the north-eastern Andaman Sea, in the southernmost part of Myanmar, and it contains approximately 800 islands. The islands have 1,700 km² of coral reefs (Russel, 2016). Hard corals were the most common in the Mergui Archipelago (a total of 287 hard coral species were observed), accounting for 33 percent of total cover (maximum 80 percent), with the largest concentration on inner reefs, followed by rock walls, and finally outer reefs (Obura *et al.*, 2014). Hard coral cover varies dramatically over the archipelago, ranging from 0% to 92 percent, with an average of 48.9% (Howard, 2018). Because of the prevalence and richness of the genus Acropora on inner reefs,

coral species diversity was highest, but overall, coral communities were dominated by Porites, particularly on outer fringing reefs (Obura *et al.*, 2014). The overall health of the reefs is average to below average, with the outer fringing reefs having the highest mortality rate (Dearden, 2016). Although the archipelago's overall coral cover is low, some individual reefs are still regarded as healthy, falling into the Good Range (51-75 percent) for hard coral cover and some falling into the Very Good Range (76-100 percent) (Howard, 2018). Massive corals dominate the archipelago's coral morphology, which is considered a sign of a reef in poor health (Cox *et al.*, 2013). For the Moscos Islands, enormous *Porites sp.* dominated the reefs, which were almost entirely located on the islands' inlet side (Howard, 2018). Reefs in the Ayeyarwady Region are limited to the Coco and Preparis offshore islands, which are far enough away from the delta's strong sediment loads (Holmes, 2014).

2.1.3. Reefs of Thailand

Coral reefs are one of the most productive marine systems in Thai waters; both in the Andaman Sea and the Gulf of Thailand (Phongsuwan et al., 2013), with 210 species of coral and are an important reservoir of biological diversity (Thailand coastal Resource Management Project). The coral reefs in Thailand cover a total area of 153 km², with around 78 km² in the Andaman Sea and 75 km² in the Gulf of Thailand (Yeemin et al., 2006). Most reefal and non-reefal coral communities in Taiwan and its offshore islets are home to Pocillopora species (Palmas et al., 2018). Approximately 55% of Thailand's major coral reef groups occur in the Andaman Sea (Thailand coastal Resource Management Project). In the Andaman Sea of Thailand, 4.6 % of reefs were rated as "excellent," 12 % as "good," 33 % as "fair," and 49.8 percent as "poor" (Yeemin et al., 2006). Phuket Island in Southern Thailand is the largest island of Thailand and has well developed coral reefs on the west coast in protected bays and on some areas along the southern coast (Sawall et al., 2010). Massive corals, together with an increasing abundance of branching species, dominate the sheltered reefs of Phuket during optimal growth circumstances (Dunne et al., 2021). Similan Islands, located 60 km off the west coast of Thailand, comprises nine small islands and on the sheltered east of the Similan Islands, where the influence of large-amplitude internal waves (LAIW) is weak, typical tropical coral reefs can be seen (Jantzen et al., 2013). The Phi Phi Islands are a group of six limestone islands located 40 km southeast of Phuket and around 30 km west of Krabi in Phang Nga Bay. On the eastern borders of the islands, especially in regions

shielded from Southwest storms, well-developed fringing coral reefs can be found (Sawall *et al.*, 2010). Until early 2010, reefs in the Andaman Sea were in better shape than the Gulf of Thailand's (Phongsuwan *et al.*, 2013). During the 2010 catastrophic coral bleaching event in the Andaman Sea of Thailand, 97 percent of coral colonies were bleached (Sutthacheep *et al.*, 2012).

2.2. OCEAN CURRENT PATTERN IN ANDAMAN SEA

The main contributor to seasonal currents in the Andaman Sea is the monsoonal winds, which are North-East wind in the winter (November-February) and Southwest wind in the rainy season (July-October) (Suwannathatsal et al., 2012). The circulation of the Andaman Sea is influenced not just by local winds but also by the remote forcing of equatorial Kelvin waves (Yu et al., 1991). Except during monsoon transition seasons (April–May and October–November), winds over the Equatorial Indian Ocean (EIO) are normally weak throughout the year (Nagura and McPhaden, 2010). At this time, westerly winds prevail in the central and eastern EIO, generating eastward equatorial currents known as Wyrtki Jets (Wyrtki, 1973, Nagura and McPhaden, 2010). When the northeast monsoon is established, the North Equatorial Current runs as a narrow current of roughly 0.3 m s⁻¹ from the Malacca straits to southern Sri Lanka, passing through the Andaman Sea en route (Brown, 2007). During the NE monsoon, surface water masses from the north of the domain enter the Andaman Sea (Rizal et al., 2012), then travel south and out of the Andaman Sea in the broad area between the Andaman Islands and Sumatra and eventually to the Indian Ocean (Rizal et al., 2012). The surface current from the southern Strait of Malacca flows northward along the west coast of Thailand into the Andaman Sea (Isa et al., 2020) and converges with the surface current from the Bay of Bengal that flowed southward (Isa et al., 2020). The surface current moves northwestward from the northwest of Sumatra to the BOB during the Northeast Monsoon before separating into two directions (Isa et al., 2020). The easterly migrating, powerful Indian Equatorial Jet (velocity 0.7 m s⁻¹ or greater), marks the shift from northeast to southwest monsoon (Brown, 2007). During the first inter-monsoon, the northward surface current from the Malacca strait travelled along the west coast of malaysian peninsula into the Andaman Sea at 7-8°N, while the current from the east of Sumatra moved northward before merging with the southerly current from the Andaman Sea (Isa et al., 2020). When the southwest monsoon is wholly established, from July to September, South West Monsoon Current which flows to the east (enters the Andaman Sea via

the Bay of Bengal), dominates the northern Indian Ocean (Brown, 2007). The surface water masses from the north reach the Andaman Sea over a broad length from Cape Negrais to the north of the Nicobar Islands during the SW monsoon (Rizal et al., 2012). While the outflow of the Andaman Sea surface water is concentrated between the south of the Nicobar Islands and Sumatra (Rizal et al., 2012). The surface current from the northern Andaman Sea flowed south before meeting the northeasterly current around 12°N and turning southward along the west coast of Thailand (Isa et al., 2020). The equatorial jet, which focuses eastward flow near the equator and reaches its peak in November and diminishes in early January when the cycle is repeated, characterises the second inter monsoon (transition before the onset of the northeast monsoon) (Brown, 2007). During the second inter-monsoon period, surface currents from the north of the Andaman sea flow southward but did not flow along the coast of the Mergui Archipelago (flowed southward into Sumatera at 12°N 96°E) (Isa et al., 2020). Also the currents flowing northward from Malacca strait flowed into the Andaman Sea along the west coast of Thailand (Isa et al., 2020). Except for June and August, when the currents are relatively weak and sometimes reversed to the south-east, the basic pattern of surface ocean current flow is constant from southwest to northwest throughout the year (Rizal et al., 2012). Fig. 2.2 shows a study by Isa et al. (2020), which illustrates how currents and SST change in the Andaman Sea with different seasons.

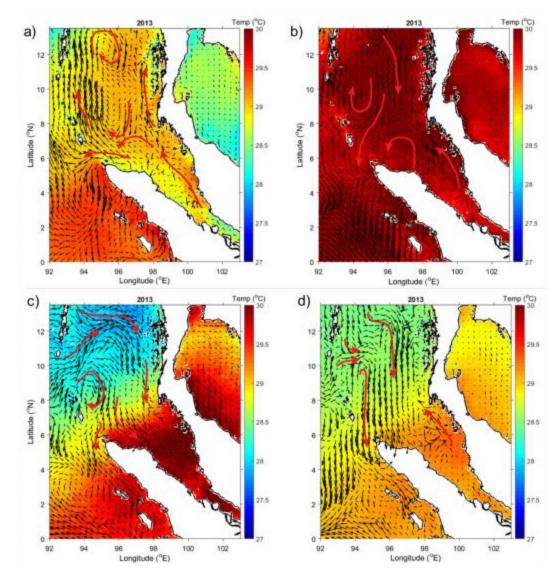


Fig. 2.2: The current flow (unit: m/s) and sea surface temperature (shade in, unit:°C) in the Andaman Sea during different seasons (a) the Northeast Monsoon (b) The first inter-monsoon season (c) the Southwest Monsoon and (d) the second inter-monsoon season. The Red arrow represents the current flow. (Adapted from Isa *et al.*, 2020).

2.3. MARINE CONNECTIVITY

Connectivity is the exchange of individuals among marine populations (Cowen and Sponaugle, 2009). Connectivity has the potential to be a significant determinant of the structure and functioning of marine communities and ecosystems (Virtanen *et al.*, 2020). Individuals within and

among populations can be dispersed in various ways due to the fluid environment in which marine populations reside (Cowen and Sponaugle, 2009). Considering the case of marine species, most of them have a pelagic early-life stage in which individuals drift away from their natal locations and transport by ocean currents (Ospina-Alvarez et al., 2020). As dispersal generally happens during the larval or spore phase in the marine environment, direct observation and mark-recapture are not feasible (Selkoe and Toonen, 2011). Many nearshore marine species have a larval stage where ocean currents significantly impact dispersal (Watson et al., 2010). The transport of larvae is highly variable with time and space in accordance with tides, winds and currents. Physical forcing like flood currents, helps in transport of the larvae from their spawning sites hugging to the coast and contributing to the population within the estuary (George et al., 2013). Even though geographical barriers are also imperative in larval retention, their role is superseded by the local hydrodynamics (George et al., 2011). So, understanding connectivity remains a significant task in marine ecology because of the technical difficulties of tracking larval dispersal (Selkoe and Toonen, 2011). Movement is often limited to the larval phase for most marine organisms with sessile, benthic, or somewhat sedentary adult phases, such as corals. Hence connectivity between geographically dispersed populations for corals is assumed to be maintained solely by dispersive larvae (Paris et al., 2013). Connectivity relates not only to the ability of larvae to move about but also to their ability to recruit, survive, and reproduce the next generation in their new environment (Gorospe and Karl, 2015). Water currents that the larvae encounter, the availability of suitable habitat, and larval biological parameters such as pelagic larval duration (PLD), larval mortality rate, settlement rate, larvae behaviour, and the number of reproductive propagules produced are expected to influence the scale of dispersal, and the magnitude of settlement and these factors can be affected by climate change (Cowen, 2002; Munday et al., 2009; Scill et al., 2015). Even in the presence of significant population mixing, habitat unsuitability can reduce connection levels (Gorospe and Karl, 2015). Coral reef connectivity is crucial for their resilience and persistence in the face of disturbances (Frys et al., 2020). Through the interchange of beneficial genotypes between populations, the degree of connectivity between populations would influence the ability of coral reef organisms to adapt to rapid climatic change (Munday et al., 2009). Connectivity via larval dispersal is crucial in establishing efficient marine reserve networks (Anadon et al., 2013). Marine population genetic analysis is employed to make assumptions about the scale of population connectivity (Selkoe and Toonen, 2011). The primary larval transport paths correlate with the

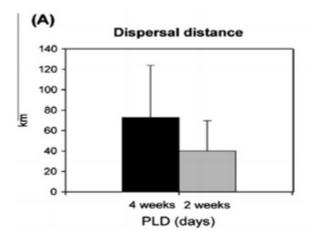
mean direction and strength of ocean surface currents, according to Lequeux *et al.* (2018). The biophysical models that simulate both the fine-scale characteristics of ocean currents and the lifehistory traits of larvae transported by these currents can be used to estimate connectivity in massive reef systems (Frys *et al.*, 2020).

