Effects of Herbivore Exclusion and Degree of Bleaching on Coral-Algal Community Dynamics

Jatdilok Titioatchasai

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of Master of Science in Biology (International Program)

Prince of Songkla University

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Author Mr. Jatdilok Titioatchasai

Major Program Biology (International Program)

Major Advisor

……………………………….….
(Dr. Jaruwan Mayakun)

Co-advisor

…………………………………..
(Assoc. Prof. Dr. Anchana Prathep)

Examining Committee:

…………………………....Chairperson
(Prof. Dr. Jeong Ha Kim)

………………………..…..Committee
(Dr. Jaruwan Mayakun)

………………………..…..Committee
(Assoc. Prof. Dr. Anchana Prathep)

………………………….....Committee
(Assoc. Prof. Dr. Pornsilp Pholpunthin)

The Graduate School, Prince of Songkla University, has approved this thesis as partial fulfillment of the requirements for the Master of Science Degree in Ecology (International Program)

……………………………………...
(Prof. Dr. Damrongsak Faroongsarng)
Dean of Graduate School

This is to certify that the work here submitted is the result of the candidate's own investigations. Due acknowledgement has been made of any assistance received.

....Signature
(Dr. Jaruwan Mayakun)
Major Advisor

....Signature
(Mr. Jatdilok Titioatchasai)
Candidate

I hereby certify that this work has not been accepted in substance for any degree, and is not being currently submitted in candidature for any degree.

....Signature
(Mr. Jatdilok Titioatchasai)
Candidate

ชื่อวิทยานิพนธ์ ผลของสัตว์กินพืชและการฟอกขาวต่อพลวัตประชาคมสาหร่ายและปะการัง

ผู้เขียน นายเจตดิลก ฐิติอัชฌาสัย

สาขาวิชา ชีววิทยา (นานาชาติ)

ปีการศึกษา 2561

บทคัดย่อ

ในปัจจุบันปรากฏการณ์ปะการังฟอกขาวและการรบกวนมีความถี่ในการเกิดเพิ่มขึ้น ซึ่งส่งผลโดยตรงต่อระบบนิเวศปะการัง โดยทำให้เกิดการเปลี่ยนแปลงจากประชาคมปะการังเด่นเป็นประชาคมสาหร่าย การจับปลาเกินขนาดเป็นการรบกวนที่สำคัญที่ส่งผลต่อการเปลี่ยนแปลงของประชาคมปะการัง จุดประสงค์ของการศึกษาเพื่อศึกษาผลของสัตว์กินพืชและความรุนแรงของการฟอกขาวต่อการเปลี่ยนแปลงประชาคมของปะการังและสาหร่าย โดยทำการศึกษาที่บริเวณแนวปะการังของเกาะแตน อุทยานแห่งชาติหมู่เกาะทะเลใต้ จังหวัดนครศรีธรรมราช ศึกษาผลของสัตว์กินพืชโดยใช้กรงสามแบบ ได้แก่ กรงปิด กรงเปิดข้าง และไม่ใส่กรง (กรงมีขนาด 25 x 25 x 25 ตารางเซนติเมตร และตาข่ายมีขนาด 2 x 2 ตารางเซนติเมตร) และศึกษาผลของการฟอกขาวโดยเลือกใช้พื้นที่การศึกษาสามแบบได้แก่ พื้นที่ที่มีปะการังสมบูรณ์ (มีปะการังปกคลุม 100%), พื้นที่ธรรมชาติ (มีปะการังปกคลุมประมาณ 10% และสาหร่ายประมาณ 90%) และ เปิดพื้นที่ว่างโดยการขัดแผ่นปะการังตาย ในการศึกษาครั้งนี้ ได้ติดตามการเปลี่ยนแปลงการปกคลุมพื้นที่ของปะการังและสาหร่ายรวมถึงรูปแบบการเปลี่ยนแปลงแทนที่ จากผลการศึกษาพบสาหร่าย 26 ชนิด โดยมีสาหร่ายสีแดงกลุ่ม turf, *Padina* และ *Lobophora variegata* เป็นสาหร่ายกลุ่มเด่น โดยสาหร่ายกลุ่ม turf เป็นกลุ่มแรกที่เข้ามาครอบครองพื้นที่หลังจากการเปิดพื้นที่ว่างและมีเปอร์เซ็นต์การปกคลุมสูงตลอดปี ซึ่งอาจเนื่องมาจากสาหร่ายสีแดงกลุ่ม turf มีการเจริญเติบโตและลงเกาะที่รวดเร็ว และมีความสามารถในการแข่งขันสูง ซึ่งส่งผลให้ต่อการเจริญเติบโตและการลงเกาะของสาหร่ายกลุ่มอื่น สัตว์กินพืชส่งผลต่อการปกคลุมของสาหร่ายสกุล *Padina* อย่างมีนัยสำคัญ ($p<0.05$) โดยพบการปกคลุมของ *Padina* ที่มีลักษณะเป็นใบพัด หรือ fan-shape สูงในการทดลองที่ใส่กรง และพบเปอร์เซนต์การปกคลุมน้อยในการทดลองที่ไม่ใส่กรง ความมากชนิดของสาหร่ายในแต่ละชุดการทดลองของสัตว์กินพืชไม่มีความแตกต่างกันอย่างมีนัยสำคัญ อาจเนื่องมาจากผลของพฤติกรรมการยึดครองพื้นที่ของกลุ่มปลาสลิดหิน เปอร์เซ็นต์การปกคลุมของปะการังมีค่าลดลงในกรงปิดของพื้นที่ธรรมชาติและของพื้นที่ปะการังสมบูรณ์ แต่อย่างไรก็ตามไม่พบผลของปลากินพืชต่อเปอร์เซ็นต์การปกคลุมของปะการัง ($p>0.05$) นอกจากนี้ยังพบการลงเกาะของปะการังวัยอ่อนหลังหนึ่งเดือนของการเปิดพื้นที่ว่างและ

Thesis Title Effect of Herbivore Exclusion and Degree of Bleaching on Coral-Algal Community Dynamics

Author Mr. Jatdilok Titioatchasai

Major Program Biology (International Program)

Academic Year 2018

ABSTRACT

In recent years, the disturbances and coral bleaching frequently occur and directly influence benthic communities shifting coral to algal dominated communities. Overfishing has been known as the one of factors driving coral-algal phase shifts. The aim of this study was to investigate the effect of herbivory and degree of bleaching on coral-algal community dynamics. These effects were experimentally tested at the subtidal reef crest at Koh Taen, Mu Ko Thale Tai National Park, Nakhon Si Thammarat Province, Gulf of Thailand. To test the effect of herbivore, cages (cage size was $25 \times 25 \times 25$ cm^3 with 2×2 cm^2) were used to exclude herbivore. There were three categories; fully cage, partial cage, and no-cage. To investigate the effect of degree of bleaching, patches; healthy coral (initially having 100% cover of live coral), natural condition (initially having 10% cover of live coral), and cleared dead coral patches (initially having 100% of dead corals). Percentage covers of corals and algae and succession were monitored for a year. In this study, twenty six algal species were found with three dominant groups: red turf algae, *Padina*, and *Lobophora variegata*. Red turf algae were dominated group and persisted for a year. It might be because red turf algae have a fast growing ability and rapid colonization on cleared spaces. In addition, red turf algae have a high competitive ability that might reduce growth rate and suppress the recruitment of the later species. For the effect of

herbivore, there was significant difference among herbivore excluded treatments (p <0.05). Fan shaped *Padina* was dominant inside the cages while *Vaughaniella* stage of *Padina* had a low cover in uncaged patches. Decreasing in coral percentage cover was showed in full caged of healthy coral and natural patches, however, there was no significance among caged treatments (p>0.05). Algal abundance was not apparently affected by herbivory. This result might be because of the territorial aggressive behaviour of damselfish excluding other herbivorous fishes from their territories and maintaining dense of turf algae. There was coral juvenile settlement after one month of clearing and died after one month of settlement. Algal colonization can contribute to the failure, delay, and inhibit corals to recover from the disturbances. So, herbivory and degree of bleaching can influence coral-algal community structure.

ACKNOWLEDGMENTS

This thesis would not be possible without the help and encouragement of these individuals. The person I most appreciated is Dr. Jaruwan Mayakun, my advisor who give advice, which is very useful in research and also helps solve various problems that occurred during data collection and writing phase. Thank you for the opportunity and advice throughout the study and also for giving me motivation to do research. I am deeply appreciative to my co-advisors, Assoc. Prof. Dr. Anchana Prathep her valuable supporting and suggestions in developing this work and revising the manuscript.

I would like to thank thesis examining committee including, Prof. Dr. Jeong Ha Kim, Department of Biological Science, Sungkyunkwan University and Assoc. Prof. Dr. Pornsilp Pholpunthin , Department of Biology, Faculty of Science, Prince of Songkla University for their suggestion to improve my work.

I would like to thank Excellence Centre for Biodiversity of Peninsular Thailand (CBIPT) for supporting the scuba diving gears during my field work. I am also thankful to Wattana Chaitongkaew, Kattika Pattarach, Panutchanat Chinklang, Suttisak Olari, Nattapong Maneeroth, Nutdanai Puttisawaong for their help on the field work.

I would like to thank all members of Seaweed and Seagrasses Research Unit, Department of Biology, Faculty of Science, Prince of Songkla University for their counsel, encouragement, and data collection.

I would like to thank Science Achievement Scholarship of Thailand (SAST) and Graduate School of Prince of Songkla University, for the financial support.

Finally, my deepest appreciation is to my parents for their supporting and encouragement all the time.

Jatdilok Titioatchasai

CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES

INTRODUCTION

Coral reefs have crucial roles in marine ecosystems and provide ecological services such as coastal protection, seafood products, and tourism (Costanza et al., 1997; Moberg and Folke, 1999; Kaiser et al., 2011). However, coral reefs are the one of the most vulnerable marine ecosystems and coral degradations have been reported worldwide causing from natural disturbances such as crown of thorn starfish, wave action, and coral bleaching and anthropogenic activities such as careless tourism, sediment run-off, overfishing (Diaz-Pulido and McCook, 2002; Pauly et al., 2005; Bruno and Selig, 2007; Bruno et al., 2009; Wiedenmann et al., 2013). These disturbances can cause coral mortality and bleaching that decrease coral abundance, species richness, and species composition and also influence community dynamics of reefs (Nystrom et al., 2000; Diaz-Pulido and McCook, 2002). In recent years, the disturbances and coral bleaching frequently occur and directly influence benthic communities. The disturbed or bleached coral reefs are likely to be dominated by turf and filamentous algae (McClanahan et al., 2001; Diaz-Pulido and McCook, 2002). This phenomenon refers to a coral-algal phase shift.

