Effects of Herbivory and Season of Clearing on Species Composition and Algal Succession at Sirinat Marine National Park, Phuket Province, Thailand

Jaruwan Mayakun

A Thesis Submitted in Partial Fulfillment of the Requirements for
the Degree of Master of Science in Ecology
Prince of Songkla University
2006

ISBN 974-11-4362-1

BRT

โครงการพัฒนาองค์ความรู้และศึกษานโยบายการจัดการทรัพยากรชีวภาพในประเทศไทย
c/o ศูนย์พันธุวิศวกรรมและเทคโนโลยีชีวภาพแห่งชาติ
อาคารสำนักงานพัฒนาวิทยาศาสตร์และเทคโนโลยีแห่งชาติ
73/1 ถนนพระรามที่ 6 เขตราชเทวี
กรุงเทพฯ 10400

Effects of Herbivory and Season of Clearing on Species Composition and Algal Succession at Sirinat Marine National Park, Phuket Province, Thailand

Jaruwan Mayakun

A Thesis Submitted in Partial Fulfillment of the Requirements for
the Degree of Master of Science in Ecology
Prince of Songkla University
2006

ISBN 974-11-4362-1

Thesis Title Effects of Herbivory and Season of Clearing on Species Composition and Algal Succession at Sirinat Marine National Park, Phuket Province, Thailand

Author Miss Jaruwan Mayakun

Major Program Ecology (International Program)

Advisory Committee :

Anchana Prathep ....Chairman

(Asst. Prof. Dr. Anchana Prathep)

..........................Committee

(Assoc. Prof. Dr. Jeong Ha Kim)

Examining Committee :

Anchana Prathep ....Chairman

(Asst. Prof. Dr. Anchana Prathep)

..........................Committee

(Assoc. Prof. Dr. Jeong Ha Kim)

..........................Committee

(Assoc. Prof. Dr. Sunthorn Sotthibandhu)

Supatra ....Committee

(Asst. Prof. Dr. Supatra Davison)

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

....

(Assoc. Prof. Dr. Surapon Arrykul)

Dean of Graduate School

ชื่อวิทยานิพนธ์ ผลของการกินของสัตว์กินพืชและฤดูกาลของการเปิดพื้นที่ว่างต่อ
องค์ประกอบชนิดและการเปลี่ยนแปลงแทนที่ของสาหร่าย
ณ อุทยานแห่งชาติสิรินาถ จังหวัดภูเก็ต
ผู้เขียน นางสาวจารุวรรณ มะยะกูล
สาขาวิชา นิเวศวิทยา (นานาชาติ)
ปีการศึกษา 2548

บทคัดย่อ

ศึกษาผลของการกินของสัตว์กินพืชและฤดูกาลของการเปิดพื้นที่ว่างต่อองค์ประกอบชนิดและการเปลี่ยนแปลงแทนที่ของสาหร่าย ณ อุทยานแห่งชาติสิรินาถ จังหวัดภูเก็ต โดยขัดแผ่นปะการังตาย ขนาด 20×20 ตารางเซนติเมตร ในระหว่างช่วงต้นฤดูร้อน (เดือน มกราคม 2547) และช่วงต้นฤดูฝน (เดือน กรกฎาคม 2548) เพื่อใช้ในการศึกษาผลของฤดูกาลของการเปิดพื้นที่ว่าง และสร้างกรงขนาด 25×25×20 ลูกบาศก์เซนติเมตร เพื่อศึกษาผลของการกินของสัตว์กินพืช เปรียบเทียบกับกลุ่มควบคุม ที่ไม่มีการขัดพื้นที่ ผลการทดลองพบว่า การเปลี่ยนแปลงแทนที่ของสาหร่ายในบริเวณนี้ อยู่ในช่วงระยะที่สอง ของการเกิด และมีรูปแบบของการเปลี่ยนแปลงแทนที่ เป็นแบบ ‘ *inhibition model’* จากการทดลองพบว่า สาหร่ายสีเขียวชนิด *Ulva paradoxa* เป็นสาหร่ายชนิดแรกที่สามารถลงเกาะได้ดีที่สุด และสามารถยับยั้งการลงเกาะของสาหร่ายชนิด *Polysiphonia sphaerocarpa* และ *Dictyerpa* stage of *Padina* ปริมาณของสาหร่ายมีความแตกต่างกัน ขึ้นอยู่กับฤดูกาลของการเปิดพื้นที่ว่าง ในขณะที่ *Ulva paradoxa* สามารถสร้างเซลล์สืบพันธุ์และลงเกาะได้ตลอดทั้งปี ผลของการกินของสัตว์กินพืชไม่มีผลต่อปริมาณของสาหร่าย อาจเป็นเพราะว่า ปลาสลิดหินพวกนี้ กันไม่ให้สัตว์กินพืชชนิดอื่นๆ เข้ามาครูดกินสาหร่ายในอาณาเขตของมัน และ ดูแลปริมาณสาหร่ายให้คงไว้ แต่มีสิ่งที่ไม่คาดหวัง คือ จากการศึกษาผลของการกินของสัตว์กินพืช พบว่า เปอร์เซ็นต์ปกคลุมของสาหร่าย *Ulva* ภายในกรงมีปริมาณน้อย อาจเนื่องมาจาก ผู้บริโภคขนาดเล็ก สามารถเข้าไปครูดกินสาหร่ายภายในกรงได้ จึงทำให้เปอร์เซ็นต์ปกคลุมของสาหร่ายลดลง การศึกษาบทบาทของผลของการกินของสัตว์กินพืช เป็นเรื่องที่ควรมีการศึกษาเพิ่มเติม เพื่อให้มีความเข้าใจที่ดีมากขึ้น และ ปัจจัยต่างๆ ที่มีผลกระทบต่อการเปลี่ยนแปลงแทนที่ของสาหร่าย ควรมีการศึกษา โดยเฉพาะในเขตน้ำขึ้น-น้ำลง ในเขตศูนย์สูตร