2.4. IMPACTS OF CLIMATE CHANGE ON MARINE CONNECTIVITY

2.4.1 Increased ocean temperatures

Based on the Intergovernmental Panel on Climate Change (IPCC) emission scenarios, estimates of projected atmospheric and oceanic CO_2 concentrations suggest that atmospheric CO_2 levels could surpass 800 ppm by the end of the century (Feely et al., 2009). Because the ocean absorbs most of the surplus heat from greenhouse gas emissions, rising atmospheric carbon dioxide levels (CO₂), an essential greenhouse gas, is the single most important element leading to global climate change and higher sea surface temperatures (Doney et al., 2014). An increase in ocean temperature can affect functional connectivity and structural connectivity, where functional connectivity is determined by an organism's biological and behavioural reactions to the physical environment (Gerber et al., 2014). In contrast, structural connectivity refers to changes in the physical and spatial structure of the environment that affect connectivity and movement (Gerber et al., 2014). The interchange of individuals, or connectivity, between distant sites is enabled through the pelagic dispersal of larvae, which is a crucial process in the life cycle of most marine populations (Lett et al., 2010). According to O'Connor et al. 2007, the temperature has a considerable effect on planktonic larval duration, such that rising temperature reduces pelagic larval duration (PLD). As a result, temperature changes have an impact on dispersal. Higher temperatures can lead to early metamorphosis of larval stages leading to early settlement than lower temperatures (Gaonkar, 2012). Increased temperature (by $+2^{\circ}C$) can impact the early life stages of corals, as the rates of larvae development were faster at high temperatures (Chua et al., 2013). On average, a 50% reduction in PLD (from 4 to 2 weeks) resulted in a 45% reduction in mean dispersal distance (Lett et al., 2010). Reduced PLD has the effect of reducing the magnitude of dispersal while increasing the level of self-recruitment (Sponaugle et al., 2006). For short PLD creatures, the spatial scale of connection is substantially smaller (Mayorga-Adame et al., 2017). In terms of connectivity, a decrease in PLD increases retention and larval exchange between nearby

populations (local connectivity) but decreases exchanges between populations further away (regional connectivity) (Ayata *et al.*, 2010). Temperature increase also increases the mortality rate of larvae (Llopiz *et al.*, 2014). Ocean warming also stresses corals and increases the bleaching of corals which is a habitat for many marine species (Hoegh-Guldberg, 1999). Reduced habitat space indicates higher isolation between some of the remaining habitats, which may reduce dispersal, colonisation, and community structure (Gerber *et al.*, 2014). Even when there is a lot of population mixing, habitat unsuitability might impede connectivity (Gorospe and Karl, 2015).



Graph showing the relationship between pelagic larval duration (PLD) and mean dispersal distance. (Adapted from Lett *et al.*, 2010 / Progress in Oceanography).

2.4.2 Ocean acidification

The dangers of carbon dioxide (CO₂) accumulating in the world's oceans and contributing to continued ocean acidification are becoming more apparent (Falkenberg *et al.*, 2020). Around 25% of CO₂ released into the atmosphere is absorbed by the oceans, where it interacts with seawater, resulting in a decrease in surface water pH of 0.3 units from current levels and 0.4 units from pre-industrial levels by 2100, representing a 2.5-fold increase in the ocean's hydrogen ion (H+) concentration relative to the start of the industrial era (Feely *et al.*, 2009). The reduction in pH and concomitant changes in carbonate chemistry may be putting additional stress on the reefs, making them more vulnerable to warming and other stressors (Lam*et al.*, 2019). Ocean acidification affects the amount of carbonate ions available to reef-building corals, reducing their ability to construct skeletons (Mollica *et al.*, 2018). Acidification is anticipated to reduce coral calcification by 15–22% on average by the end of the century (Chan and Connolly, 2013). With less suitable habitats, such as corals, not only will fewer larvae be produced, but settlers may have to travel longer distances (Gerber *et al.*, 2014), and this also affect the species that depend on corals (Hoegh-Guldberg *et al.* 2007) because reduced habitat reduces structural connectivity (Gerber *et al.*, 2014). When pH reduces, some larvae avoid or fail to detect auditory or olfactory signals that suggest excellent settling circumstances (Bashevkin *et al.*, 2020). Due to increased ocean acidification, orange clownfish (larvae) tended to avoid positive settlement cues and were attracted to negative stimuli, resulting in a settlement in a poor or even non-existent settlement environment (Munday *et al.*, 2009). The timing of settling in damselfishes (Pomacentrus spp.) is likewise affected by acidification (Devine *et al.*, 2012a). Due to acidity, Cardinalfish (adults) have difficulty in distinguishing between home and foreign places (Devine *et al.*, 2012b). Increases in pH enhance PLD, and the effects of ocean acidification could theoretically override those of temperature in warmer temperate seas, resulting in net increases in larval duration, while the opposite occurs in cold waters (Gaylord *et al.*, 2015).

2.4.3 Ocean Deoxygenation

Bopp *et al.* (2009), discovered a decrease in oceanic O_2 due to climate change in their analyses to examine the long-term influence of the ocean on atmospheric O_2/N_2 ratios. The ocean warms as it absorbs the majority of the excess heat from greenhouse gas emissions (Doney *et al.*, 2014), resulting in ocean deoxygenation. Hypoxia is a condition caused by a lack of oxygen in the ocean. Hypoxia reduces oyster larvae feeding by lowering their intake rates (Widdows *et al.*, 1989). The larval settlement will be significantly less in hypoxic conditions (Baker and Mann, 1992). Baker and Mann (1992) found a decline in juvenile oyster growth in hypoxic treatments and a complete loss of growth in anoxic treatments. Marine invertebrates' vision is particularly sensitive to oxygen availability, and oxygen-impaired retinal function may alter critical visual behaviours in these marine larvae (McCormick *et al.*, 2019). Dead zones, places where extreme hypoxia causes mass mortality or migration of megafauna (e.g., fish and big invertebrates), can arise when dissolved oxygen levels in coastal waters are severely depleted (Nelson and Altieri, 2019). Deficient oxygen (hypoxia) episodes are hazardous to coral reefs in shallow tropical waters (Hughes *et al.*, 2020) and may cause mass mortality events on the reefs (Nelson and Altieri, 2019).

2.4.4 Altered salinity

Low salinity causes barnacle larvae to cease swimming, and fluctuations in the larval release are caused by changes in external salinity (Cawthorne and Davenport, 1980). Some marine species can die as a result of salinity stress (Holliday, 1969). A study on salinity-induced morphological changes in *Pisaster ochraceus* by Pia *et al.* (2012) indicates that low salinity can induce developmental abnormalities. Vazquez and Young, (1996) investigated larvae swimming behaviour in response to acute laboratory haloclines and discovered that low salinity could affect larvae swimming behaviour. Heavy rainfall can lead to lower salinity which can ultimately lead to larval mortality (Gaonkar, 2012). Coral diversity, abundance, and survivorship are projected to decline in low and changing salinity locations (Lirman *et al.*, 2003), affecting structural connectivity. The effects of high rainfall on the Great Barrier Reef have been linked to coral deterioration (Butler *et al.*, 2015).

2.4.5 Turbidity

Turbidity near the coast will rise due to heavy rainfall and increased storm strength (Bashevkin *et al.*, 2020). Because releasing their larvae under those conditions could safeguard their larvae by swamping possible predators, adult barnacles responded to high turbidity levels and demonstrated a peak in larval numbers with the passing of winter (Gyory and Pineda, 2011). When turbidity is low, clam larvae proliferate (Davis, 1960) because increased turbidity affects filter-feeding larvae by obstructing their filtration structures and reducing their feeding efficiency (Lohrer *et al.*, 2006). Under moderate suspension, larval Pacific herring may feed faster than under clear water, but this ability decreases as the suspension level rises (Boehlert and Morgan., 1985). Turbidity provided a safe refuge for larvae, and light is a significant factor in feeding regulation in the absence of predators indicating that long-term turbidity is critical for small larvae that must eat continually to survive (Lehtiniemi *et al.*, 2005). Increased water turbidity and poor water quality do not always kill adult coral colonies, but they do slow coral recruitment and reduce connectivity (Fabricius, 2005).

2.4.6 Increased storm intensity

From 1970 to 2004, the number and severity of tropical and subtropical cyclones increased, most likely in response to rising sea surface temperatures (SST) (Bashevkin *et al.*, 2020). Heavy rains accompanied by storms can lower salinity and increase turbidity in the coastal seas. Both a drop in salinity and a rise in turbidity can have an impact on marine connectivity. Aside from that, various physical factors (e.g., seasonal wind events, tropical cyclone timing, and magnitude) combined to impact dispersal at various stages and influenced crab recruitment patterns (Etherington and Eggleston, 2003). Tropical storms and hurricanes increase the capacity of blue crab nurseries, with the highest settlement occurrences generally associated with 'onshore' storm tracks (Eggleston *et al.*, 2010). Because of the fall in sea temperatures connected with high winds coincident with all hurricanes and tropical storms, the passage of a hurricane can alleviate thermal stress on coral reefs (Manzello *et al.*, 2017). However, if storms become more severe and carbonate materials become weaker as a result of more acidic waters, reef corals will become more vulnerable to mechanical injury (Madin *et al.*, 2008).

2.5. MARINE CONNECTIVITY PARAMETERS

The larval behaviour and species life-history features help to determine dispersal distance and connectivity (Shanks, 2009). Individual species represent a unique suite of life history parameters, including spawning dates, pelagic larval duration (PLD), larval competency, larval behaviour, and larval mortality (Treml and Halpin, 2012). The propagule duration and dispersal distance have a strong relationship (Shanks *et al.*, 2003). Estimates of the pelagic duration of larval dispersive stages have historically been used to determine the spatial extent of larval dispersal in marine systems (Cowen *et al.*, 2007). The time during which larvae remain viable and capable of settling is known as pelagic larval duration (PLD), and it varies by species (Crochelet *et al.*, 2016). When employing a dispersal model to evaluate connectivity, the following characteristics are usually required: spawning time, pelagic larval duration, settlement behaviour, and larval mortality (Schill *et al.*, 2015).