Over the past several decades, loss of herbivory has been suggested as the one of causative factors driving phase shifts from coral to algal dominated communities on tropical reefs (Littler and Littler, 1984; McCook, 1999; Smith et al., 2001, 2004; Stimson et al., 2001; Szmant, 2001; Thacker et al., 2001; McManus and Polsenberg, 2004; Idjadi et al., 2006). The role of herbivory in determining the community structure and dynamics on coral reefs is well-documented (McClanahan et al., 2003; Mumby et al., 2006; Mantyka and Bellwood 2007; Mayakun et al., 2010). Numerous studies have demonstrated that herbivory can increase community diversity by clearing spaces for algal and coral recruitments (Diaz-Pulido and McCook, 2002; McClanahan et al., 2003; Hughes et al., 2007; Burkepile and Hay, 2010; Rasher et al., 2012; Ramos et al., 2014) and removing dominant species. Herbivores can also decrease abundance, species composition, standing stock and diversity of algae by grazing preferred algal species and altering algal succession (Littler et al., 1991; McCook, 1999; Stachowicz and Hay 1999; Lirman, 2001; McCook et al., 2001; Belliveau and Paul, 2002; McClanahan et al., 2002; McClanahan et al. 2003; Ceccarelli et al., 2011). However, all over the world, overfishing has severely occurred reducing the densities of herbivorous fishes and decreasing grazing on coral reefs. Then, reduced herbivory might result in the overgrowth of algae. When reefs are overgrown by macroalgae, it can lead coral to mortality and reef degradation by reducing coral cover and coral growth (Lirman, 2001; Jompa and McCook 2002; Nugues and Bak, 2006; Titlyanov et al., 2007), inhibiting coral recruitment (Miller and Hay, 1996; Fitz et al., 1983), coral settlement (Fitz et al., 1983), decreasing coral reproduction (Tanner, 1995), and triggering the coral disease (Nugues et al., 2004).

Mass coral bleaching driven by elevated sea temperatures and high irradiance is a major factor affecting reef ecosystems leading reef degradation. The reefs might change from coral to algae dominance because there are dead coral skeletons which are favorable substrates for algae to colonize (Littler and Littler, 1984; Glynn, 1993; Nystrom et al., 2000; McClanahan et al., 2001; Diaz-Pulido and McCook, 2002; Hughes et al., 2007). Colonizing algae might inhibit coral settlement, coral growth (McCook et al., 2001), and delay the regeneration of coral tissue (Diaz-Pulido et al., 2009). Disturbed or bleached corals might recover or die depending on magnitude, frequency of disturbance, and the species of coral and algae (McCook et al, 2001;

Diaz-Pulido and McCook, 2002; Jompa and McCook, 2003). Recently, coral bleaching events are predicted to become more frequent (Brown, 1997; Hoegh-Guldberg, 1999). However, the pattern and dynamics of algal succession in tropical subtidal coral reef community are not well understood. Additionally, the ability and potential of community to recover from disturbance are still unclear.

In Thailand, degraded coral reefs along the Andaman Sea and the Gulf of Thailand have been reported causing from natural (strong wave, disease, coral bleaching) and anthropogenic disturbances (loss of herbivory and nutrient enrichment) for decades (Chou et al., 2002; Cheevaporn and Menasveta, 2003; Yeemin et al., 2006; Boonchuwong and Dechboon, 2008; Yeemin et al., 2009; Reopanichkul et al., 2010; Plathong et al., 2011). These reefs undergo changes from coral to algal dominance (Yeemin et al., 2006). However, much less is known about the effect of herbivore exclusion and degree of bleaching on coral-algal community dynamics; insights into the recovery of corals, and algal and coral recruitments. Understanding the community dynamics and the potential of reef to recover from disturbances are needed and becoming important. Then, the aim of this study was to determine the effects of herbivory and degree of bleaching on coral-algal community dynamics, insight into coral-algal percentage covers, number of coral and algal species, and coral and algal recruitments in a subtidal coral reef community.

LITERATURE REVIEW

Coral reefs where have high biodiversity and productivity are very important marine ecosystems that can provide food and shelter for other reef organisms, sand, and can protect islands and coastal areas during typhoons and storms. Reefs not only provide biological value but also provide economic value such as fisheries, and tourism. However, past several decades, coral reefs around the world are threatened from natural disturbances such as storm, crown-of-thorns starfish, wave action (Endean, 1982; Diaz-Pulido et al., 2007; Kayal et al., 2012) and anthropogenic disturbances such as fishing, burning of fossil fuels, careless tourism, and nutrient enrichment (Goreau and Hayes, 1994; Dubinsky and Stambler, 1996; Brown, 1997; Hoegh-Guldberg, 1999). These disturbances associated together with global climate change are causing coral bleaching and mortality affecting reef community structure (Richmond, 1993; Brown, 1997; Hoegh-Guldberg, 1999; Cesar et al., 2003; Wilkinson and Souter, 2005; Bruno and Selig, 2007; Bruno et al., 2009). Reef degradation and bleaching have dramatically increased in recent years and the reefs worldwide have shifted from coral to algal dominated communities (McCook, 1999; McClanahan et al., 2001; Diaz-Pulido and McCook, 2002; Hughes et al., 2007; Bruno et al., 2009; Cheal et al., 2010).

When degraded and bleached corals occur, algae will flourish and succeed occupying cleared substrates inhibiting coral recruitment and settlement and reducing resilience that has resulted in increased algal cover on many coral reefs (McManus and Polsenberg, 2004). The recovery of coral reefs after disturbance and timeframe of phase-shift might depend on many factors such as frequency, magnitude, and intensity of disturbance (Foster, 1975; Benedetti-Cecchi and Cinelli, 1993; Kim and

DeWreede, 1996), seasonal availability of propagules and life-history traits of dominant species (Kim et al., 2017), and level of coral recruitment, as well as the intensity of herbivory.

The effect of top-down control by herbivory has been used to explain the phase shifts. High intensity of grazing giving positive to corals by maintaining coral abundance and controlling algal abundance while decreasing in grazing activities affected directly coral reef community, allowing algal overgrow and kill corals then community will shift from coral dominated to algal dominated community (Figure 1) (Littler and Littler, 1984).

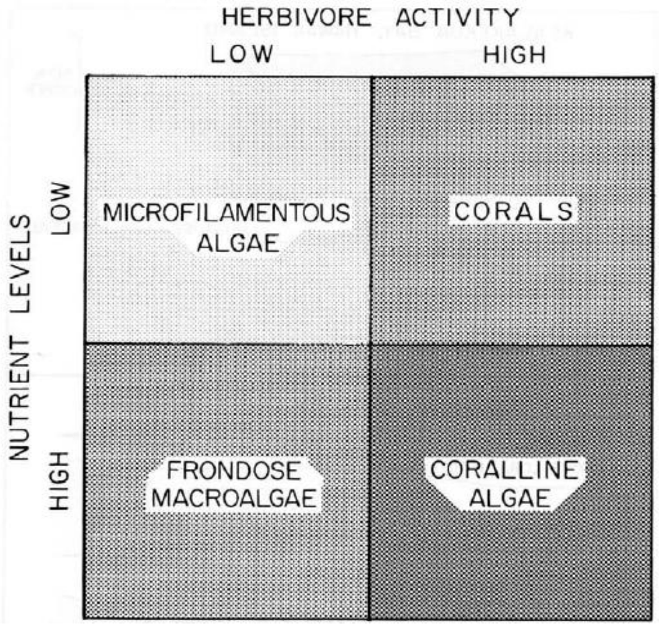

Figure 1. Conceptual diagram of the proposed influence of fish excretion and nutrient run-off on corals and macroalgae (Littler and Littler, 1984).

Numerous studies have demonstrated that herbivory can regulate algal abundance, composition, diversity, and mediate competition between algae and corals

(McCook, 1999; McCook et al., 2001; Thacker et al., 2001; Miller et al., 1999; Belliveau and Paul, 2002; McClanahan et al., 2002; McClanahan et al., 2003; Mantyka and Bellwood, 2007; Sotka and Hay, 2009; Burkepile and Hay, 2010). High grazing rates can control algal growth, cover, abundance by removing algal production, enhancing coral growth, and helping facilitate recovery of corals (Mcclanahan et al., 2002; Burkepile and Hay, 2010; Vermeij et al., 2010; Ceccarelli et al., 2011; Rasher et al., 2012). while, loss of herbivores due to overfishing (Pauly et al., 2002; Pauly et al., 2005) can cause an increase in algal covers and algae become abundant preventing coral settlement and growth (Fitz et al., 1983; Miller and Hay, 1996; McCook, 1999; Stachowicz and Hay, 1999; Lirman, 2001; Lotze et al., 2001; Jompa and McCook, 2002; McClanahan et al., 2003; Diaz-Pulido and McCook, 2002; Nugues and Bak, 2006; Hughes et al., 2007; Titlyanov et al., 2007; Burkepile and Hay, 2008,2009; Adam et al., 2011; Ceccarelli et al., 2011). However, not many studies demonstrate the effects of herbivory when dealing with different degrees of coral bleaching and the dynamics of algal-coral recruitment and succession on bleached corals (Diaz-Pulido and McCook, 2002).

Decreased coral cover occur around the world causes by coral bleaching (Bruno and Selig, 2007; Bruno et al., 2009) and there are many factors inducing coral bleaching such as increasing seawater temperature, changing salinity, solar ultraviolet radiation, and sedimentation. These factors can affect zooxanthellae in coral tissue and then cause coral bleaching (Glynn and D’Croz, 1990; Jokiel and Coles, 1990; Fitt and Warner, 1995; Gleason and Wellington, 1993; Van Woesik et al. 1995; Brown, 1997; McClanahan et al. 1999, McClanahan et al. 2001, Muhando and Mohammed, 2002).

In Thailand, mass coral bleaching and anthropogenic activity decrease coral cover from both the Andaman Sea and the Gulf of Thailand (Tissier and Brown, 1996; Yeemin et al., 2006; Tanzil et al., 2009; Hoeksema and Matthews, 2011; Plathong et al., 2011). For the bleaching event in 2010, around 75 % of coral bleaching were found in the Andaman Sea (Chanmethakul and Plangngan, 2016) and mostly Thai reefs already degraded and dominated by algae. There are several researches studying on coral-algal community by looking at the percentage cover, however not many studies working and investigating on coral-algal community dynamics and recruitment patterns of both organisms and the effects of herbivore exclusion and degree of bleaching on coral-algal community structure. Hence, in this study, we investigated and determined the effects of herbivore exclusion and degree of bleaching on coral-algal community dynamics.

Hypothesis

It was hypothesized that coral-algal community dynamics can be altered by herbivore and degree of bleaching, so where there are differences in the level of herbivore activity and degree of bleaching, there will be differences in the pattern of algal-coral recruitment and species composition. It will also be predicted that when there is loss of herbivores, community will shift from coral to algal dominated community.

Objective

The aim of this study was to demonstrate the effect of herbivore and degree of bleaching on coral-algal community dynamics; insights into coral-algal percentage covers, number of coral and algal species, and coral and algal recruitments in a subtidal coral reef community.

RESEARCH METHODOLOGY

Study site

The study was carried out at the subtidal reef crest at Ko Taen, Mu Ko Thale Tai National Park, (9° 19′ 20″ N, 99° 46′ 80″ E), Gulf of Thailand, Southern Thailand (Figure 2). There are two seasons, a rainy season dominated by northeast monsoon (October – January) and a dry season dominated by southwest monsoon (February – September) and the tides are semi-diurnal with tide range was about 0.8–3 m (Coppejans et al., 2010). In this area, approximately sixty species of benthic algae were reported including 23 species of Chlorophyta, 19 species of Ochrophyta, 16 species of Rhodophyta and 2 species of Cyanobacteria (Coppejans et al., 2010; Prathep et al., 2011) with four common genera, red turf algae, *Padina*, *Sargassum* and *Turbinaria*. For corals, massive coral, Genus *Porites* is dominant. Mean percentage cover of *Porites* was around ten percent in this area (Personal observation). *Abudefduf vaigiensis*, *Abudefduf bengalensis*, *Abudefduf sexfacsiatus*, and *Neoglyphidodon nigroris* are dominant herbivorous fish species in this study site (Personal observation) (Figure 3 and 4).