Thesis Title	Effects of Herbivory and Season of Clearing on Species Composition and Algal Succession at Sirinat Marine National Park, Phuket Province, Thailand
Author	Miss Jaruwan Mayakun
Major Program	Ecology (International Program)
Academic Year	2005

ABSTRACT

The effects of herbivory and season of clearing on species composition and algal succession were experimentally tested in a tropical intertidal shore, Phuket Island, Thailand. To determine the effect of season of clearing on algal succession, dead coral patches were cleared, and cages were set up to exclude fish herbivory. The experimental design comprised 1 gap size of clearing (20 cm × 20 cm), 2 seasons of clearing (January 2004 and July 2004) and 2 categories of herbivory: five fully caged (25 cm × 25 cm × 20 cm, mesh size was 2 cm ×2 cm) and five uncaged plots both experimental and control plots. The results indicated that the pattern of algal community development during succession was in the middle stage and algal succession followed *'an inhibition model'*. In this succession process, an ephemeral alga, *Ulva paradoxa* was the early colonist which inhibited the settlement of the later species, *Polysiphonia sphaerocarpa* and *Dictyerpa* stage of *Padina.* Seasons of clearing influenced the abundances in the algal succession. *U. paradoxa* was able to reproduce and recruit throughout the year. Algal abundance was not influenced by grazing. It might be a result of resident herbivorous damselfishes excluded other herbivores from their territories and maintained algae as algal farms. Unexpectedly, the *Ulva* cover in the caged plots (without fish), had a lower algal coverage. These excluded fish plots might allow smaller grazers to feed on the new colonized algae, thus reducing the algal cover within the cages. Further experiments on these roles of herbivory are still needed for a better understanding of their roles and other aspects of disturbances on algal succession should be investigated in this tropical intertidal shore.

ACKNOWLEDGEMENT

I would like to express my gratitude to Associate Professor Sunthorn Sotthibandhu, Assistant Professor Anchana Prathep and Associate Professor Jeong Ha, Kim for their support and guidance. They always encourage and inspire me to aim high and to be a competent phycologist. Surely, I have been immensely motivated. I have always been guided with enthusiasms and a great deal of personal commitment.

I am also very much grateful to Dr. Raymond J. Ritchie and Dr. Pauline Ross, University of Sydney, Australia for suggesting ideas which were of great contribution to this thesis.

I am indebted to the team of Seaweed and Seagrasses Research Unit and CRAB, PSU who assisted me with the field work, Mr. Sira Keereerat for providing shelter. Also, Mr. Kittipan Subkhoon is thanked for believing in my ideas.

The financial support from the TRF/BIOTEC Special program for Biodiversity Research and Training grant BRT T_348001 made this thesis possible. This work was partly funded by the Graduate School, Prince of Songkla University, Hat Yai, Songkhla, Thailand; Project Aware Foundation, Project AWARE Asia Pacific, Australia. I gratefully acknowledge the Faculty of Science, Prince of Songkla University, Thailand for financially supporting to visit the Department of Biological Science, Sungkyunkwan University, Suwon, South Korea.

Finally, special thanks go to my parents and sisters for their support. They might not understand why my algal succession study is interesting. However they always support me unconditionally to go on.