Biological Parameters of Larvae	Description
Time of spawning	This defines the larval release times in the model
Maximum pelagic larval duration (PLD)	The PLD representing the maximum amount of time larvae can spend in the water column.
Settlement behaviour	Probability of larvae settling if larvae come upon an appropriate habitat cell.
Larval mortality	Daily mortality rate of larvae while dispersing.

Table 2.1: Larval biological parameters needed (in the model) to study connectivity.(Adapted from Scill *et al.*, 2015).

2.6. EXISTING CONNECTIVITY MODELS

Variety of methods are used to assess coral reef connectivity. For the first time, Baums *et al.* (2006) discovered a direct link between effective dispersal distances and gene flow in a marine organism based on oceanographic and life history parameters. To follow the dispersal of marine larvae, a technique called element fingerprinting was devised (DiBacco & Levin, 2000). Tripp *et al.* (2020) discovered that the chemical of larval otoliths can be used to estimate regional productivity and connectivity. For determining the coral reef connectivity pattern, Torres *et al.* (2018) used a biophysical model that included ocean currents and larval biology. To determine the influence of geographic and hydrodynamic limitations on dispersal or retention of barnacle larvae, (George *et al.*, 2013) used Eulerian hydrodynamic model as well as a Lagrangian particle analysis model. Particle transport modelling can be an effective tool and decision support system in identifying the locations that are potential nursery areas for fish larvae (George *et al.*, 2011). Roberts *et al.* (2010) created the Marine Geospatial Ecology Tools (MGET) that includes Connectivity Analysis tool. The Connectivity Analysis tools analyse the connectivity of marine ecosystems, and this tool simulates the spread of coral larvae from reefs by ocean currents using an

Eulerian advection-diffusion algorithm implemented in MATLAB, and outputs a graph structure depicting the connections between reefs, based on the method developed by Treml *et al.* (2008) (Roberts *et al.*, 2010). Treml *et al.* (2012) improved this method by applying the Multidimensional Positive Definite Advection Transport Algorithm (MPDATA) (Smolarkiewicz and Margolin, 1998) to ocean currents to circulate larvae around the study area.

MATERIAL AND METHODS

CHAPTER 3

MATERIAL AND METHODS

3.1 STUDY AREA

The study was conducted in the Andaman Sea, which lies on the eastern edge of the Indian Ocean, circumscribed towards the west by an arc of islands extending from northern Sumatra to the Irrawaddy delta. The study area lies between 92°E to 100°E and 4°N to 20°N Grid.

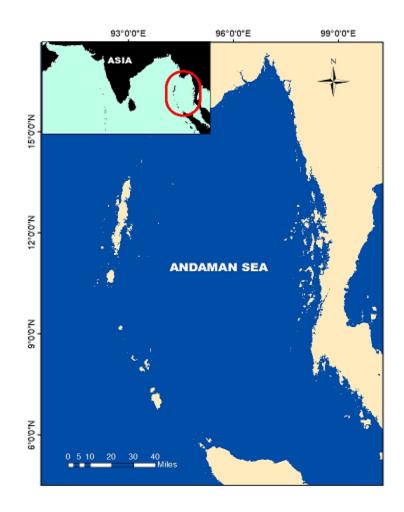


Fig. 3.1: Location map of study area.

The Andaman Sea is not small. Its surface area (6, 70,572 km²) is practically 25% of that of the Bay of Bengal (2,139,717 km²) (Chatterjee *et al.*, 2017), and its entire basin lies within the Exclusive Economic Zones of India, Myanmar, Thailand, and Indonesia (Chatterjee *et al.*, 2017). Andaman Sea is one of the least-observed regions in the Indian Ocean, and this is because most portions of the Andaman Sea are part of the surrounding nations' national exclusive economic zones (EEZs), and some data policy issues prevent access to existing datasets (Liu *et al.*, 2018). Fringing reefs are plentiful in the Andaman and Nicobar Islands (India) (Reddiah, 1977), Mergui Archipelago (Myanmar), west coasts of Thailand and Malaysia, and northwest Sumatra (Indonesia) (Brown, 2007). The Andaman Sea has a long geological history, diverse seafloor topography, a highly dynamic oceanography, and a large tidal range (2–5 m) with frequent sealevel depressions (Brown, 2007).

3.2 SPECIES OCCURRENCE DATA

The coral *Pocillopora damicornis* (Linnaeus, 1758), also known by the common name 'Cauliflower Coral,' was the coral selected for this study. The occurrence records of *Pocillopora damicornis* were collected from open source database GBIF (Global Biodiversity Information Facility) (GBIF.org (18 March 2021) GBIF Occurrence Download https://doi.org/10.15468/dl.eyqmd3) and other published literature. The distribution points of the *Pocillopora damicornis* was plotted using ArcGIS software.

3.3 SELECTION OF ENVIRONMENTAL PARAMETERS

The environmental parameters were obtained from the Bio-ORACLE (Tyberghein *et al.*, 2012), and the data are available at a spatial resolution of five arcmins (approximately 9.2 km at the equator). Environmental parameters taken were of benthic layers average values. A correlation matrix was made with the help of R software (R Development Core Team 2008), and nine environmental variables were selected after avoiding the collinear variables. All variables were checked for multicollinearity using the function raster.cor.plot embedded in the ENMTOOLS package. The environmental parameters selected include current velocity mean, chlorophyll mean,

dissolved oxygen mean, dissolved oxygen range, pH, light bottom mean, nitrate range, temperature mean, and salinity mean. Current velocity maximum, iron mean, bathymetry mean, and phosphate mean were avoided to achieve the lowest collinearity among parameters.

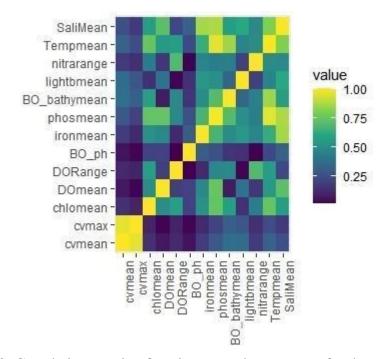


Fig. 3.2: Correlation matrix of environmental parameters for the study area.

3.4 SPECIES DISTRIBUTION MODEL

Species Distribution modelling was done using Biomod 2 (Thuiller *et al.*, 2009) package implemented in R, a freeware, open-source package. It is an important upgrade of BIOMOD (BIOdiversity MODelling) in 2009, called biomod2. Biomod2 is an ensemble platform for species distribution modelling. This package permits to run consistently up to 10 single models and combine them into an ensemble model and make ensemble projections. All the nine environmental parameters chosen were made into the extent of the study area and WGS84 as their projection. The species occurrence data obtained from GBIF were presence only data, while the modelling techniques implemented in BIOMOD requires presence and absence data. Since the data were presence-only, pseudo-absences were generated. To extract a range of pseudo-absence data, three

algorithms have been implemented in Biomod: 'random,' 'SRE,' and 'disc' (Georges and Thuiller, 2013). Here we use random algorithm for this purpose (Thuiller *et al.*, 2009). Models like Generalised Linear Models (GLM, McCullagh and Nelder, 1989), Generalized Boosting Model (GBM, Ridgeway 1999) or usually called Boosted Regression Trees, Classification Tree Analysis (CTA, Breiman *et al.*, 1984), Surface Range Envelop (SRE, Busby 1991), Flexible Discriminant Analysis (FDA), Random Forest (RF) and Maximum Entropy (MAXENT.Phillips, Phillips *et al.*, 2006) were computed.

In BIOMOD, we also do model evaluation. Receiver Operating Characteristic (ROC) and True Skill Statistics (TSS, Allouche *et al.*, 2006) were used as two modes of criteria for model effectiveness. Models with TSS score less than 0.8 and ROC values less than 0.9 are excluded. Now with the chosen model, an ensemble model is created. After the model has been validated and calibrated, we project the species' probable distribution over space and time (Georges and Thuiller, 2013). Biomod also gives relative explanatory variable importance. The parameter "VarImport" allows for a direct comparison of the importance of explanatory variables across models (Thuiller *et al.*, 2008).

3.5 BIOLOGICAL PARAMETERS

The scale of dispersal of larvae relies upon the species' life-history characteristics (Kinlan *et al.*, 2005). A study on several corals suggests mortality is often variable in time (often higher earlier in the larval duration period) but generally on the order of 5% day⁻¹ to 10% day⁻¹ (Connolly and Baird, 2010, Schill *et al.*, 2015). For this study mortality rate was chosen as 7.5% day⁻¹. Maximum Pelagic Larval Duration (PLD) of *Pocillopora damicornis* was taken as 100 days and period of larval settlement-competency as 100 days (Harii and Kayanne, 2002, Richmond, 1987, Cumbo *et al.*, 2013) from various published literature reviews. The Peak month of spawning for *Pocillopora damicornis* is taken to be May (Fan *et al.*, 2002). When larvae acquire competency and are over coral habitat, their settling rate is estimated to be 80% per day. It is also the default value of the connectivity model used in this study. A study by Schill *et al.*, 2015 using coral larvae of PLD for 30 days uses settlement rate to be 75 % per day. Since larvae are pelagic, the HYCOM depth layer to download currents is taken as 0 m to study larvae that float at or near the surface.

These biological parameters were utilised to run the connectivity model to estimate the coral reef connectivity in the Andaman Sea.

3.6 RUNNING THE CONNECTIVITY MODEL

A biophysical modelling approach (Treml and Halpin, 2012) was used to estimate the coral larval dispersal between the reefs of the Andaman Sea and for studying the coral reef connectivity. The Connectivity Analysis Tool available in the Marine Geospatial Ecology Tools package (Roberts *et al.*, 2010) (version 0.8a73), attached to ArcGIS version 10, was used. Using an Eulerian advection-diffusion algorithm implemented in MATLAB, this tool simulates the dispersal of coral larvae from reefs by ocean currents and generates a network structure depicting the relationships between reefs (Roberts *et al.*, 2010).