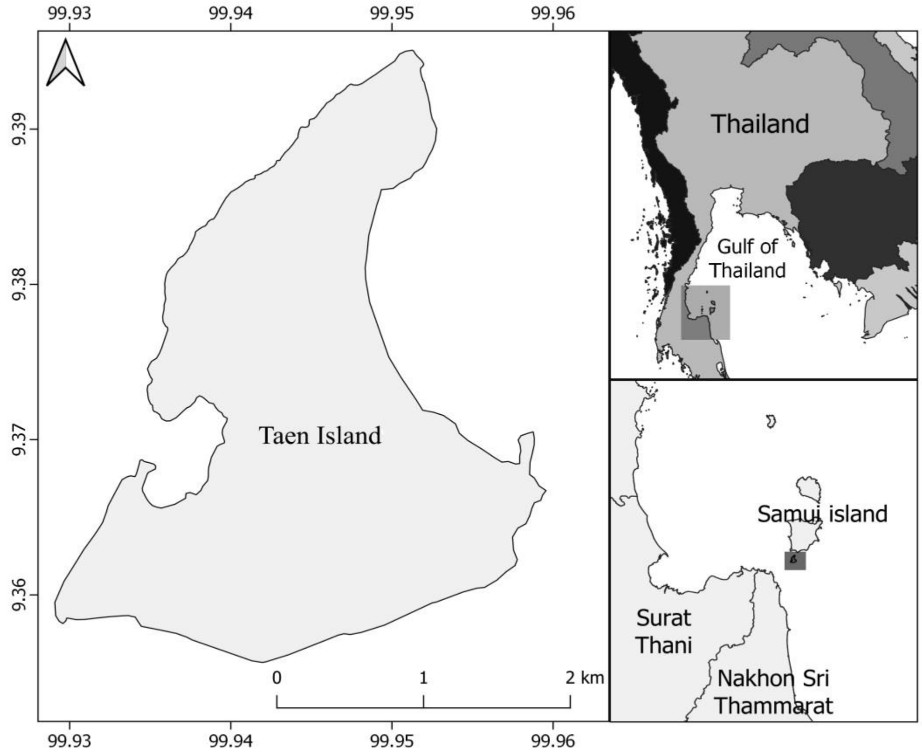

Figure 2. Map of study site Koh Taen, Mu Ko Thale, Surat Thani Province, Southern Thailand.

Figure 3. The dominant herbivorous fishes in this study site were *Neoglyphidodon nigroris, Abudefduf sexfasciatus* and *Abudefduf vaigiensis*.

Figure 4. Natural reef condition with 10% of coral cover.

Materials and methods

The effects of herbivore exclusion and degree of coral bleaching on coral-algal community dynamic were experimentally tested in the subtidal reef. To test the effect of degree of bleaching; healthy coral (initially having 100 percentage cover of live coral, tissue with no dead and bleaching), natural condition (initially having 10 percentage cover of live coral, tissue with no dead and no algal colonization), and cleared dead coral patches (initially having 100 percentage cover of dead coral, no coral and algal settlements) were chosen (Figure 5). Dead massive coral patches (20cm × 20 cm) were cleared by hand chiseling and scraped by wire brush. The uncleared patches were marked as control. Thirty cleared, thirty natural (10 percentage cover of healthy coral) and thirty healthy coral (100 percentage of healthy coral) were marked and labeled with concrete nails and was besieged patch with white nylon.

To investigate effect of herbivore exclusion, three categories of herbivory were used: fully caged, partial caged, and uncaged (Figure 6). There were ten full cages, ten partial cages, ten uncages in each bleaching treatment. Cages made of a stainless-steel frame covered with wire mesh. Cage size was 25 × 25 ×25 cm^3 (larger than the patches (20×20 cm^2) to eliminated edge effects). Mesh size was 2 × 2 cm^2 that allows water flow through the cage and can exclude herbivorous fishes (Mayakun et al., 2012). Partial cage was opened both lateral sizes, allowing the herbivore fishes to go inside cage (Jompa and McCook, 2002; Ramos et al., 2014) and partial cage was used to test the effect of an artifact on algal cover (Sotka and Hay, 2009). Cages were fixed on the top of massive coral patches with concrete nails and plastic cable tiles. Cages were cleaned of algae, sediment, and settling organism every month with wire brush. Sediment was also cleared from patches every month. To test effect of artifact, water current and light intensity were measured. Water current and light intensity outside and inside cages were measured using gypsum ball (Komatsu and Kawai, 1992) and HOBO data logger (Pendant® Temperature and light data logger Model: UA-002-64, Onset Computer Corporation, United State America).

In all patches, percentage cover of each algal and coral species and species composition were monitored every month from April 2017 to July 2018. The photos of all patches were taken using an underwater digital camera (Olympus TG-5, Japan). Unknown algal specimens were collected and taken to the laboratory for identification using algal taxonomical identification guides such as Coppejans et al., 2010. Fish density and fish species were recorded by digital camera (Olympus TG-5, Japan) along six of 30 m × 2m and were identified using fish identification (based on Human and Deloach, 2002). Environmental factors such as light intensity and sea water temperature were recorded using Onset HOBO data logger. Water samplings were kept in dark and cool and then sent to Central Equipment Division, Faculty of Science, Prince of Songkla University to analyze nitrate and phosphate using Photometric method.

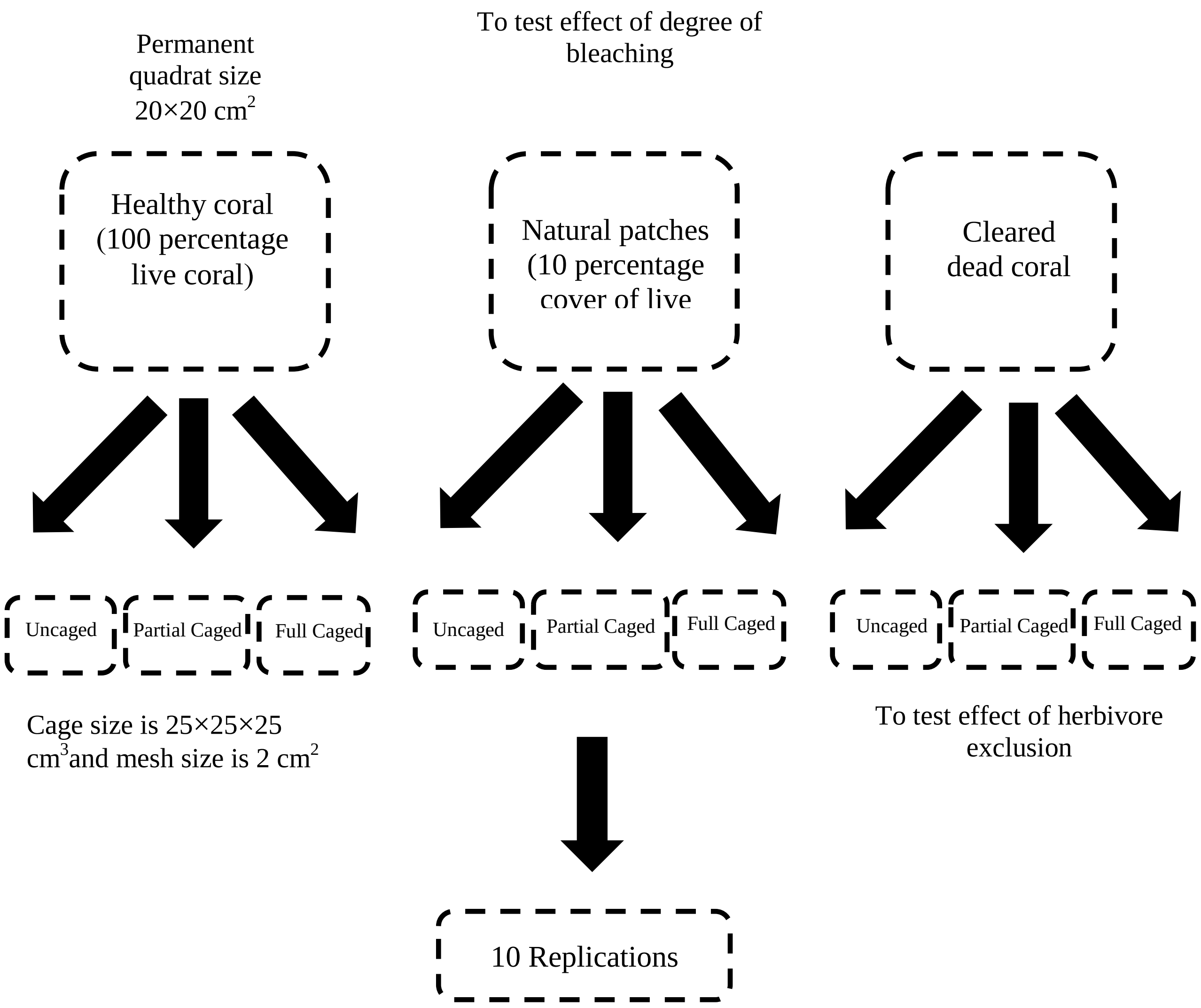

Figure 5. Flow chart of experimental design

Figure 6. Herbivore exclusion, A) Full-caged, B) Partial caged, and C) Uncaged.

Statistical analysis

Percentage covers of coral and four alga dominant species were analyzed using a Repeated Measures Analysis of Variance (RM-ANOVA). Two-way Repeated Measured ANOVA (Herbivory × Time) was applied for each of the four dominant species and coral for each different coral bleaching treatments. Mauchly's test indicated that the assumption of sphericity has been violated, therefore degrees of freedom were corrected using the Greenhouse-Geisser estimates of sphericity. Species diversity was calculated using Shannon-Weiner index. Light intensity and water velocity between outside and inside cage were tested by *t*-test. All data were analyzed using the computer program SPSS for Windows version 16.0.

RESULTS

The results are divided into two parts:

Part1) Effects of herbivore exclusion and degree of bleaching on coral-algal community dynamics.

Part 2) Pattern of algal succession in the tropical subtidal coral reef community at Koh Taen, Mu Ko Thale Tai National Park, the Gulf of Thailand.

Part1) Effects of herbivore exclusion and degree of bleaching on coral-algal community dynamics

Light intensity and water current

Cages decreased water current by 0.79±0.53% compared between outside and inside. Cage decreased light intensity by 3.78-18.85% compared with uncaged patches. Water current and light intensity were not significant different between outside and inside cage (p>0.05, *t*-test). Total light intensity is much greater than the level needed for saturation of photosynthesis.

Seawater temperature, light intensity, nitrate and phosphate concentrations

Seawater temperature at study site varies between 29–33°C. The light intensity varied around 760–1300 µmole photon·m^{-1}·s^{-1}. The highest average seawater temperature was 32.58±0.09°C in May 2017 while the lowest average was 28.90±0.02 °C in November 2017. For light intensity, the highest light intensity was found in May 2018 with 1295.97±35.17 µmole photon·m^{-1}·s^{-1} while November 2017 had the lowest average light intensity with 63.82 ± 86.09 µmole photon·m^{-1}·s^{-1} (Table 1).

Nitrate and phosphate concentrations at study site were ≤ 0.015 and ≤ 0.030 mg/L over the year (Table 2).

Diversity and abundance of fishes

Nineteen fish species were found in this study including ten herbivorous fishes; *Abudefduf vaigiensis*; *Abudefduf sexfasciatus*; *Abedefduf bengalensis Neoglyphidodon nigroris*; *Neopomacentrus bainkieri*; *Neopomacentrus cyanomos*; *Neopomacentrus filamentosus*; *Siganus javus*; *Pomacentrus chrysurus* ; *Pomacentrus moliuccensis* and nine carnivorous fishes including *Alepes vari*; *Chaetodon octofasciatus*; *Chelmon rostratus*; *Halichoeres chloropterus*; *Halichoeres leucurus* ; *Halichoered melanurus* ; *Halichoeres nigrescens*; *Lutjanus carponotatus* ; *Lutjanus russellii*.