Jaruwan Mayakun

CONTENT

LIST OF TABLES

LIST OF ILLUSTRATIONS

LIST OF ILLUSTRATIONS (CONTINUED)

LIST OF ILLUSTRATIONS (CONTINUED)

1. INTRODUCTION

Disturbance and subsequent patch recovery in the disturbed area are paramount in the understanding of the variability of community structure and dynamics in many habitats. Disturbance can be defined as any process that removes much of the living biomass in a community (Farrell, 1991) or otherwise disrupts the community by influencing the availability of space or food resources, or by changing the physical environment. In marine habitats, the formation of gaps is of considerable significance to sessile organisms or sedentary species which require an open space. Natural disturbance events produce patches of cleared space which may undergo different patterns of species recovery (Dayton, 1971; Sousa, 1979a, 1984b). Community succession varies greatly in space and time depending on the characteristics of the disturbance regime, the intrinsic vulnerability to disturbance of resident organisms, and life-history traits of the species involved (Sousa, 1984a, b; Benedetti-Cecchi and Cinelli, 1993).

Most studies on the disturbance and succession in marine habitats, however, have been conducted on temperate rocky shores. Not many studies have been carried out in tropical habitats. Among those studies, more researches were carried out in coral reefs and subtidal zones, whereas tropical rocky shores and intertidal zones are largely unexplored. There were some succession studies in tropical coral reefs and subtidal zones which were demonstrated by several researchers such as Hixon and Brostoff (1996) off Hawaii and McClanahan (1997) off Kenya. Those studies investigated the effect of herbivore on algal succession while few studies have been conducted on other aspects of disturbance on succession.

Herbivory is an important source of a biotic disturbance (Sousa, 1979b; Benedetti-Cecchi and Cinelli, 1993; McClanahan, 1997) that has received considerable attention because it is now considered to have major direct and indirect influences on the abundance, species composition and succession of algae (McClanahan, 1997). Herbivorous fishes are capable of maintaining the diversity of subtropical and tropical benthic algae similar to the results demonstrated in Australia, Belize, Hawaii and Southeast Brazil (Kennelly, 1983; Sammarco, 1983; Lewis, 1986; Hixon and Brostoff, 1996; Ferreira *et al.*, 1998). In addition, the influence of herbivory on algal succession is also well known from field studies in both the Caribbean and Pacific (Carpenter, 1986; Lewis, 1986; McClanahan *et al.*, 1994; McClanahan, 1997).

Damselfish also is well known for its effect on algal succession and benthic organisms. In the last two decades, numerous investigations on the relationships between these fish and their habitats have advanced the knowledge of damselfish and their effects on benthic communities (Sammarco, 1983; Ferreira *et al.*, 1998). Resident herbivorous damselfish exclude other herbivores from their territories and reduce the grazing pressure within these territories. They also maintain dense stands of filamentous algae as algal farms (Hata and Nishihira, 2002; Hata and Kato, 2003). Sammarco (1983) suggested that the damselfish excluded herbivorous fish from its territory, creating undergrazed patches with characteristic "algal lawns" and algal species diversity was relatively high within damselfish territories. Ferreira *et al.*, (1998) also found that damselfish, *Stegastes fuscus*, strongly influenced the algal community in its territories, keeping it in an early succession stage and preventing dominance by *Jania* spp., the later succession species. These patterns were reported for other tropical areas (Russ, 1987; Klumpp and Polunin, 1989; Hixon and Brostoff, 1996).

The timing of disturbance can have a significant effect on algal abundance and succession patterns even when reproduction is stimulated by the disturbance event itself (Sousa, 1979a; 1984b; Foster *et al.*, 2003). Time or season has been known to determine early successional algal assemblages because of the seasonal availability of propagules of certain species (Foster, 1975a; Paine, 1977; Emerson and Zedler, 1978; Sousa, 1979a; Hawkins, 1981; Dayton *et al.*, 1984; Breiburg, 1985; Kennelly, 1987; Benedetti-Cecchi and Cinelli, 1993; Kim and DeWreede, 1996). Such initial variability may influence subsequent colonization, so that the gaps created in different seasons become dominated by different organisms in later succession stages (Jara and Moreno, 1984; Kim and DeWreede, 1996).