Three rasters were initially required, namely water mask raster, patch IDs raster, and patch cover raster to simulate larval dispersal using this tool, The water mask raster shows which cells are land and which are water. The value 0 or No Data indicates land, and all other values indicate water. During the simulation, larvae will be allowed to move between water cells, but they cannot enter land cells. Patch ID raster specifies the locations and IDs of habitat patches, and Patch cover raster specifies the extent of each cell's area occupied by habitat from which larvae can be delivered or upon which larvae can settle. Water mask raster can be produced from bathymetry datasets from General Bathymetric Charts of the Ocean (GEBCO, GEBCO Compilation Group 2020). Using the raster calculator in ArcGIS, value =0 is given to land and value =1 is given for water. To create a patch cover raster, it is necessary to know how much percent of each cell occupies the habitat. So initially, we did species distribution modelling to understand the habitat suitability of *Pocillopora damicornis*. The raster that was obtained after SDM was opened in ArcGIS to make the patch cover and patchID raster. For this, it was first converted to a vector point, and thus we get reef nodes. The attribute table was then edited to give an ID and patch cover for each reef node. The output from SDM already tells us how much percentage of each cell has habitat. So to make a patch cover raster whose values should be greater than or equal to 0 and less than or equal to 1, we use the analysis from SDM. The value 1 indicates the entire cell occupies a suitable habitat while 0.5 indicates that only 50 % of the cell occupies the habitat. After giving ID

and patch cover value for each reef node, it is then made into two separate rasters to get the patch ID raster and path cover raster. All the three rasters are made with cell size 9 Km and World Mercator Projection. Once the three rasters were created, they were used to create larval dispersal simulation using the MGET tool. After creating the simulation with the three rasters, ocean current data was loaded into the Larval Dispersal Simulation using the MGET. Ocean current data were acquired from the HYCOM Global GLBa0.08 dataset (HYCOM + NCODA Global 1/12 Degree Analysis (GLBa0.08) (obtained through MGET), which has a resolution of about 9 km and uses a Mercator projection. After loading the current for the dates required, larval dispersal simulation was executed using the Treml et al. (2012) algorithm. The start date for the currents to load into the simulation was selected based on the reports of spawning occurrence from the region. The duration for simulation was taken as 100 days because the pelagic larval duration (PLD) of Pocillopora damicornis is 100 days (Harii et al., 2002, Richmond, 1987, Cumbo et al., 2013). The last step of running the MGET tool was visualise larval dispersal simulation results. A line feature class showing connections between patches was obtained as the output. The attribute table of the output from MGET shows the probability of larvae recruiting to each reef node from each source reef node and the length of dispersal of larvae. A connectivity matrix indicating the strength of larval connectivity among the islands was developed using R. To understand the local connectivity, the reef nodes were sub-grouped based on the islands in the region.

3.7 ESTIMATION OF THE DISPERSIVE POTENTIAL OF THE CORAL LARVAE DURING IOD POSITIVE AND IOD NEGATIVE YEARS

Indian Ocean Dipole is a coupled ocean-atmosphere phenomenon in the Indian Ocean (Saji *et al.*, 1999). A positive (negative) IOD is associated with greater than average SST (cooling) over the western equatorial Indian Ocean with corresponding cooling (warming) off the Sumatran coast (eastern Indian Ocean). An extreme negative IOD was observed in 2016 (Lu *et al.*, 2018), and an unusual positive IOD was observed in 2015 (Zhang *et al.*, 2018). During 2016, the event began in May, peaked in July, weakened in August, then rebounded to reach its second peak in September (Iskandar *et al.*, 2018). In order to understand the influence of IOD on the connectivity of the reefs of the Andaman Sea, we run the simulation for two phases for 2016. Since there are two peaks in

2016, we have selected the HYCOM data from May 2016 to August 9, 2016 (phase 1), indicating the first peak phase. The HYCOM data from August to November 9 of 2016 (phase 2) was selected as the second peak phase. From mid-August to mid-November 2015, the Indian Ocean saw a positive phase of IOD, with a peak intensity of 1.17°C at the end of September (Avia and Sofiati, 2018). Unlike 2016 there are no two peaks in 2015. So for understanding the pattern of connectivity in the IOD positive phase, HYCOM data were selected from August to November 9 of 2015. All the simulations were run, and the connectivity matrices were compared.

3.8 ESTIMATION OF THE PATTERN OF CORAL LARVAL CONNECTIVITY DURING DIFFERENT SEASONS

The SST and surface currents distribution in the Andaman Sea varied seasonally due to the monsoons (Rizal *et al.*, 2012). During Northeast Monsoon (December-January-February) and Southwest Monsoon (June to September), cooler SST was detected in the Andaman Sea compared to the first inter-monsoon season (March to May), during which the Andaman Sea is much warmer (Isa *et al.*, 2020). So to understand the pattern of coral larval connectivity during different seasons, simulations were run for four periods: a) Northeast monsoon (December-January-February), b) First inter-monsoon season (March to May), c) Southwest monsoon (June to September), and d) Second inter-monsoon (October to November). Since PLD for *P. damicornis* is 100 days, all the simulations should run for 100 days. So we have selected the HYCOM data for the following dates: a) December 2016 to March 11 of 2017 for Northeast monsoon, b) March to June 9 of 2017 for the first inter-monsoon season, c) June to September 9 of 2017 for Southwest monsoon and d) October 2017 to January 9 of 2018 for second inter-monsoon. All the simulations were run, and the connectivity matrices were compared.

3.9 SST TREND ANALYSIS

A time-series map of average SST and SST anomaly is plotted to understand how the sea surface temperature (SST) in the Andaman Sea varies. The monthly mean SST data from 1889– 2021 May were obtained from COBE SST data provided by the NOAA (National Oceanic and Atmospheric Administration)/OAR/ESRL PSL, Boulder, Colorado, USA. COBE SST data set is freely available online. Sea Surface Temperature anomalies data from 1889 to 2020 was obtained from GISS Surface Temperature Analysis (GISTEMP), version 4 in NASA's Goddard Institute for Space Studies website. For the processing of data, the ndf4 package in R is used. The time-series map is obtained using R. Packages like tidyverse, ggplot are used to make more customized plot of time series map of average SST and SST anomaly.

The monthly average SST in the Andaman Sea during the year 2017 is plotted to understand how SST changes in the Andaman Sea seasonally and compare it with the connectivity pattern during different seasons. The monthly mean SST data for 2017 is obtained from NOAA Coral Reef Watch (CRW). Using Grid Analysis and Display System (GRADS), the average SST value for each month in the Andaman Sea is found. The monthly average SST in the Andaman Sea is then plotted using Microsoft Excel.



CHAPTER 4

RESULTS

4.1 SPECIES DISTRIBUTION MODEL

We predicted the current spatial distribution of a significant hard coral species, *P. damicornis*, in the Andaman Sea (Northern-Eastern Indian Ocean). The environmental suitability is indicated on the map by the legend from grey to green. Green represents a highly suitable habitat, whereas grey represents the least.

4.1.1 Prediction of the current distribution

4.1.1.1 Model Evaluation Score

The two modes of criteria used for determining the model effectiveness were Receiver Operating Characteristic (ROC) and True Skill Statistics (TSS). TSS is a simple and intuitive measure for the performance of species distribution models when expressing the obtained predictions as presence-absence maps (Allouche*et al.*, 2006). Fig. 4.1 shows the model evaluation score graph of seven models used. The model that occurs on the top right corner of the graph has the best performance.

Among the seven models used, Generalised Boosting Model (GBM) has the best model performance, followed by Random Forest (RF) (Allouche *et al.*, 2006). We decided to eliminate any models with a TSS score of less than 0.8 and ROC value less than 0.9 in ensemble modelling. So the model SRE is excluded in ensemble modelling (BIOMOD_EnsembleModeling combines individual models to build some meta-model). Except for SRE, all the models used have a ROC value greater than 0.9. Models with ROC value greater than 0.9 indicates that they have excellent model performance.

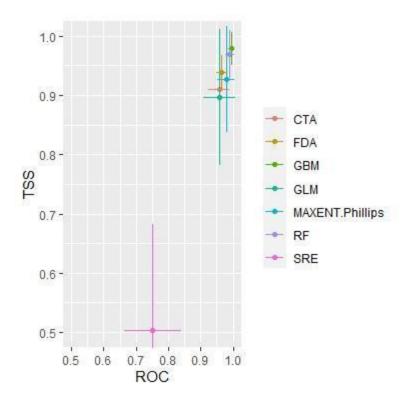


Fig. 4.1: Graph showing Model Evaluation Score of seven models

4.1.1.2. Analysis of variable contributions

The importance of each variable is one minus the correlation score between the original prediction and the prediction made with a permuted variable (Thuiller *et al.*, 2008). High values will therefore reveal a high importance of the variable whereas a value of 0 means that there is no importance. Most models showed "light bottom mean" has high variable importance followed by "salinity mean" and "pH" has low variable importance.

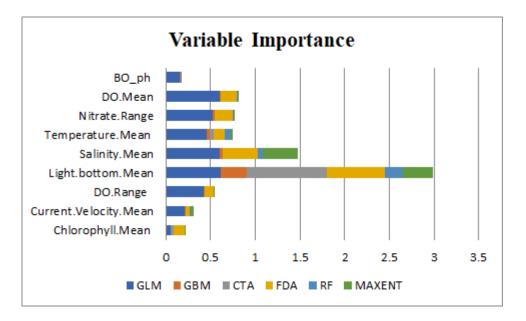


Fig. 4.2: Variable importance by seven models

4.1.1.3. Response curves of variables used

Visually inspecting species response curves is typically beneficial when using models to estimate potential distributions in different places or timeframes (Austin and Gaywood, 1994). BIOMOD does this by employing an implementation of the "evaluation strip" approach (Elith *et al.*, 2005), which allows for the extraction of species response curves irrespective of the model's algorithm (Thuiller *et al.*, 2009). These curves show how each environmental variable affects model prediction. The response curves for the *P. damicornis* model showed the change in predicted probability when the corresponding variable is used in isolation. The plots below demonstrate the dependence of predicted suitability on the selected variables as well as on the dependencies induced by correlations between each variable and other variables for each model independently.

a) Generalized Linear Model (GLM)

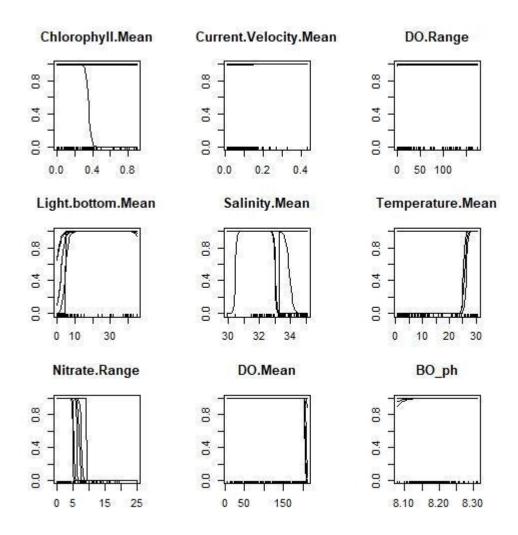


Fig. 4.3: The response curves of GLM

b) Generalized Boosting Model (GBM)