Pomacentridae was common family in this study site and there were four common damselfishes; such as *A. vaigiensis*, *A. sexfasciatus*, *A. bengalensis, and N. nigroris. A. bengalensis* had the highest density (59.44±21.16 individual/100m^2) (Figure 7). Grazing scars of parrotfish have been found on uncaged patches.

General patterns of coral and benthic macroalgae community

Twenty-six algal species were found in this study. Algal species diversity was around 0.75-2.26 and the highest algal species diversity was found in October 2017 (*H´*=2.26) (Figure 10) and decreased afterward. There was significant difference in algal diversity among months (Figure 8). Red turf algae were dominant specie with the highest average percentage cover in October 2017 (49.50±7.52%) (Mean ± SE) (Figure 11D) and their percentage cover fluctuated through time while cover of

Padina sp., *Lobophora variegata* (J.V.Lamouroux) Womersley ex E.C.Oliveira, and *Cladophora* sp. had around 20% throughout the year. For massive coral, the percentage cover of *Porites* spp. remained around ten percent through time (Figure 9D).

Effects of herbivore exclusion

Algal species diversity of the healthy coral patches differed between the uncaged, partial caged, and caged patches ($p<0.05$, *t*-test) while there were no significant differences in algal species diversity between herbivory treatments of both the natural condition and dead coral patches ($p>0.05$, *t-test*). The highest algal species diversity was found in the uncaged patches of the natural condition ($H'=0.26$). Herbivory significantly affected *Padina* cover of both dead coral patches and natural condition patches ($p<0.05$ and $p<0.05$, respectively) (Table 3 and 4) while herbivory had no effect on red turf algae ($p>0.05$ and $p>0.05$, respectively) and *L. variegata* ($p>0.05$ and $p>0.05$, respectively) (Table 3 and4). The cover of *Padina* in the full caged was higher than uncaged patches of all degrees of coral bleaching treatments (Table 3, 4, and 5). In addition, percentage cover of *Padina* and its morphology were different between the full caged and uncaged treatments. From observation, filamentous form of *Padina* presented in the uncaged and the partial caged treatments while fan shape form appeared so dense in the full caged patches. *Padina* had the highest percentage cover in the full caged of dead coral treatment and remained high cover until October 2017 (43.12±11.80%) (Figure 9C). Red turf algae dominated in the uncaged and partial caged patches (59.33±12.04% and 56.33±10.59%) while *Padina* dominated in the full caged patches (59.75±9.49%) (Figure 9C).

For the dead coral patches (initially having no coral and benthic macroalgae), algal species diversity index among caged treatments was no significant (*p*>0.05). For uncaged of cleared coral patches, species diversity fluctuated over a year. Species diversity increased continuously from first month and had the highest species diversity in August 2017 (H'=1.75). Species diversity in partial caged increased to the highest value in August 2017 (H'=1.50) and decreased afterward. In full caged treatment, species diversity increased steadily from first month and had the highest species diversity index in October 2017 (H'=1.62). Succession of algae varied among caged treatments. In uncaged and partial caged, succession began with red turf algae, *Padina*, and *L. variegata.* Red turf algae dominated over a year with up to 35% of relative abundance. The cover of red turf algae fluctuated through time. In uncaged and partial caged patches, red turf algae occupied with high percentage cover after one month of settlement. Red turf algae had the highest percentage cover in November 2017 and February 2018 (59.33±12.04% and 56.33±10.59%, respectively). *Padina* occupied patches with low cover over a year. While *L. variegata* cover increased steadily by increasing from 1.11±1.11% to 16.44±7.21% in uncaged plots and from 0.11±0.11% to 17.22±5.84% in partial caged plots in May 2018. For full caged patches, algal succession began with red turf algae, *Padina,* and *L. variegata. Padina* was dominant group during early stage of succession and had the highest percentage cover in August 2017 (63.00±8.68%) and decreased afterward to below ten percent during February - April 2018. However, the cover of *Padina* then increased to 42.38±13.90% in May 2018. There was a significant different in *Padina* percentage cover among caged treatments (*p*<0.05). *L. variegata* increased over a year, but no more than twenty percent. There was no significant difference in *L.*

variegata cover among caged treatments (*p*>0.05, Figure 9A, 9B, 9C, and Table 3). Coral settlement has been found in all caged treatments with around one percentage cover after two to three months of settlement.

For the natural condition (initially having 10 percentage cover of coral), There were no significant different about algal species diversity index among caged treatments (*p*>0.05). Species diversity of uncage patches increased continuously from May 2017 to October 2017 with the highest percentage cover (*H´*=2.26) and decreased afterward. Species diversity in partial caged increased to the highest value in February 2018 (*H´*=1.88) and decreased afterward. In full caged treatment, species diversity increased steadily from first month and had the highest species diversity index in June 2017 (*H´*=1.88). Red turf algae, *Padina*, and *L. variegata* were the first group of colonizers. Red turf algae predominated with highest relative abundance. Red turf algae percentage cover in uncaged and partial caged patches and had the highest percentage cover in October and November 2017 with 59.50±7.52% and 50.10±9.56%, respectively. Red turf algae percentage cover fluctuated throughout a year. *Padina* cover was significant difference among caged treatment (*p*<0.05). Full caged patches were dominated by *Padina* and had the highest percentage cover was 38.80±10.32% in June 2017 and decreased significantly to 1.50±1.06% in February 2018. While partial caged and uncaged patches had highest percentage cover 10.70±7.21% and 14.12 ±5.33 in May 2018 and June 2017 respectively. *L. variegata* increased throughout a year. However, *L. variegata* had no significant difference among caged treatments (*p*>0.05). The percentage cover of *Porites* spp. in partial caged and uncaged patches remained nearly ten percent throughout a year. Coral percentage cover in full caged decreased to 6.40±0.94% in May 2018; however, there was no significant difference of coral cover among all caged treatments ($p>0.05$, Figure 9D, 9E, 9F, and Table 4).

For the healthy coral patches (initially having 100 percentages cover of coral), algal species diversity index among caged treatments were no significant difference ($p>0.05$). For uncaged of cleared dead coral patches, there was increasing trend in species diversity over a year and had the highest species diversity in May 2018 ($H'=0.50$). Species diversity in partial caged increased to the highest value in April 2018 ($H'=0.63$). In full caged treatment, species diversity increased steadily from first month and had the highest species diversity index in May 2018 ($H'=0.75$). All of caged treatments were dominated by *Porites* spp. Coral cover remained consistently in uncaged and partial caged patches while percentage cover of coral decreased in full caged patches in November 2017 (91.11±5.82%) from 99.40±0.56% in October 2017 and decreased afterward to 80.33±12.38% in May 2018; however, there was no significant difference among caged treatments ($p>0.05$, Table 5). Dead coral tissues in the full caged patches were replaced by turf algae within first month with low percentage cover (0.56±0.56%). Red turf algae appeared in all caged treatments and remained around two percent in uncaged and partial caged patches while remained lower ten percent in the full caged patches. *Padina* cover was significantly different among caged treatments ($p<0.05$, Table 5). *Padina* was observed in October 2017 and August 2017 in the partial and the full caged patches. *Padina* remained below one percent throughout a year in the partial caged patches while *Padina* showed increasing trend in the full caged patches. *L. variegata* also was observed in the partial and the full caged patches in the last three months with around one percent until May 2018 (Figure 9G, 9H, and 9I).

Effects of degree of bleaching

After coral bleaching occurred, coral tissue was replaced by turf algae rapidly. Algal species diversity increased in the first month of dead coral patches while there was less species diversity in the healthy coral patches (*H´*= 0.63 and *H´*= 0.00, respectively) (Figure 8). Red turf algae were dominant group in all the degree of bleaching treatments and fluctuated through time while coral percentage cover had slightly increased in the natural patches and the healthy coral patches.

In the dead coral patches, algal species diversity increased more rapidly after one month of clearing. The lowest and highest species diversity were found in May 2017 and August 2017 with *H´*= 0.63 and *H´*= 1.75, respectively. Four algal species recruited in the plots. Red turf algae dominated in the first month with 36.67±10.83% and fluctuated throughout a year. *Padina* sp., *L. variegata* and *Cladophora* sp. recruited in May 2017 with 13.22±7.11%, 1.11±1.11%, and 5.00±2.89%, respectively (Figure 9A). Coral settlement was found in June 2017 (0.56±0.56%) and disappeared after two months of settlement.

Algal species diversity in the natural condition patches increased rapidly after one month. There were the highest species diversity in October 2017 (*H´*= 2.26) and the lowest species diversity (*H´*= 0.75) in April 2018. Natural condition patches were dominated by red turf algae with average percentage cover around 49.50±7.53%. *Cladophora* sp., *L. variegata* and *Padina* sp. recruited after one month with the average percentage cover around 2.25±0.75%, 8.14±3.86%, and 8.75±3.10%, respectively (Figure 9D). Red turf algae had the highest percent cover in October 2017 (49.50±7.53%) and fluctuated through time. Coral percentage cover had increased steadily trend throughout a year; however, there was no significant difference through time (p>0.05, Table 4).

Healthy coral patches had low species diversity throughout a year. The highest species diversity presented in May 2018 with H'= 0.50. The lowest species diversity was H'= 0.00 in May 2017, July 2017, August 2017, October 2017, November 2017, and February 2018. There was less percentage cover of red turf algae in the healthy coral patches (0.50±0.40%). Also, there was no significant difference changing of *Porites* spp. in the healthy coral patches (p>0.05, Table 5, and Figure 9G).

Coral tissue discoloration

Pigmentation response was observed on coral tissue in the natural patches and the healthy coral patches in all caged treatments. Pink pigmentation was occurred in May, June, and October 2017 and showed in February 2018. Pink spot percentage cover was significantly different between the healthy coral and the natural condition patches (p<0.05). There was no significant difference of percentage cover of pink spot cover among herbivore treatments (p>0.05). For the natural condition patches, there was the highest percentage covers in the uncaged patches with 1.25±1.25% in August 2017 while the partial caged patches of the healthy coral patches had the highest percentage cover of pink spot with 5.00±2.74% in May 2018 (Figure 10). In the healthy coral patches, there were scars and mucus on coral tissue in the natural condition treatment. In some patches, coral could recover after pink band disease appearance.

Table 1. Seawater temperature and light intensity at study sites at Koh Taen, Mu Koh Thale Thai National Park, Nakorn Sri Thammarat Province, Southern Thailand.

Sampling times	Sea temperature(°C)	Light intensity (µmole photon·m^{-1}·s^{-1})
May 2017	32.58±0.09	1149.30±57.33
June 2017	31.52±0.09	1102.87±35.19
July 2017	32.30±0.26	1245.07±41.05
August 2017	31.33±0.16	1101.87±65.05
October 2017	31.46±0.20	1187.96±70.85
November 2017	28.90±0.02	763.82±86.09
February 2018	30.22±0.24	1085.92±68.20
March 2018	30.23±0.06	870.999±51.66
April 2018	30.70±0.04	1004.73±30.21
May 2018	32.29±0.07	1295.97±35.17

Table 2. Nutrient at study sites at Koh Taen, Mu Koh Thale Thai National Park, Nakorn Sri Thammarat Province, Southern Thailand.