Sediment is another disturbance factor which reduces stability and limits the diversity of animals, both on rocky shores and in soft-bottom communities (Prathep *et al.*, 2003). Sedimentation is believed to influence the distribution and diversity of seaweeds and the local structure and diversity of the assemblage through affecting patterns of growth of the algal turf (Stewart, 1983, Airoldi and Cinelli, 1997). Direct effects of sediment on algae in marine habitats include smothering and scouring and not providing a solid substrate for settlement (Airoldi and Cinelli, 1997). Thus, sediment could interfere with the recruitment of algae. The effects of sediment on algal communities on the intertidal and subtidal zones have been reported. (Stewart, 1983; Airoldi and Cinelli, 1997; Prathep *et al.*, 2003) However not many studies have been investigated on algal succession.

Experimental studies of herbivorous fish and season of clearing on algal succession have traditionally been conducted in coral reef habitats and subtidal zone. Compared to relatively large amounts of information from subtidal coral reefs, less in known about the effect of herbivory and season of clearing on algal succession on tropical intertidal shores. The published research on successional stages in the intertidal and subtidal zones in Southeast Asia, such as Thailand is scant. Hence, algal succession in the intertidal zones is essential in order that we can get a better understanding of the ecological dynamics in the intertidal zone and whether they follow similar patterns to those of other shores around the world.

Review of literature

When a disturbance opens up space or frees up resources in a community for the establishment of new individuals or colonies, organisms quickly begin to occupy the space and to use the liberated resources. The early or pioneer species tend to dominate the area after disturbance and then are replaced by later species. The sequence of colonization and species replacement that occurs after a site is disturbed is called "Ecological succession" (e.g. Connell and Slatyer, 1977; Olson, 1985; Farrell, 1991). This general definition encompasses a range of successional sequences that occur over widely varying time scales and often as a result of quite different underlying mechanisms. Interacting populations of species in ecological communities form dynamic assemblages that are constantly changing. The process of succession is an integral part of most community studies (Littler and Littler, 1985) and generally common to all environments, both terrestrial and aquatic habitats (Smith and Smith, 2001).

Disturbance is defined as any process that reduces that much of the living biomass in an area and opens up space or frees up resources in community for the establishment of new individuals or colonies (Olson, 1985; Farrell, 1991; Begon *et al.*, 1996; Kim and DeWreede, 1996). Recurrent patchy disturbance is characteristic of most natural systems. On rocky shores or coral reefs, gaps in algal or sessile animal communities may be formed as a result of severe wave action during hurricanes, storms, tidal waves, battering by logs or moored boats, by the fins of careless scuba-divers or by the action of predators. A major source of damage in seagrasses and coral reefs are boat anchors and outboard motor propeller. In forests, they may be caused by high winds, lightening, earthquakes, elephants, lumberjacks (Begon *et al.*, 1996). The formation of gaps is of considerable significance to sessile organisms or sedentary species which require open space (Kim and DeWreede, 1996). It matters much less in the lives of mobile animal species for which space is not the limiting factor (Begon *et al.*, 1996).

There are two different types of succession, primary and secondary succession. The first one occurs on a site previously unoccupied by a community e.g. a newly exposed surface such as the concrete and cement blocks in the rocky intertidal zone. It is often found that succession on concrete and cement blocks is different from that found on natural rocks. In contrast, secondary succession occurs on previously occupied (i.e. vegetated) sites following disturbances such as on rocky shores or coral reefs. Gaps in algal or sessile animal communities may be formed as a result of severe wave action or by the action of predators.

Ecological succession is one of the oldest ideas in community ecology and has received a great deal of theoretical and empirical attention (e.g. Connell and Slatyer, 1977; Sousa, 1979a; Olson, 1985; Dean and Connell, 1987a). The study of ecological succession began in the early 20th century by plant ecologists and there were many hypotheses of successional mechanisms. In 1916 Clements (see Sousa 1979a) represented "community development" as an emergent property of the community analogous to the embryological development of an organism. Succession in his view was a highly deterministic and predictable process. He suggested that early species altered the environment, making it more favorable for later species but less favorable for established species (Wootton, 2002). He proposed the facilitation model as an integral part of his view that climax communities are "superorganisms" (Foster and Sousa, 1985). This view was challenged by Gleason in the 1920s who believed in individualistic concept. He maintained that species dynamics was independent of each other. Later workers noted that differences in the time that species invaded an area could also play a role in the temporal pattern of species replacement and early species might inhibit the invasion of later-arriving species (Keever, 1950; Wootton, 2002).