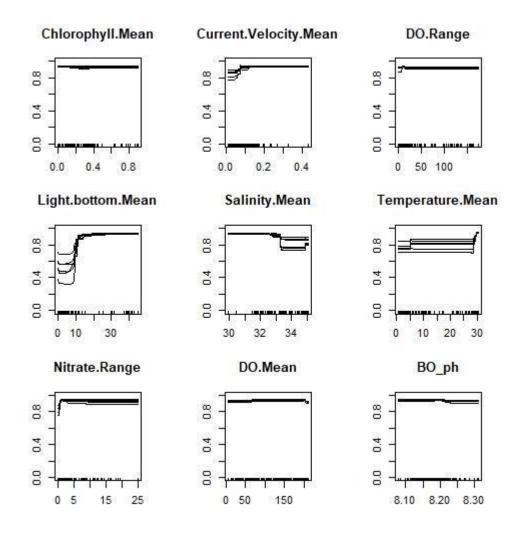


Fig. 4.4: The response curves of GBM

c) Random Forest (RF)

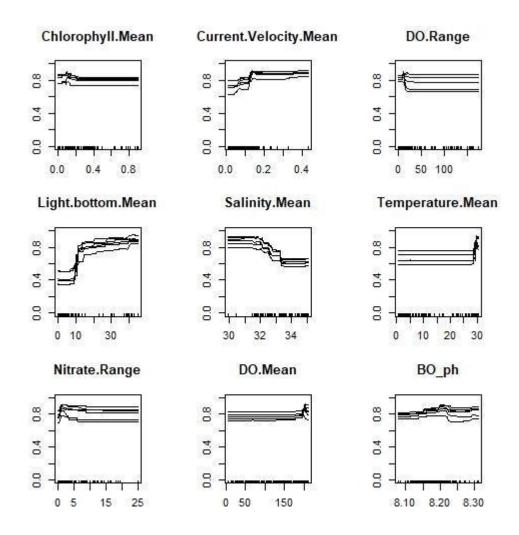


Fig. 4.5: The response curves of RF

d) Classification Tree Analysis (CTA)

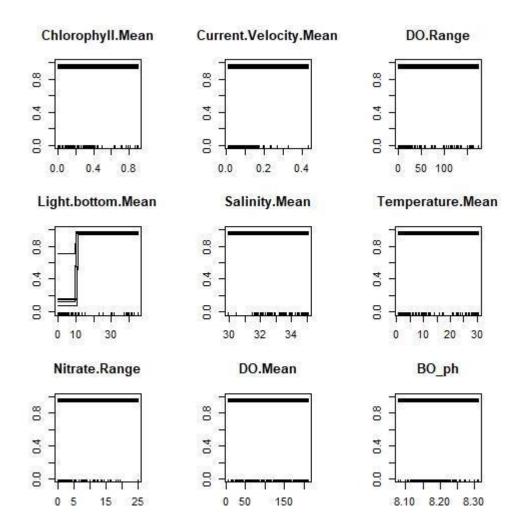


Fig. 4.6: The response curves of CTA

e) Flexible Discriminant Analysis (FDA)

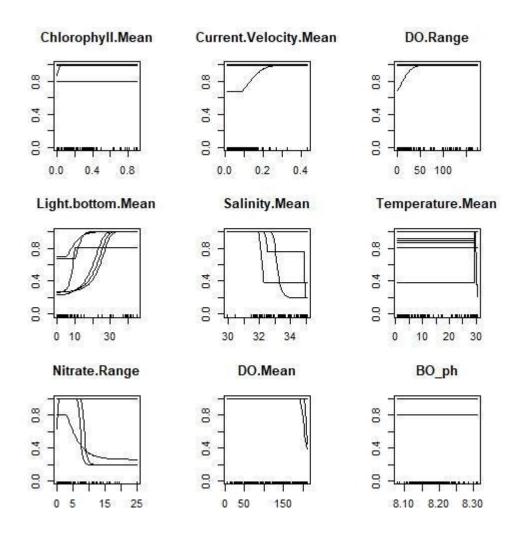


Fig. 4.7: The response curves of FDA

f) MAXENT.Phillips

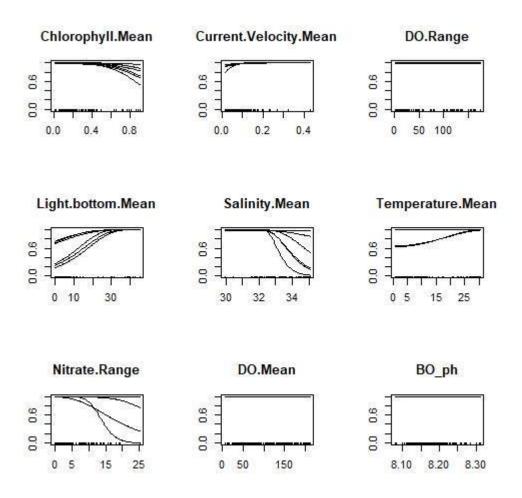


Fig. 4.8: The response curves of MAXENT.Phillips

4.1.4 Evaluation Score of Ensemble Model

Table 4.1: shows the evaluation score of the ensemble model. The ensemble model has TSS score of 0.957 and ROC value of 0.99 which indicates that the ensemble model has excellent accuracy.

Accuracy	AUC	Kappa/TSS	
Excellent/High	0.9 - 1	0.8 - 1	
Good	0.8 - 0.9	0.6 - 0.8	
Fair	0.7 - 0.8	0.4 - 0.6	
Poor	0.6 - 0.7	0.2 - 0.4	
Fail/null	0.5 - 0.6	0 - 0.2	

Index for classifying model accuracy

	Testing.data	Cutoff	Sensitivity	Specificity
KAPPA	0.789	701.5	85.714	98.561
TSS	0.957	320	100	95.683
ROC	0.99	321.5	100	95.683

Table 4.1: Evaluation score of the Ensemble model

4.1.1.4. The predicted habitat suitability of *Pocillopora damicornis* in the Andaman Sea

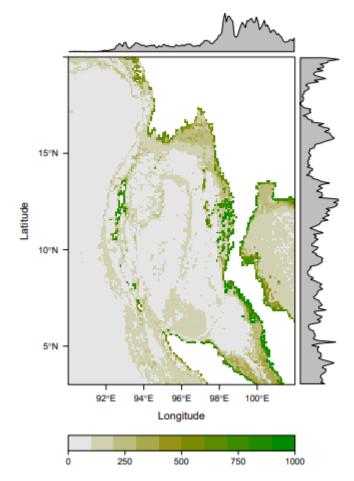


Fig. 4.9: Map showing the predicted habitat suitability of *P. damicornis* in the Andaman Sea in the present condition

Fig. 4.9 shows that the predicted distribution of *P. damicornis* in the Andaman Sea (Northeastern Indian ocean) with suitability ranging from 0 to 1000, low to high indicated by a legend of grey to dark green. *P. damicornis* shows higher habitat suitability (80-97%) along the Andaman and Nicobar Islands, Mergui Archipelago, Phuket, western coast of Thailand, and the north-eastern coast of Sumatra. The western coast of Sumatra and Myanmar (east to Moscos Island) and the southern tip of the Irrawaddy delta showed medium to high suitability (50-80%).

4.2. CONNECTIVITY MATRIX

Connectivity matrices for IOD positive and negative year and for different seasons were derived. Fig. 4.10 provides a detailed view of coastal and island reefs in the Andaman Sea (obtained using the output from species distribution modelling for *P. damicornis*) and their identification name used in the connectivity matrix.

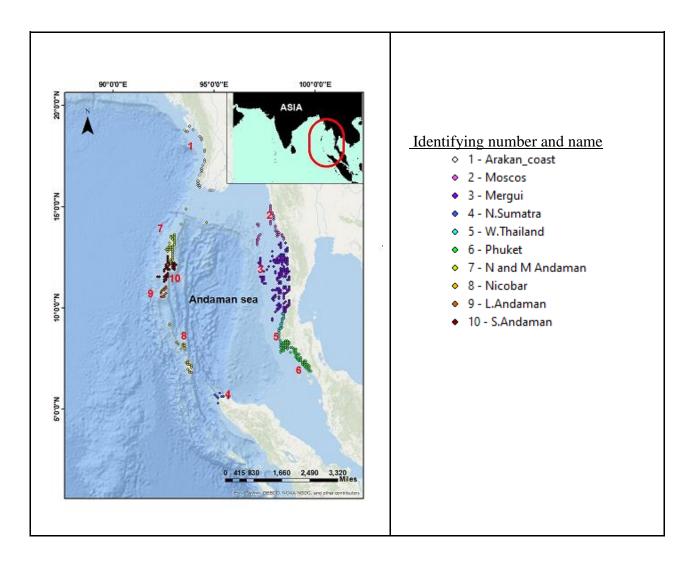


Fig. 4.10: Coastal and island reefs in Andaman Sea and their identification name used in connectivity matrix

4.2.1. Different seasons

4.2.1.1. Northeast Monsoon

Connectivity matrix displaying the coral larvae (Pocillopora damicornis) exports and imports between reefs in Andaman Sea during Northeast Monsoon (June to September) is derived (Fig. 4.11). Fig. 4.11 illustrates the strength and direction of potential connections between the reefs in the Andaman Sea by showing the probability of *Pocillopora damicornis* larvae settling to each reef. Here the X - axis shows the destination reef, meaning the reef on which the larvae settle and the Y - axis shows the source reef, meaning the reef from which the larvae disperse. The diagonal shows the self-recruitment. The colour in the Fig. indicates the probability of larval settlement or the probability by which the larvae is recruited to the destination reef. Here the red colour indicates the highest probability; yellow to orange colour also indicates a good probability while grey colour indicates the lowest probability. Ten "source-destination" sub-regions (coastal and island reefs) are visually identified on the connectivity matrices (the reef nodes were subgrouped based on the location - see Fig. 4.10): S.Andaman indicates: South Andaman, L.Andaman: Little Andaman, Nicobar: Nicobar Islands, N&M Andaman: North and Middle Andaman, Phuket: Reefs around Phuket Island, Phi Phi Islands and southwestern coast of Thailand in Andaman Sea, W. Thailand: western coast of Thailand above Phuket, N. Sumatra: Northern tip of Sumatra, Mergui: Mergui Archipelago, Moscos: Moscos islands and Myanmar coast which lies east of Moscos, Arakan coast: western Arakan (Rakhine) coast and the southern Irrawaddy (Ayeyarwady) deltaic coast.