Sampling times	Nitrate concentration (mg/L)	Phosphate concentration (mg/L)
May 2017	≤ 0.015 mg/L	≤ 0.030 mg/L
August 2017	≤ 0.015 mg/L	≤ 0.030 mg/L
November 2017	≤ 0.015 mg/L	≤ 0.030 mg/L
May 2018	≤ 0.015 mg/L	≤ 0.030 mg/L

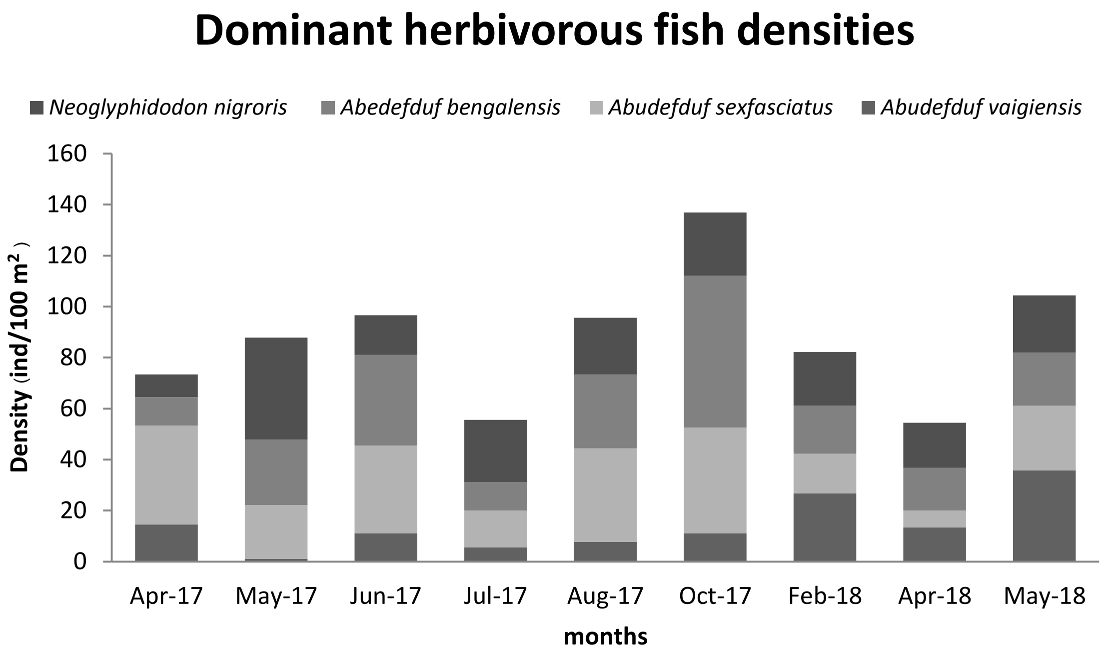

Figure 7. Density of dominant herbivorous fishes from April 2017 - May 2018 (Individual/100 m^2).

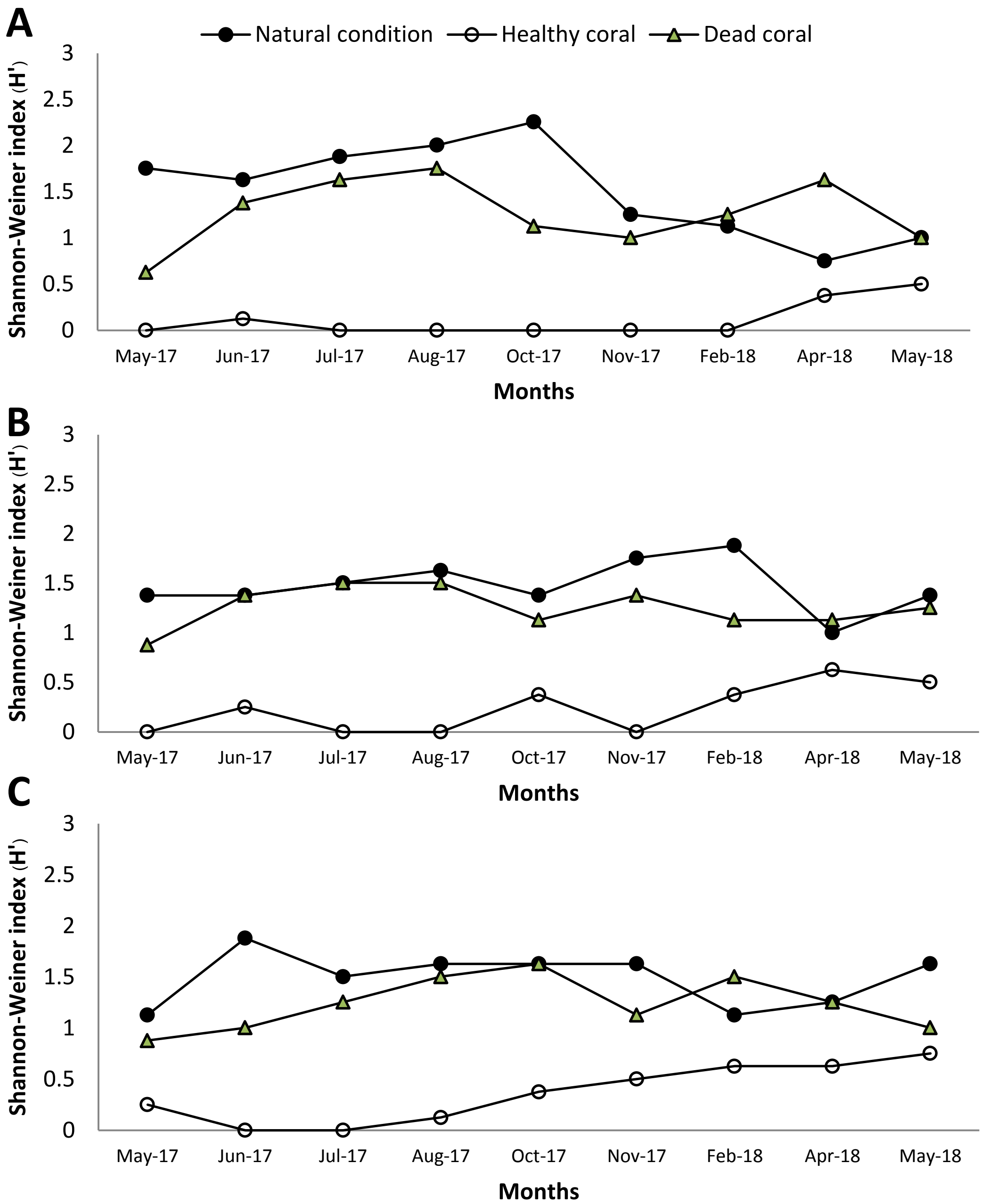

Figure 8. Species diversity (Shannon Wiener) of benthic macroalgae in (A) No caged, (B) Partial caged, and (C) Fully caged patches of each different degree of bleaching from May 2017–May 2018. (●= Natural condition, ○= Healthy coral patches, and ▲= Dead coral patches).

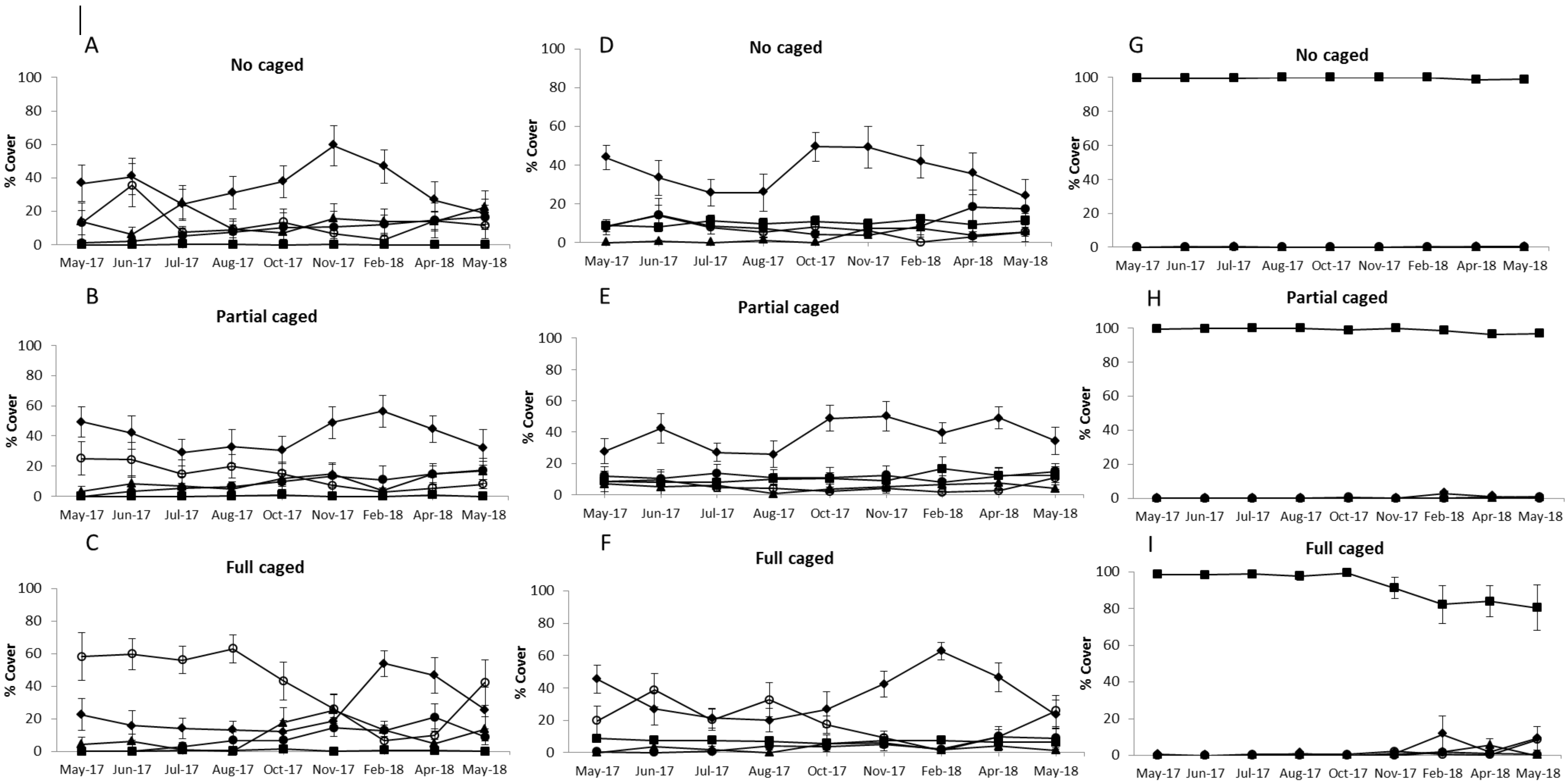

Figure 9. Percentage covers of coral, 3 dominant benthic algae, bare substratum, and coral in (A–C) Dead coral patches, (D–F) Natural condition patches, and (G–I) Healthy coral from May 2017–May 2018 (mean ± S.E., n = 10). (■ = Coral, ◆ = Red turf, ○= *Padina* sp., ●= *L. variegata* and ▲= Bare substratum).