A total of 2462 possible connections were found between the reefs. The maximum dispersal distance was 984.3742 km, which occurred for larvae released off the Phuket (Fig. 4.10, identifying number - 6) and settled to North and Middle Andaman (7) in Andaman Sea. The minimum distance travelled by larvae is 8.366 km between adjacent reefs of Phuket (6). North & Middle Andaman act as a sink for most of the coastal and island reefs but probability of larval settlement is not high. From sources like Mergui Archipelago (3), Phuket (6), western Thailand coast (5), Myanmar coast east to Moscos (2), South Andaman (10), and Nicobar Islands (8), the larvae are recruited to here. Though the number of larvae recruited to South Andaman is less compared to North & Middle Andaman, it also acts as a sink for most of the coastal and island reefs in the Andaman Sea, but more larvae are settled here from sources like the Nicobar Islands

and North and Middle Andaman. Larvae are dispersed from Phuket and the western coast of Thailand to the Andaman and Nicobar Islands, but the probability they settle is low. The Arakan coast of Myanmar (region 1 in Fig. 4.10) does not act as a source for any other reefs. Though Phuket and Mergui Archipelago do not act as a source for one another, they are sources of coral larvae for North & Middle Andaman, South Andaman, and Little Andaman. Apart from self-recruitment, Nicobar Islands receive more larvae from Phuket.

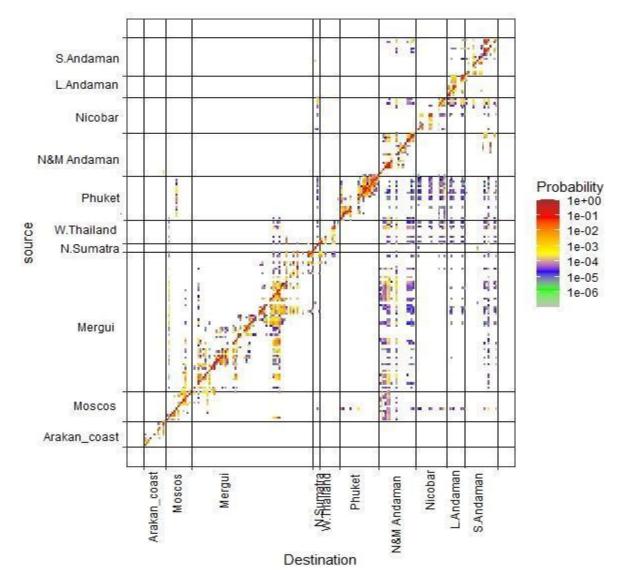


Fig. 4.11: Connectivity matrix indicating the probability of *Pocillopora damicornis* larvae recruiting to reef site (horizontal axis - destination reef), originating from a reef site (vertical axis - source reef) for northeast monsoon season

4.2.1.2. First inter-monsoon

Fig. 4.12 illustrates the coral larval connectivity pattern during the first inter-monsoon. A total of 2352 possible connections were found between the reefs. This indicates that connectivity between reefs is decreased during the first inter-monsoon compared to Northeast monsoon.

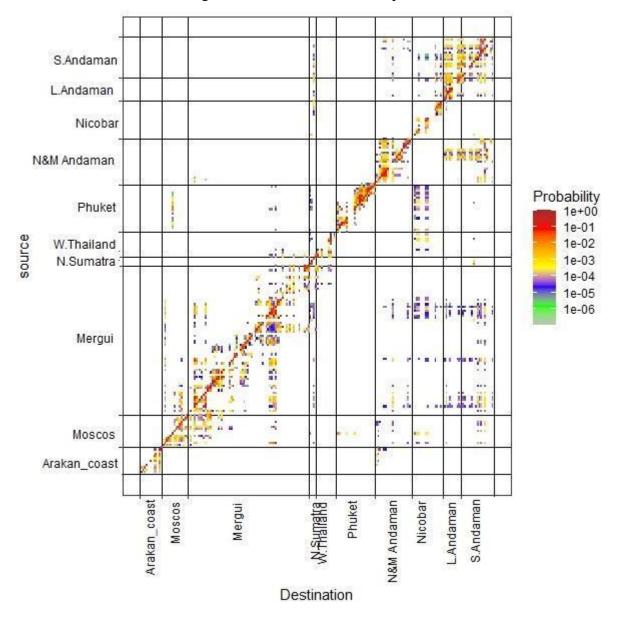


Fig. 4.12: Connectivity matrix of P. damicornis larvae during the first inter-monsoon season

The maximum dispersal distance was 735.3386 km, which occurred for larvae released off the Mergui Archipelago (Fig. 4.10, region - 3) and settled to Nicobar Islands (8) in Andaman Sea.

The maximum distance the larvae can travel is decreased during this season. The minimum distance travelled by larvae is 8.366 km between adjacent reefs of Phuket (6). There is no or low connectivity between Phuket and Mergui Archipelago. The larval recruitment to North & Middle Andaman from other coastal and island reefs is highly reduced compared to Northeast monsoon, but the number of larvae settled at the south and little Andaman is increased. The probability that the larvae settle at the Nicobar Islands coming from the source reef Phuket and the western coast of Thailand is increased in this season. Unlike the Northeast monsoon, there is no recruitment of larvae to the Andaman Islands from Phuket and the western coast of Thailand.

4.2.1.3. Southwest Monsoon

The pattern of coral larval connectivity during Southwest Monsoon (June to September) is derived (Fig. 4.13). A total of 2567 possible connections were found between the reefs. The maximum dispersal distance was 755.2713 km, which occurred for larvae released off the Nicobar Islands (Fig. 4.10, identifying number - 8) and settled to Mergui Archipelago (3) in Andaman Sea. During the Northeast monsoon, larvae are dispersed to a greater distance than during the southwest monsoon. However, the maximum distance travelled by larvae during the Southwest monsoon. However, the maximum distance travelled by larvae during the first intermonsoon. The minimum distance travelled by larvae is 8.366 km between adjacent reefs of Phuket (6). Unlike Northeast monsoon, where North & Middle Andaman was a sink (though the probability of larval settlement was not high) for many coastal and Island reefs, during southwest monsoon larvae are recruited to North and Middle Andaman only from South Andaman and self-recruitment. The Mergui Archipelago acts as a good sink during the Southwest monsoon. Larvae are recruited to here mainly from the sources like North & Middle Andaman (region- 7 from Fig. 4.10), South Andaman (10), Little Andaman (9), and Nicobar Islands (8). The Mergui Archipelago also acts as a source for Moscos Islands and the adjacent Myanmar coast.

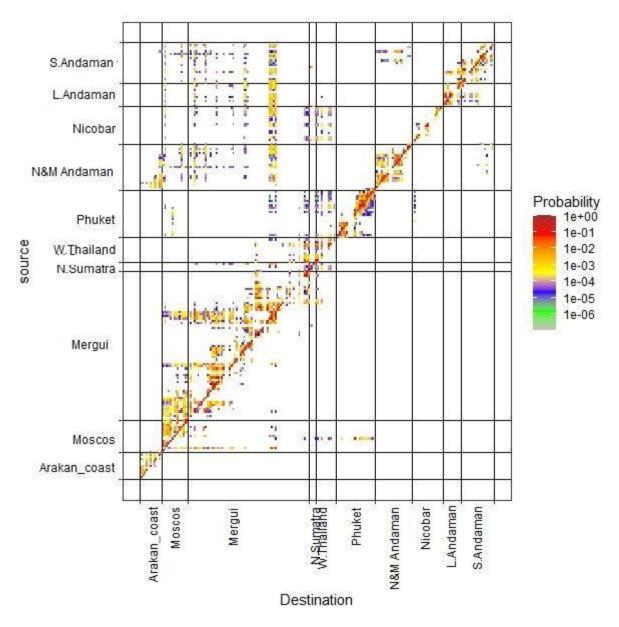


Fig. 4.13: Connectivity matrix of *P. damicornis* larvae during southwest monsoon season.

4.2.1.4. Second inter-monsoon

The pattern of coral larval connectivity during the second inter-monsoon (October to November) is derived (Fig. 4.14). A total of 2061 possible connections were found between the reef, which is less compared to the Northeast and Southwest monsoon. The maximum dispersal distance was 929.590 km, which occurred for larvae released off the Phuket (Fig. 4.10, identifying number - 6) and settled to South Andaman (10) in the Andaman Sea. This is greater than the

Southwest monsoon but less than the maximum dispersal distance seen in the Northeast monsoon. The minimum distance travelled by larvae is 8.366 km between adjacent reefs of Phuket (6). No reef acts as a good sink, but the self-recruitment rate remains high. There is no connectivity seen between the reefs of Phuket and the Mergui Archipelago. Little Andaman is seen to recruit larvae to its adjacent South Andaman. Though the number of larval dispersal between the islands within the Mergui Archipelago is reduced, for the dispersed larvae their probability of settlement is good.

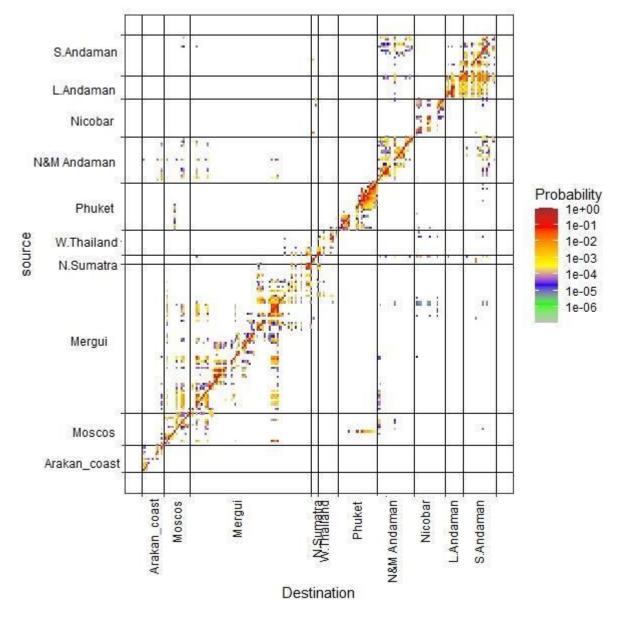


Fig. 4.14: Connectivity matrix of *Pocillopora damicornis* larvae during the second inter-monsoon season

4.2.2. Different climatic conditions

4.2.2.1. Extreme negative IOD year - 2016

4.2.2.1.1. PHASE 1- First peak phase (May to August 9)

The 2016 significant negative IOD event in the tropical Indian Ocean had two peaks: one in July and one in September, with the second peak being more potent than the first (Iskandar*et al.*, 2017). In order to understand the pattern of coral larval connectivity between the reefs of the Andaman Sea for the year 2016 (extreme negative IOD year) during its first peak phase, the simulation was run from May to August 9 of 2016, and a connectivity matrix is derived (Fig. 4.15).