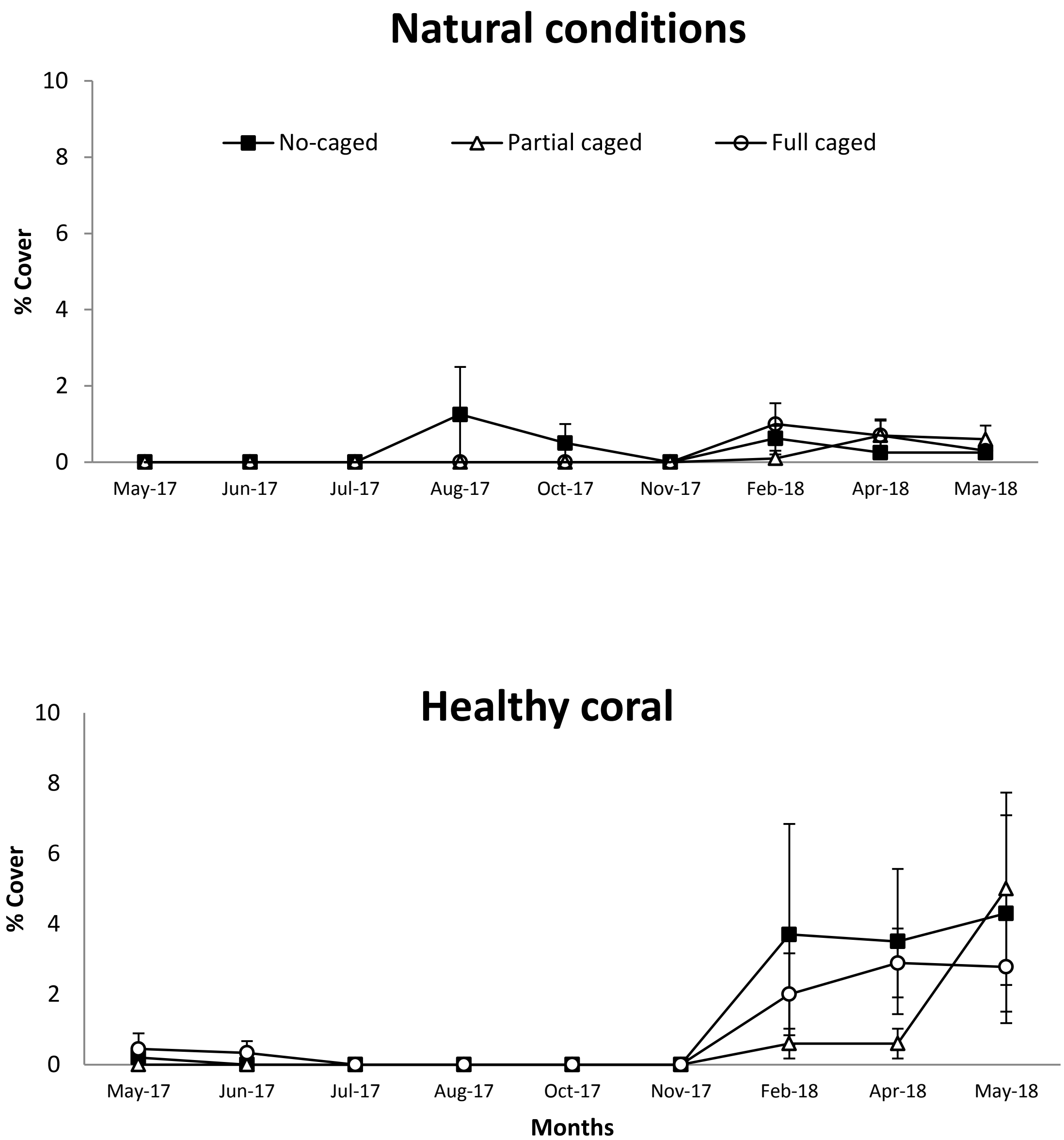

Figure 10. Percentage covers of pink band syndrome in each degree of bleaching and herbivory from May 2017–May 2018. (Mean ± S.E., n =10): (■ = No caged, ●= Partial caged, and ○= Full caged).

Table 3. Effect of herbivore on percentage covers of three dominant algae and coral; Red turf, *Padina* sp., *Lobophora variegata*, and *Porites* spp. of dead coral patches.

Source of variation	Dead coral											
	Red turf			*Padina* sp.			*L. variegata*			Coral		
	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Between Subject												
Cages	**2**	**3484.302**	**1.949** ^{ns}	**2**	**15041.275**	**14.757** **	**2**	**211.172**	**0.172** ^{ns}	**2**	**0.444**	**0.145** ^{ns}
Error	**12**	**1788.129**		**12**	**1019.281**		**12**	**1228.881**		**12**	**2.756**	
Within subject												
Months	**8**	**2391.321**	**2.856** *	**8**	**3243.724**	**6.465** ***	**8**	**634.759**	**3.203** **	**8**	**1.845**	**1.796** ^{ns}
Months x Cages	**16**	**923.540**	**2.102** *	**16**	**627.001**	**1.676** ^{ns}	**16**	**39.448**	**0.351** ^{ns}	**16**	**1.385**	**1.042** ^{ns}
Error	**96**	**439.415**		**96**	**374.084**		**96**	**112.376**		**96**	**1.329**	

$*P < 0.05$; $**P < 0.01$; $***P < 0.001$; ns, not significant. Repeated measures ANOVA was applied to 10 months of data. Univariate within subject *F* and probability was the adjusted values after the Greenhouse-Geisser estimator. df, degrees of freedom ; F, F-statistic; MS, mean square; ns, not significant.

Table 4. Effect of herbivore on percentage covers of three dominant algae and coral; Red turf, *Padina* sp., *Lobophora variegata*, and

	Natural condition											
Source of variation	Red turf			*Padina* sp.			*L. variegata*			Coral		
	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Between Subject												
Cages	**2**	**150.130**	**0.160** ns	**2**	**3299.241**	**6.084***	**2**	**1546.181**	**1.693** ns	**2**	**386.755**	**2.325** ns
Error	**14**	**937.246**		**14**	**542.246**		**14**	**913.212**		**14**	**166.342**	
Within subject												
Months	**8**	**2398.213**	**4.233****	**8**	**847.324**	**3.711****	**8**	**217.521**	**2.596***	**8**	**44.307**	**0.870** ns
Months x Cages	**16**	**865.520**	**2.069***	**16**	**195.569**	**0.925** ns	**16**	**98.920**	**1.627** ns	**16**	**43.723**	**1.376** ns
Error	**112**	**418.315**		**112**	**211.538**		**112**	**60.797**		**112**	**31.698**	

**P* < 0.05; ***P* <0.01; ****P* <0.001; ns, not significant. Repeated measures ANOVA was applied to 10 months of data. Univariate within subject *F* and probability was the adjusted values after the Greenhouse-Geisser estimator. df, degrees of freedom ; F, F-statistic; MS, mean square; ns, not significant.

Table 5. Effect of herbivore on percentage covers of three dominant algae and coral; Red turf, *Padina* sp., *Lobophora variegata*, and
Porites spp. of healthy coral patches.

	Healthy coral											
Source of variation	Red turf			*Padina* sp.			*L. variegata*			Coral		
	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Between subject												
Caged	**2**	**344.945**	**2.717^{ns}**	**2**	**52.457**	**1.168^{ns}**	**2**	**3.704**	**1.000^{ns}**	**2**	**2695.470**	**2.761^{ns}**
Error	**16**	**64.317**		**16**	**89.765**		**16**	**3.704**		**16**	**976.246**	
Within subject												
Months	**8**	**75.316**	**1.556^{ns}**	**8**	**21.880**	**1.244^{ns}**	**8**	**1.157**	**1.000^{ns}**	**8**	**245.680**	**2.938^{ns}**
Months x Cages	**16**	**50.665**	**1.138^{ns}**	**16**	**24.003**	**1.255^{ns}**	**16**	**1.157**	**1.000^{ns}**	**16**	**170.276**	**2.342****
Error	**128**	**44.051**		**128**	**19.129**		**128**	**1.157**		**128**	**72.721**	

*P < 0.05; **P <0.01; ***P <0.001; ns, not significant. Repeated measures ANOVA was applied to 10 months of data. Univariate within subject *F* and probability was the adjusted values after the Greenhouse-Geisser estimator. df, degrees of freedom ; F, F-statistic; MS, mean square; ns, not significant.

DISCUSSIONS

Algal succession patterns

In this study, red turf algae were dominated group and persist for few years because red turf algae have a fast-growing ability and rapid colonization, suppressing the recruitment of other algae (Kendrick, 1991; Diaz-Pulido and McCook, 2002; Fong and Paul 2011; Duran et al., 2016). In addition, red turf algae have high total reproductive capacity producing large number of propagules throughout the year (Dayton 1975; Sousa, 1979; Littler and Littler, 1980; Vuki and Price, 1994). Red turf algae also have a high competitive ability that might reduce growth rate of the later species (Parenti and Rice, 1969; Connell, 1973). Moreover, turf algae can inhibit algal and coral settlements and colonization by trapping and accumulating sediments (Sousa, 1979; Sousa et al., 1981; Diaz-Pulido and McCook, 2002; Eriksson and Johansson, 2003; Birrell et al., 2005). *Padina* in *Vaughaniella* stage and *L. variegata* were also the first colonizers but their percentage covers were low throughout the year. This might be because they are not good competitors, slower colonizers, have slower growth rates (Mayakun et al., 2010), however, they might play a greater role in dynamics later. Many studies suggested that fleshy macroalgae were dominant group after two to three years of succession (Hixon and Brostoff, 1981; Diaz-Pulido and McCook, 2002). In this study, the results seem to support the inhibition model proposed by Sousa (1979) stating that the pioneer or early species modify or make an environment less suitable for later successional species to recruit. For the successional pattern, it is followed a typical successional pattern, dominating by turf and filamentous algae (Diaz-Pulido and McCook, 2002).

Effect of herbivore exclusion

Algal abundance was not affected significantly by herbivory. The dead coral patches and the natural patches were occupied by red turf algae showing similar percentage cover among herbivore exclusion treatments. This result might be cause of territorial aggressive behavior of damselfish excluding other herbivorous fishes from their territories and maintaining dense of turf algae (Brawley and Adey, 1977; Ceccarelli et al., 2001; Arnold et al., 2010; Mayakun et al., 2010). For brown macroalga, *Padina*, it had higher percentage cover in caged patches treatment comparing with uncaged patches.

Red turf algae were dominated algal groups in all of herbivore treatment. Damselfishes were dominant herbivorous fishes in this study that might influence red turf algae percentage cover. Damselfishes maintain favorable red filamentous algae in their territory by eliminating other algal group from their patches (Ceccarelli et al., 2001; Ceccarelli, 2007). This result was similar to the study of Ceccarelli et al. (2005), showing that turf algae were dominated inside territory area while outside territory area dominated by fleshy macroalgae. Ceccarelli et al (2001) suggested that different damselfish species had different algae species composition. Damselfish maintained red turf algae in their territory because red turf algae have rich of necessary nutrition and good for digestion (Frédérich and Parmentier, 2016).

Grazing has directly affected algal abundance, form, and algal growth (Mcclanahan et al., 2002; Hughes et al., 2007; Burkepile and Hay, 2008; Vermeij et al., 2010; Ceccarelli et al., 2011). Percentage cover of macroalgae increased when herbivore exclusion. Reduction of herbivore pressure influenced *Padina* sp. percentage cover and *Padina* sp. morphology. *Padina* had the highest percentage cover and appeared in fan shaped form in the caged patches while filamentous form (*Vaughaniella* stage) was found in the uncaged patches. This result showed the morphological plasticity of *Padina* that regulated by herbivory. Many studies reported that this morphological plasticity is phenotypic response to the different levels of grazing pressure and *Padina* can change its form from turf to fan-shaped form when grazing pressure is low (Lewis, 1983; Diaz-Pulido et al., 2007).

Grazing activities were important factor driving coral reef ecosystem by decreasing algal abundance that provide advantages for coral cover (Lirman, 2001; Mcclanahan et al., 2002; Sotka and Hay, 2009; Vermeij et al., 2010; Ceccarelli et al., 2011). Coral cover in the caged patches decreased throughout a year while coral cover in the uncaged patches had constant cover or increased steadily. This result was similar to the result of Jompa and McCook (2002) showing that there was coral tissue mortality in caged treatment after three months of caging experiment. After coral died, turf algae and fleshy macroalgae can settle and replace corals that cause a shift from coral to algal dominated communities (Littler and Littler, 1984; McCook, 1999; McManus and Polsenberg, 2004; Bruno, 2009; Cheal et al., 2010). Macroalgae have competitive abilities on coral that affect negatively on coral such as decrease in coral growth rate, coral reproduction, coral survivorship (Tanner, 1995; Lirman, 2001; McCook et al., 2001; Jompa and McCook, 2003; Titlyanov et al., 2007; Thurber et al., 2012). Additionally, increasing in macroalgae abundance can inhibit coral settlement, and recruitment (Kuffner and Paul, 2004; Kuffner et al., 2006; Hughes et al., 2007). Many studies have illustrated that herbivores were important factor driving coral reef ecosystem by decreasing algal cover and abundance that provide advantages for coral recruitment (Lirman, 2001; McClanahan et al., 2002; Vermeij et al., 2010; Ceccarelli et al., 2011).

Effect of degree of bleaching

The dead coral patches were colonized by red turf algae with the highest percentage cover compared to other patches and no colonization on the healthy coral patches. Algae become more abundant on the dead coral patches because of more bare spaces for algal settlement (Diaz-Pulido and McCook, 2002; Bruno et al., 2009). Moreover, there were other factors induce directly on algal bloom on coral reef ecosystem such as bottom-up (nutrient enrichment) and top down (overfishing) (Hughes et al. 1999; Lapointe, 1999). Algal colonization can contribute to the failure, delay, and inhibit corals to recover from the disturbances (Diaz-Pulido and McCook, 2002; Birrel et al., 2005; Linares et al., 2012). However, coral cover in the healthy coral and natural condition patches were constant. This result was similar to the study of Diaz-Pulido and McCook (2002) showing that the healthy coral patches had a few percentages of algal percentage cover over a year. Coral percentage cover had constant trend due to healthy corals have ability to clean themselves or to avoid algal competitors by producing a mucus layer that serves as a defensive mechanism against algal colonization (Lang and Chornesky 1990; Glynn, 1993). So, the live corals in the healthy coral patches are not easily overgrown by algae compared with dead corals.

Coral tissue discoloration

In this study, pink spot or pink line has been found on coral tissue between the dead and healthy tissue of coral colony in all of the caged patches and the occurrence increased dramatically in summer. Ravindran and Raghukumar (2006) found that the pink spot was caused by the infected of cyanobacterium, *Phormidium valderianum* and related to environmental factors such as increasing seawater temperature, nutrient enrichment, and pollution. High sea surface temperature was a key factor that induce pink line syndrome occurrence because *P. valderianum* can growth and reproduce more rapidly under higher seawater temperature (Ravindran et al., 2016). Parrotfish grazing scar has been found in some patches of the partial caged and the uncaged patches that might induce pink spot on coral tissue. However, there was no research illustrating about parrotfish grazing scar can drive the pink line syndrome. Aeby (2003) and Benzoni et al (2009) reported that trematode larvae also be the cause of pink spot. After trematode larvae infected in coral polyps, it might lead coral stress and had pink spot on coral tissue. Coral-alga contact also can cause coral disease. Nugues et al (2004) reported that coral-algal contact can trigger coral disease and coral tissue mortality by infection of pathogen from algae. However, studies in the pink line syndrome are essential to allowing us to obtain a better understanding of the impact of parrotfishes on pink line syndrome and what environment factors can trigger coral pigmentation.

Part 2) Pattern of algal succession in the tropical subtidal coral reef community at Koh Taen, Mu Ko Thale Tai National Park, the Gulf of Thailand.

Introduction

Disturbance is an event or force that removes living biomass from a habitat or disrupts the community by influencing the usable space and food resources, or modifying the environment in such ways that can change the habitat to a mosaic type (Pickett and White, 1985; Townsend and Hildrew, 1994; Kim et al., 2017). Disturbances caused by natural and anthropogenic activities are important factors influencing subtidal communities in terms of species abundance, species richness, and species composition (Ebeling et al., 1985; Duffy and Hay, 1994; Levin and Hay, 1996; Hay, 1997; Stachowicz and Hay, 1999; Nystrom *et al*., 2000; Diaz-Pulido and McCook, 2002; Jompa and McCook, 2002; Marshall and Baird, 2000; Sotka and Hay, 2002; Bruno and Selig, 2007; Bruno et al., 2009; Smith et al., 2010; Vermeij et al., 2010; Hurd et al., 2014). However, the impact of disturbance on community and the pattern of community recovery after disturbance vary both in space and time, depending on frequency, magnitude, and intensity of disturbance, size of disturbed patches, location, time and seasonality (Foster, 1975; Benedetti-Cecchi and Cinelli, 1993; Kim and DeWreede, 1996), as well as seasonal availability of propagules and life-history traits of dominant species (Kim et al., 2017).

In a subtidal coral community, coral reefs are subjected to disturbances such as decreased grazing, eutrophication, and elevated sea water temperature that cause coral bleaching and coral mortality (Brown, 1997; McClanahan et al., 2002; Sotka and Hay, 2009). Disturbance has influenced the species diversity, community structure and dynamics of reefs (Diaz-Pulido and McCook, 2002). Reefs have undergone disturbances that might cause a change from coral to algae dominance (coral-algal phase shift) because there are dead coral skeletons which are favorable substrates for algae to colonize (Littler and Littler, 1984; Glynn, 1993; Nystrom et al., 2000; McClanahan et al., 2002; Diaz-Pulido and McCook, 2002; Hughes et al., 2007). Colonizing algae might inhibit coral settlement, coral growth (McCook et al., 2001), and delay the regeneration of coral tissue (Diaz-Pulido et al., 2009). Disturbed or bleached corals might recover or die, depending on the magnitude and frequency of disturbance, and the species of coral and algae involved (McCook et al, 2001; Diaz-Pulido and McCook, 2002; Jompa and McCook, 2003). However, the pattern and dynamics of algal succession in tropical subtidal coral reef communities are not well understood. Additionally, the ability and potential of a community to recover from disturbance are still unclear.

In Thailand, degraded coral reefs along the Andaman Sea and the Gulf of Thailand have been reported, and this situation has been caused by natural (strong waves, disease, coral bleaching) and anthropogenic (loss of herbivory and nutrient enrichment) disturbances for decades (Cheevaporn and Menasveta, 2003; Yeemin et al., 2006; Reopanichkul et al., 2010; Plathong et al., 2011). These reefs have undergone a shift from coral to algae dominance (Yeemin et al., 2006). However, much less is known about changing coral-algal dynamics and algal succession patterns after disturbance. A better understanding of community dynamics and the potential of reefs to recover from disturbances is needed. Thus, the aim of this study was to determine the algal succession pattern in a subtidal coral reef community in the southern Gulf of Thailand.

Materials and Methods

Study site

The study was carried out at the subtidal reef crest at Ko Taen, Mu Ko Thale Tai National Park, (9° 19′ 20″ N, 99° 46′ 80″ E), Gulf of Thailand, Southern Thailand. There are two seasons in this area: the rainy season, dominated by the northeast monsoon (October–January) and the dry season, dominated by the southwest monsoon (February–September). Tides along the gulf coast are semi-diurnal, and tidal range varies from 0.8 to 3.0 m (Coppejans et al., 2010). In this area, there were approximately 60 species of marine benthic algae found, including 23 species of Chlorophyta, 19 species of Ochrophyta, 16 species of Rhodophyta and two species of Cyanobacteria (Coppejans et al., 2010; Prathep et al., 2010), with four common genera: red turf algae, *Padina, Sargassum* and *Turbinaria*. The massive coral *Porites* was the dominant coral genus. *Abudefduf vaigiensis*, *Abudefduf bengalensis*, *Abudefduf sexfacsiatus*, and *Neoglyphidodon nigroris* were dominant herbivorous fish species at this study site (personal observation).

Experimental design and methods

For the succession experiments, dead coral patches (20 cm × 20 cm) were cleared by hand chiseling and scraping with wire brush in April 2017 to remove all organisms as much as possible. Uncleared areas with natural conditions (initially having 10 percent coverage of healthy coral) were marked as control. Ten natural patches and ten cleared dead coral patches were marked and labeled with concrete nails and surrounded with nylon thread.

In all permanent patches, percentage cover of each algal species was estimated and monitored monthly from May 2017 – May 2018. Photos of all patches were taken using an underwater digital camera (Olympus TG–5, Japan). Unknown algal specimens were collected and taken to the laboratory for identification using algal taxonomic identification guides (Coppejans et al., 2010).

Statistical analyses

Percentage cover of three dominant algal species was analyzed using repeated measures analysis of variance (RM-ANOVA). One-way ANOVA was separately applied for each of three dominant algal species. Species diversity was calculated using Shannon-Weiner index. All data were analyzed using the computer program SPSS for Windows version 16.0.

Results and Discussion

In control patches, twenty-one algal species were found, with four dominant taxa: *Padina* in *Vaughaniella* stage, *Lobophora variegata* (J. V. Lamouroux) Womersley ex E. C. Oliveira, *Cladophora* sp. and red turf algae (Table 5). Red turf algae were dominant with the highest percent cover of 50.10 ± 9.57% (Mean ± SE) (Figure 12). The coverage of red turf algae fluctuated over time, while the coverage of *Padina* in *Vaughaniella* stage, *L. variegata*, and *Cladophora* sp. was approximately 20% for each species throughout the year. For the massive coral *Porites* spp., coverage remained near 10% throughout the study, with a slight increase from 10.10 ± 0.23% in April 2017 to 12.30 ± 4.70% in May 2018 (Figure 12). However, there was no significant difference in coral cover among months (p>0.05). Algal species diversity in the control patches ranged from 0.98 – 2.13; diversity increased during the first five months and then decreased afterwards. The greatest species diversity (*H´* = 2.13) was found in August 2017 (Figure 11). There was no significant difference in algal species diversity among months (p>0.05) (Table 7).

In the cleared coral patches, nineteen algal species recruited, with three predominant species: *Padina* in *Vaughaniella* stage, *L. variegate,* and red turf algae (Table 6) (Figure 12). These three algae taxa were the first colonizers that recruited after one month of clearing. Red turf algae quickly and extensively colonized the cleared patches with the highest percentage cover (56.33 ± 10.59%). *Padina* in *Vaughaniella* stage and *L. variegata* had a low percentage cover until the end of the study. Their highest cover was 25.00 ± 11.02% and 17.22 ± 5.84%, respectively (Figure 12). Algal species diversity in the cleared patches ranged from 0.80–1.78, and the greatest species diversity (*H´* = 1.78) was found in August 2017 (Figure 11). The diversity increased during the first four months and then decreased afterwards. The patches began to recover in May 2017, one month after clearing, and took three to four months to reach levels similar to the control plots (Figure 12). Coral juveniles settled in the cleared coral patches in August 2017, however they disappeared after one month of settlement.