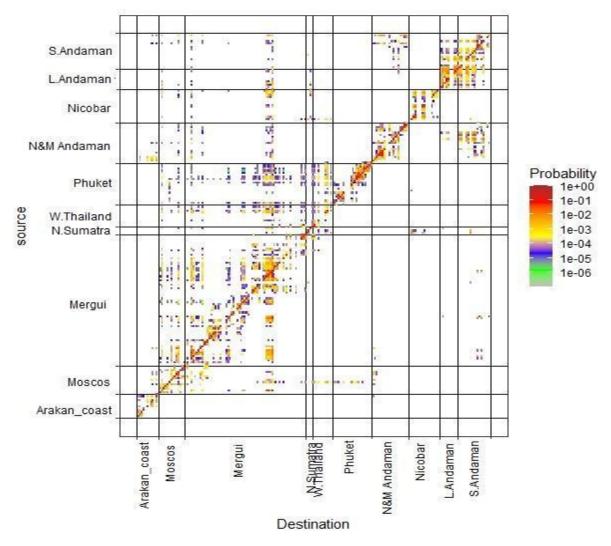


Fig. 4.15: Connectivity matrix of *P. damicornis* larvae during extreme negative IOD year - during its first peak phase

A total of 2683 possible connections were found between the reefs for 100 days PLD. The maximum dispersal distance was 774.278 km, which occurred for larvae released off the Phuket (Fig. 4.10, identifying number - 6) and settled to Moscos Island (2) in the Andaman Sea. The minimum distance travelled by larvae is 8.366 km between adjacent reefs of Phuket (6). Fig. 4.15 depicts that the rate of self-recruitment of larvae is high. Though there is a connection among subregions, the probability of larvae recruited between sub-regions is low compared to self-recruitment. From the network, it is evident that the Mergui Archipelago is a sink for most of the coastal and island reefs in the Andaman Sea, but the probability of larval settlement is low. Little Andaman (9) and South Andaman (10) act as a source and sink for each other, but there is no recruitment of larvae to Nicobar Islands (8) from these regions.

4.2.2.1.2. PHASE 2- Second peak phase (Stronger than first peak)

To understand the pattern of coral larval connectivity between the reefs of the Andaman Sea for the year 2016 (extreme negative IOD year) during its peak phase of negative IOD, the simulation was run from August to November 9 of 2016, and a connectivity matrix is derived (Fig. 4.16). A total of 1861 possible connections were found between the reefs for 100 days PLD, which is very low compared to the first peak phase indicating that negative IOD affects connectivity in the Andaman Sea negatively. The maximum dispersal distance was 667.414 km, which occurred for larvae released off the Little Andaman (Fig. 4.10, identifying number - 9) and settled to Phuket (6) in the Andaman Sea. The maximum dispersal distance was also significantly reduced during the peak phase of negative IOD. The minimum distance travelled by larvae is 8.366 km between adjacent reefs of Phuket (6). Fig. 4.16 depicts that the rate of self-recruitment of larvae is high. Though the probability of larval settlement was low, there was connectivity between Phuket and the Mergui Archipelago during the first peak phase, but during the second peak, which was stronger than the first, there is no larval recruitment from Phuket to Mergui Archipelago. Though not so high, there is larval recruitment from Andaman and Nicobar Islands to the Mergui Archipelago. Connectivity is greatly reduced during this phase compared to the previous peak in 2016.

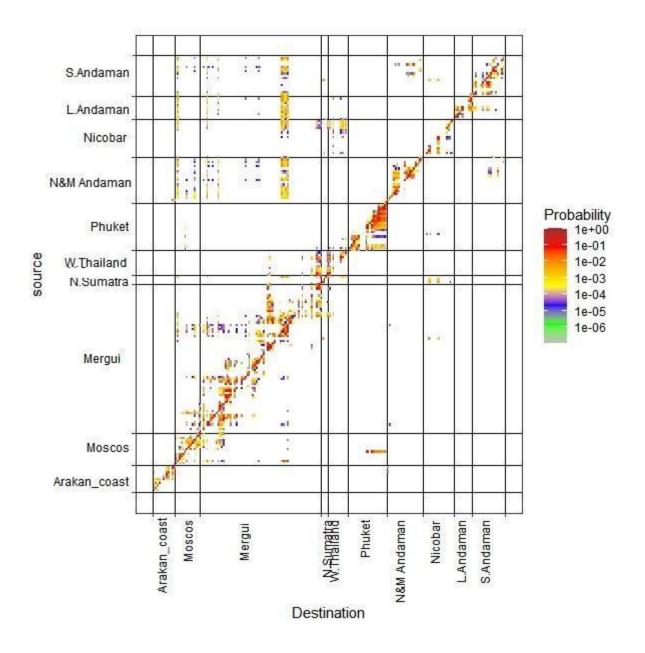


Fig. 4.16: Connectivity matrix of *P. damicornis* during extreme negative IOD year - during the second peak phase which is stronger than the first peak.

4.2.2.2 Positive IOD year - 2015

4.2.2.2.1. Positive IOD Peak phase (August to November 9)

The Indian Ocean saw a positive phase of IOD from mid-August to mid-November 2015, with the highest condition occurring at the end of September 2015 with an intensity of 1.17° C.

(Avia and Sofiati, 2018). Fig. 4.17 illustrates a simulation run from August to November 9, which includes the peak month of positive IOD.

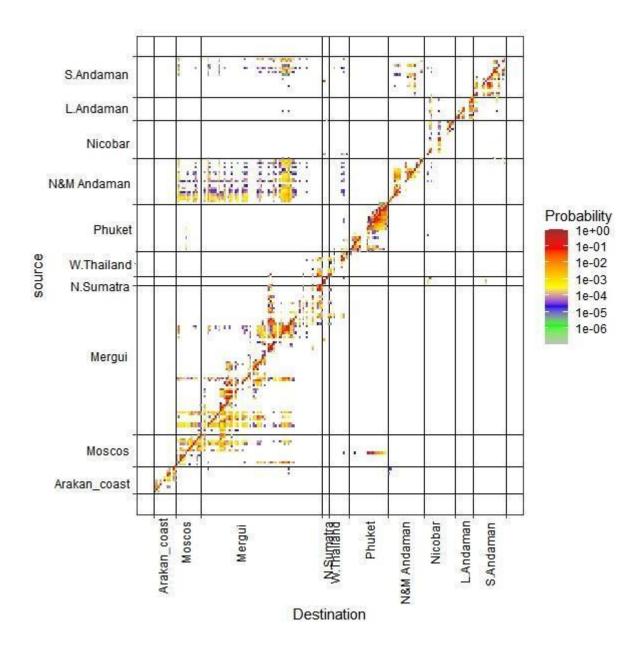


Fig. 4.17: Connectivity matrices of *P. damicornis* larvae during positive IOD phase.

A total of 2340 possible connections were found between the reefs for 100 days PLD. The maximum dispersal distance was 872.503 km, which occurred for larvae released off the North and

Middle Andaman (Fig. 4.10, identifying number - 7) and settled to the Northern tip of Sumatra (4) in the Andaman Sea. The minimum distance travelled by larvae is 8.366 km between adjacent reefs of Phuket (6). Fig. 4.17 depicts that the rate of self-recruitment of larvae is high, and compared to other reefs, it is evident that the Mergui Archipelago acts as a sink. Apart from receiving larvae from the reefs within the same island, no reefs except the Mergui Archipelago and adjacent Moscos (2) receive many larvae from other reef islands or coastal islands. North and Middle Andaman act as a source for the Mergui Archipelago and adjacent Moscos (2). When connectivity during positive IOD is compared to the peakest negative IOD months, it is seen that connectivity is greatly reduced during the strong negative IOD event.

4.3. SST TREND ANALYSIS

Fig. 4.18 illustrates the long-term time series of the SST anomalies in the Andaman Sea. It is used to estimate the regional trend of sea surface temperature in the Andaman Sea. In the Andaman Sea, the warming trend with SST anomalies has reached more than 1.5 ^oC, whereas cooling SST anomalies is around 1.5 ^oC during the period 1889–2020. That means, from 1889 and 2020, both warming and cooling trends in SST anomalies were seen in the Andaman Sea. A time-series map of SST in the Andaman Sea from 1889 to May 2021 is also derived and shown in Fig. 4.19. Analysis of time series data for sea surface temperature for the Andaman Sea (Fig. 4.18 and 4.19) indicates an increasing pattern of SST.

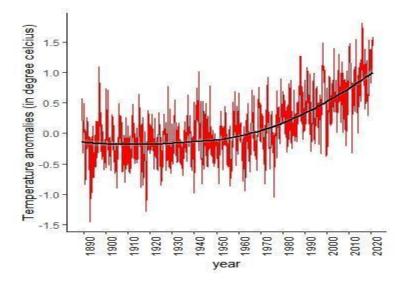


Fig. 4.18: Time series map of SST Anomaly in the Andaman Sea for the year 1889 to 2020.

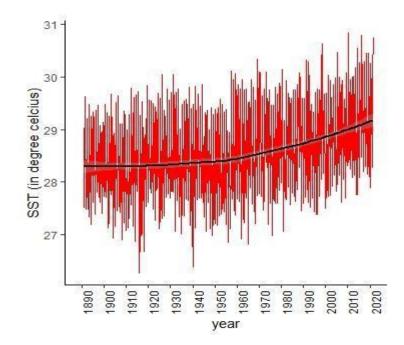


Fig. 4.19: Time series map of SST in the Andaman Sea from 1889 to 2021 May.

Fig. 4.20 depicts the monthly average SST in the Andaman Sea during the year 2017. The SST reached a high point in May. A rise in SST was seen from March to May (first intermonsoon), and this is thought to be the cause of the severe lack of connectivity during the first inter-monsoon.