This study showed an early stage of succession. Red turf algae were the dominant species that recruited and colonized the cleared patches within one month after clearing, and covered the patches until the end of the study. Meanwhile, the other two species recruited the cleared patches with a very low percentage cover throughout the year. The difference might be due to the ability of red turf algae to grow quickly and rapidly colonize cleared spaces, and then persist for a few years, suppressing the recruitment of other algae (Kendrick, 1991; Diaz-Pulido and McCook, 2002; Fong and Paul 2011; Duran et al., 2016). Red turf algae also have a highly competitive ability that might reduce the growth rate of the later-arriving species (Parenti and Rice, 1969; Connell, 1973). Additionally, from field observations, the cleared patches were covered with sediments. It has been found that turf algae can trap and hold sediments to form a mat, causing an unsuitable surface and inhibit algal and coral settlement and colonization (Sousa, 1979; Sousa et *al*., 1981; Diaz-Pulido and McCook, 2002; Eriksson and Johansson, 2003; Birrell et al., 2005). *Padina* in *Vaughaniella* stage and *L. variegata* were also among the first colonizers, and recruited the cleared patches, but the percentage cover was low for both species throughout the year. This might be because they are not good competitors, slower colonizers, and have slower growth rates (Mayakun et al., 2010); however, they might play a greater role in community dynamics later.

In this study, the results seem to support the inhibition model proposed by Sousa (1979), stating that the pioneer or early species modify or make an environment less suitable for later successional species to recruit. For the successional trends, algal colonization in this study followed a typical successional pattern, dominated by turf and filamentous algae (Diaz-Pulido and McCook, 2002).

Red turf algae had a high percentage cover both in the control and cleared patches, while the other two species had very low coverage, which might be the result of the resident herbivorous damselfishes such as *Neoglyphidodon nigroris* (personal observation). These damselfishes can exclude other herbivorous fishes from their territories and maintain dense stands of red filamentous algae and turf lawns (Vine, 1974; Brawley and Adey, 1977; Ceccarelli et al., 2001; Arnold et al., 2010).

Damselfishes prefer red filamentous algae because they are palatable and high in nutrients, easily digested, and have high productivity (Frédérich and Parmenntier, 2016).

Many studies reported that turf algae might inhibit and delay coral settlement and recruitment by occupying the available space and trapping sediment (Birrell et al., 2005). In addition, the chemicals produced by filamentous algae can kill coral tissue (Jompa and McCook, 2003).

In recent years, disturbances and coral bleaching have occurred frequently, and these directly influence benthic communities. The disturbed or bleached coral reefs are likely to be dominated by turf and filamentous algae, which might influence reef recovery. Thus, this research can provide a better understanding of community dynamics and the algal successional pattern, and the consequences of disturbance or bleaching.

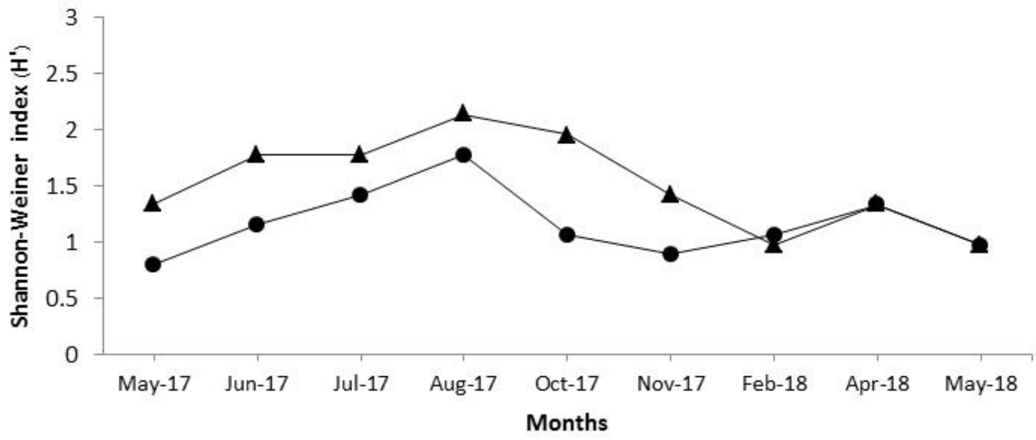

Figure 11. Species diversity (Shannon Wiener) in control and cleared patches of a coral reef in the Gulf of Thailand, from May 2017 – May 2018. (▲= Control patches and ●= Cleared patches).

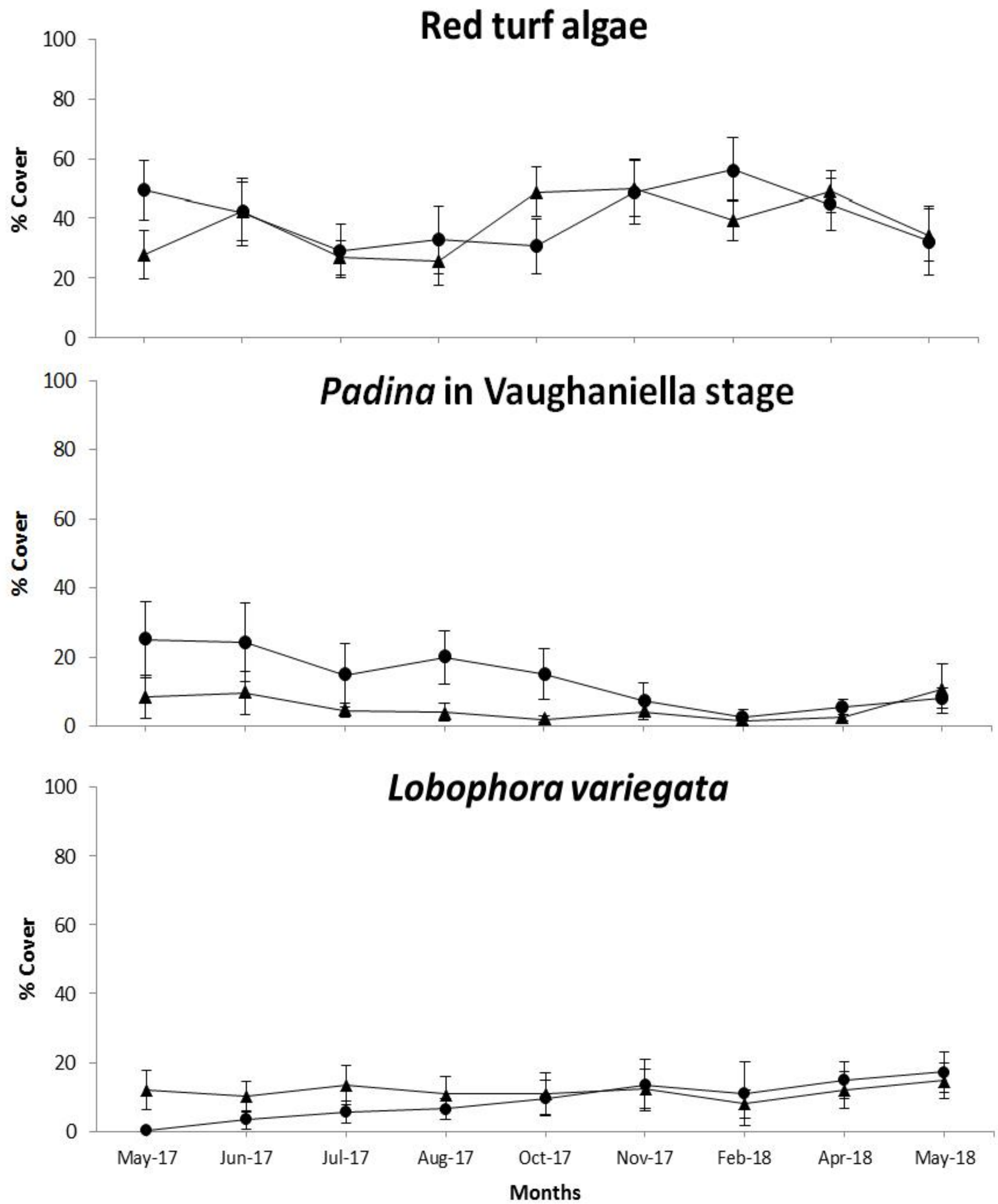

Figure 12. Percentage cover of the three dominant algal species; Red turf algae, *Padina* in *Vaughaniella* stage, and *Lobophora variegata* in control and cleared patches from May 2017 – May 2018 (mean ± S.E., n = 10): ▲ = Control patches and ●= Cleared patches.

Table 6. Algal species and occurrence on a coral reef in the Gulf of Thailand. C: common (≥ 10% in at least 1 sample); R: rare (≤ 10%); X: no occurrence.

Taxa	Abundance	
	Control patches	Cleared patches
Division Chlorophyta		
Caulerpa verticillata	R	X
Cladophora sp.	C	R
Dictyosphaeria sp.	R	R
Green turf algae	R	R
Parvocaulis sp.	R	R
Rhipidosiphon sp.	X	R
Division Rhodophyta		
Amphiroa sp.	R	X
Ceramium sp.	R	R
Ceratodictyon spongiosum	R	X
Champia sp.	R	X
Chondrophycus sp.	R	R
Hypnea spp.	R	R
Polysiphonia sp.	R	R
Red turf algae	C	C
Red crustose algae	R	R
Class Phaeophyceae		
Dictyota sp.	X	R
Lobophora variegata	C	C
Padina sp.	C	C
Sargassum spp.	R	R
Turbinaria conoides	R	R
Turbinaria decurrens	R	R

Table 7. Percentage cover of three dominant algae (red turf algae, *Padina* in *Vaughaniella* stage, *Lobophora variegata),* and coral (*Porites* spp.) in cleared patches of a reef in the Gulf of Thailand. Repeated measures ANOVA was applied to nine months of data. *P <0.05; **P <0.01; ***P <0.001; ns, not significant.

Source of variation	Red turf algae			*Padina* in *Vaughaniella* stage			*Lobophora variegata*		
	df	MS	F	df	MS	F	df	MS	F
Within subjects									
Month	8	888.181	1.276^{ns}	8	690.306	2.017^{ns}	8	185.687	4.786^{***}
Error	56	695.847		56	342.278		56	8.795	

CONCLUSION

From this study, our results can provide the information on the effects of herbivory and degree of bleaching on coral-algal community dynamics in the subtidal zone where the benthic communities can be disturbed by both physical and biological disturbances. Recently, the disturbances intensively occur that can change the communities by influencing the benthic biomass, diversity, recruitment and successional pattern. We can assume that coral-algal community structure and dynamics varies depending on degree of bleaching and herbivory. Losing in grazing activities provide positive effect on macroalgae by significantly increasing in percentage cover and species diversity. In addition, herbivory can influence algal morphology. *Padina* had fan shape in caged treatment. The different degree of bleaching affected different in coral recovery and algal settlement. In healthy coral, there were low or rare in percentage cover and species diversity of benthic macroalgae while dead coral patches were occupied by macroalgae. Coral recruitment has been found in the dead coral patches, however, coral juveniles died after two months of settlement that might be because corals cannot compete against with macroalgae.

From the succession study, our results showed the early successional pattern. Red turf algae, *Padina* in *Vaughaniella* stage, and *L. variegata* were pioneer groups colonizing the cleared patches. Red turf algae were dominant groups and covered the patches over a year. After establishment, red turf algae inhibited coral settlement and slowed the recovery of the reefs.

Our results provide the information on coral-algal community dynamics after disturbance that might be useful to assess the effects of disturbances such grazing and bleaching on coral–algal community on tropical coral reef. However, the further studies would allow us to get a better understanding on effects of other disturbances on community structure and the recovery of coral reefs.

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VITAE

Name Mr. Jatdilok Titioatchasai
Student ID 5910220017
Educational Attainment

Degree	Name of Institution	Year of Graduation
Bachelor of science (Biology) (Second Class Honors)	Prince of Songkla University	2016

Scholarship Awards during Enrolment

Science achievement scholarship of Thailand (SAST)

List of Publication and Proceeding

Pattarach, K., Titioatchasai, J., Darakrai, A. and Mayakun, J. 2018. Effects of wave exposure and shore level on seagrass abundance and distribution in the intertidal community. Songklanakarin Journal of Science and Technology 40: 1446-1450.

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