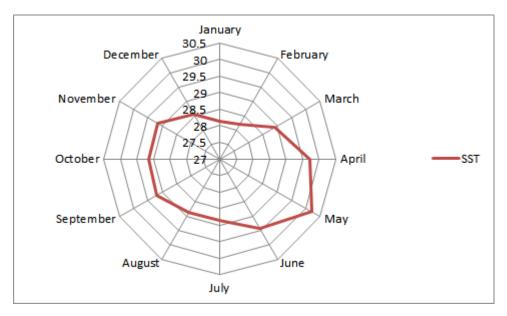


Fig. 4.20: The monthly average SST during the year 2017

DISCUSSION

CHAPTER 5

DISCUSSION

The Andaman Sea is part of the Asian monsoon system, and so the SST and surface current distributions in the Andaman Sea vary seasonally due to the monsoons (Rizal *et al.*, 2012). Currents play an essential role in the dispersal of coral larvae. Moreover, biological activities such as dispersal and survival of coral larvae may be influenced by changes in water temperatures (Gerber *et al.*, 2014). River discharges from Irrawaddy also change the salinity of the sea (Sprintall & Tomczak, 1992). All these features can affect the coral larval connectivity in the Andaman Sea. This study clearly portrays how the coral larval connectivity patterns of the Andaman Sea are affected during different seasons and changes in climatic conditions (IOD positive and negative year).

Pocillopora damicornis, one of the dominant corals in the Andaman Sea, especially in the wave-exposed reefs (Brown, 2007) was used for the study. It has a Pelagic larval duration (PLD) of 100 days (Harii et al., 2002, Richmond, 1987, Cumbo et al., 2013), abling it to disperse large distance and the planulae of the corals are competent as soon as 12 h after release (Isomura and Nishihira, 2001). An ensemble modeling approach is used in this study to understand the habitat suitability of the *P.damicornis*. The ensemble modelling approach has the benefit of using multiple diverse models, and hence prediction performance is better. The criteria used to select highperformance models for ensemble modelling are Receiver Operating Characteristic (ROC) and True Skill Statistics (TSS). Six models were selected among the seven models (GLM, GBM, CTA, FDA, SRE, RF, and MAXENT) (except SRE). All the six models used in this ensemble modelling give excellent performance as the ROC value for all models had shown above 0.9. Models with ROC value greater than 0.9 indicates that they have excellent model performance. SRE with a TSS score less than 0.8 and a ROC value less than 0.9 was excluded from ensemble modelling. The ROC and TSS scores of the Ensemble model were 0.99 and 0.975 respectively. Analysis of variable importance for each model showed that light bottom mean has high variable importance for most models, and this is because coral survival and physiology are influenced by light intensity and photoperiod in corals that contain symbiotic zooxanthellae. According to some studies,

Acropora millepora tended to have a broader range tolerance of light intensity than *Pocillopora* damicornis (Kuanui *et al.*, 2020). The second important variable for most models was salinity mean, and it is because of the fact that scleractinian corals are relatively stenohaline with less ability to tolerate salinity fluctuations, and they die if the salinity is < 25 ppt or > 45 ppt (Kuanui *et al.*, 2015).

The model (SDM) predicts higher habitat suitability (80-97%) for *P.damicornis* along the Andaman and Nicobar Islands, Mergui Archipelago, Phuket, western coast of Thailand, and the north-eastern coast of Sumatra. Studying habitat suitability alongside genetic connectivity is necessary because habitat unsuitability can reduce connectivity even when there is a lot of population mixing (Gorospe and Karl, 2015). So for this study, the output from the species distribution model (SDM) of *P.damicornis* is used to access the coral patches in the Andaman Sea for studying the pattern of larval connectivity of *P.damicornis* among the reefs of the Andaman Sea. The connectivity matrix obtained showed that the larval connectivity is not uniform in all seasons. The reef, which acted as a sink during the southwest monsoon, does not receive many larvae during the northeast monsoon. The probability of larvae settled on each reef showed a difference with different seasons. Connectivity refers not just to larvae's ability to move about but also to their ability to recruit, survive, and reproduce in their new environment (Gorospe and Karl, 2015). So higher probability of larval settlement indicates good connectivity among the reefs. Selfrecruitment rate is seen high during all seasons and during both IOD positive and negative years, while the recruitment of larvae to each reef from other source reefs (other than self-recruitment) is highly varying. One of the reasons for such heterogeneity lies in the changes in ocean circulation of the Andaman Sea. Since the Andaman Sea is a part of the Asian monsoon system, both SST and currents change with seasons (Northeast monsoon, first inter-monsoon, Southwest monsoon, and Second inter monsoon).

Our result shows that during the southwest monsoon both the number of connections between the reefs and the probability of larval settlement are high. This indicates that coral larval connectivity in the Andaman Sea is high during the Southwest monsoon compared to other seasons (Northeast monsoon, first inter-monsoon, and second inter-monsoon). The Mergui Archipelago is also found to be a good source and sink during the southwest monsoon. During the Northeast monsoon, North and Middle Andaman receive larvae from the Mergui Archipelago, Phuket, and western Thailand but the probability of larval settlement is low. Though the Mergui Archipelago does not receive many larvae from other island reefs, it is found that there is a good dispersal of larvae within the reefs of Mergui Archipelago during the Northeast monsoon. Moreover, the probability of larval settlement is also good in the Mergui Archipelago. Compared to other Island reefs, Mergui Archipelago can be said to be a good source during most of the seasons. This finding can be helpful while demarcating conservation areas or marine spatial planning in the Andaman Sea because the Mergui Archipelago can act as a source for seeding the affected coral by larval dispersal. During the first inter-monsoon, we found a reduction in the number of possible connections between the reefs compared to the Northeast monsoon. Moreover, the maximum distance the larvae could travel was the least during this season. This was because of the high sea surface temperature during the first inter-monsoon. An increase in SST can increase the metabolic rate of larvae is decreased, and hence the dispersal distance is reduced (Lett *et al.*, 2010). An increase in SST also increases the mortality rate of larvae.

The pattern of coral larval connectivity in the Andaman Sea can be related to surface currents in the Andaman Sea during different seasons. During the Northeast monsoon, the surface currents from the Malacca strait flow northward along the west coast of Thailand and converges with the currents flowing southward from the Bay of Bengal (Isa *et al.*, 2020). Our result shows that the maximum dispersal distance the larvae could travel during this period is from Phuket of Thailand to North and Middle Andaman. This shows that the maximum distance the larvae traveled is also along the path of currents. In addition, during the Northeast monsoon, the main source reefs for North and Middle Andaman were Mergui Archipelago, Phuket, and western Thailand, which all come along the path of the current flowing northward from Malacca strait to the Andaman Sea. During the first inter-monsoon and second inter-monsoon, the surface current did not flow along the coast of Mergui Archipelago (Isa *et al.*, 2020). That is why we could not see any connectivity between Phuket and the adjacent Mergui Archipelago during both seasons.

To understand how the pattern of larval connectivity is affected during climatic conditions like IOD positive and negative year, an extreme negative IOD year 2016 and positive IOD year 2015 was chosen for this study. Since a peak negative IOD phase was seen in September for extreme negative IOD year 2016 and a peak positive IOD phase at the end of September for positive IOD year 2015, comparing the connectivity matrix for the simulation run from August to November for both years gives us an idea on how positive and negative IOD affects connectivity. The result obtained showed that connectivity was highly reduced during negative IOD compared to positive IOD year. A connectivity matrix was also obtained for the simulation run for May to August 9 of 2016 because there was also a peak in July though it was less compared to the peak in September. Comparing these two connectivity matrices obtained in 2016 showed that connectivity is reduced when negative IOD becomes stronger.

<u>SUMMARY</u>

CHAPTER 6

SUMMARY

The pattern of coral reef connectivity in the Andaman Sea varies with the seasons because the pattern of currents and SST in the Andaman Sea also changes with the seasons. A high reduction in maximum dispersal distance the larvae travel is also seen during the first intermonsoon (March to May) due to high SST during this period. Compared to other seasons, connectivity is high during Southwest monsoon season. Furthermore, during negative IOD years, there is a significant decline in connectivity. There is a link between negative IOD and greaterthan-average SST over the eastern Indian Ocean, and because the Andaman Sea lies in the eastern Indian Ocean, this rise in SST would impact coral reef connectivity. A study by O'Connor et al. 2007 indicates that an increase in SST can decrease the pelagic larval duration and reduce the dispersal distance and hence the connectivity. This study also portraits this fact by showing a low connectivity when negative IOD becomes stronger. Increased SST impacts coral reef habitats as well, limiting the amount of substrate available for coral larvae to settle on, lowering recruitment. Because many species rely on coral reefs for survival, maintaining a healthy and resilient coral reef is essential. Connectivity is critical for replenishing destroyed coral because resilient reefs act as the source for seeding the affected reefs by larval dispersal. However, this study shows that climatic circumstances strongly influence connectivity, and since climate change is a reality, it is critical to safeguard coral reefs. The importance of coral reefs is as much as a rainforest to terrestrial organisms.

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CHAPTER 7

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LARVAL CONNECTIVITY AMONG THE CORAL REEFS OF THE ANDAMAN SEA

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ABSTRACT

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ABSTRACT

Coral reefs are one of the world's most vital and ecologically rich ecosystems. They are home to 34 % of all known marine species despite making up only a small percentage of the world's oceans. Reefs on the other hand are undergoing considerable damage, which will be expedited by climate change since they are among the most vulnerable ecosystems to climate change, being particularly vulnerable to ocean warming, ocean acidification, ocean deoxygenation, and other climatic conditions. As a result, maintaining a healthy and robust environment is critical and it requires the process of connectivity to be maintained. Since corals are sessile, connectivity is maintained by the dispersal of coral larvae which are pelagic. Here we study the pattern of coral larval connectivity among the reefs of the Andaman Sea during different seasons and evaluate changes in the connectivity network among these reefs during changes in climatic conditions. The study was conducted in the Andaman Sea which lies on the eastern edge of the Indian Ocean. Since its entire basin lies within the Exclusive Economic Zones of India, Myanmar, Thailand, and Indonesia, it is one of the least-observed regions in the Indian Ocean. Here we did a species distribution model of coral Pocillopora damicornis, to understand the habitat suitability of the coral. Biomod2, which is an ensemble platform for species distribution modelling was used and thus we obtained coral reef data in Andaman Sea. The potential dispersal of the coral larvae between the reefs is obtained using a biophysical modeling approach. The larval connectivity model using the Treml et al. (2012) approach employed in the Marine Geospatial Ecology Tools, an add-on to ArcGIS was used for this purpose and a connectivity matrix was developed to analyze the pattern of connectivity. Our result clearly shows that there is a significant decline in connectivity during the extreme negative IOD phase. In addition, the analysis of the pattern of connectivity during different seasons in the Andaman Sea highlights the fact that currents significantly affect the connectivity pattern. Compared to other seasons, connectivity is high during the Southwest monsoon season. The Mergui Archipelago is found to be a good source of coral larvae compared to other reefs in the Andaman Sea, especially during the South west monsoon season. A high reduction in maximum dispersal distance the larvae travel is seen during the first inter-monsoon (March to May) due to high sea surface temperature (SST) during this period. The results from this study can help in providing the foundation for marine spatial planning including the protected area networks in the region.