The models of ecological succession have been produced by Connell and Slatyer (1977). They proposed three general models based on how the early colonists affect the establishment of the later colonists. Early colonists can promote the establishment of the later colonists (facilitation model), have no effect on the establishment of the later colonists (tolerance model), or slow the establishment or growth of the later colonists (inhibition model). More recent studies, however, have placed increasing emphasis on the inhibition model of succession (Connell and Slatyer, 1977; Sousa, 1979a; Farrell, 1991). In the recent models of Tilman (1985), species alter the nutrient environment sufficiently that other species become favored in competition and Huston and Smith (1987) provide a different approach to modeling succession, concentrating on successional patterns produced by differences in competitive ability and life history at the level of the individual, rather the species (see Wootton, 2002 for references). Understanding succession requires more than knowing just the model of succession. It is also important to determine the mechanism of succession, which is defined as the actual causal pathway that produces the net effect of the early colonists on the later successional species (Farrell, 1991).

In marine habitat, since the 1920s, there have been many studies carried out in marine habitats which have examined the process of succession in intertidal algal communities. Algal succession has been investigated by placing artificial substrata on the sea bottom (Breitburg, 1985; Dean and Connell, 1987a,b; Benedetti-Cecchi and Cinelli, 1993; Serisawa and Ohno, 1995 a, b; Hixon and Brostoff, 1996; Serisawa *et al.,* 1998; Somsueb *et al.*, 2001) and/or by removing seaweeds from natural substrata (Wilson, 1925; Kitching, 1937; Rees, 1940; Northcraft, 1948; Saito *et al.*, 1976, 1977, Niell, 1979; Sousa, 1979a; Farrell, 1991; Kim *et al.*, 1992; Benedetti-Cecchi and Cinelli, 1996; Kim and DeWreede, 1996; Foster *et al.*, 2003). There are, however, advantages and disadvantages of each experimental design. Where manipulation and sampling of natural substrata is difficult, artificial substrata can be used. Artificial substrata vary, however, in their colour, reflectivity, chemical characteristics, surface roughness, macrotopography, and porosity which may affect algal settlement and species composition (Foster, 1975b; Harlin and Lindbergh, 1977 see Foster and Sousa, 1985). While, using natural substrata, it would be more species occurred because surface heterogeneity provided more microhabitats and refuge from grazing pressure, which makes this substratum preferable.

Many studies have examined the process of succession in a wide variety of associations; forests (Eggeling, 1947); coral reefs (Glynn, 1976; Lonya, 1976; Hixon and Brostoff, 1996), rocky intertidal algal communities (Dayton, 1971, 1975; Lubchenco and Menge, 1978; Sousa, 1979a, b, 1984; Paine and Levin, 1981; Dayton *et al.*, 1984; Dethier, 1984; Breitburg, 1985; Farrell, 1991; Benedetti-Cecchi and Cinelli, 1993, 1996; Kim and DeWreede, 1996; Underwood, 1998, 1999; Connell and Anderson, 1999; Foster *et al.*, 2003); marine epifaunal invertebrates (Paine, 1976; Osman, 1977; Sousa, 1979b; Anderson and Underwood, 1997) and rocky intertidal invertebrate communities (Connell, 1961, 1970; Paine, 1966; Dayton, 1971; Sousa, 1979b; Dean and Connell, 1987a, b). Investigators have studied various aspects of disturbance on succession and community structure such as frequency (Connell, 1978; Sousa, 1979a, b; Miller, 1982; Kim and DeWreede, 1996), size (Sousa, 1984a; Benedetti-Cecchi and Cinelli, 1993, 1996; Kim and DeWreede, 1996), location (Foster, 1975a), intensity (Sousa, 1980; Kim and DeWreede, 1996) and time or seasonality of the disturbance (Foster, 1975a; Benedetti-Cecchi and Cinelli, 1993, 1996; Kim and DeWreede, 1996; Foster *et al.*, 2003) and including grazing effects (Breitburg, 1985; Anderson and Underwood, 1997; Underwood, 1998) and herbivory (Lubchenco, 1982; 1983; Jara and Moreno, 1984; Farrell, 1991; Benedetti-Cecchi and Cinelli, 1993; Hixon and Brostoff, 1996; Hata *et al.*, 2002; Hata and Kata, 2003).

In marine algal communities, Sousa (1979a) has demonstrated the classical study of algal communities in southern California. Succession was divided into three distinct stages. The first one known as the *initial stage*, or early successional species, often referred to as pioneer species, are usually small size with a high degree of dispersal and high rates of population growth (r-selected species). This initial stage was dominated by green algae especially *Ulva* and *Enteromorpha* and this early stage lasts about one year. When time passing, succession will be in the *middle stage* of succession. This stage has more diverse assemblage of more persistent green and red algae, although the early successional *Ulva* and *Enteromorpha* remain in greatly reduced amounts. Red algae become very common at this stage. The red algal species commonly found were *Gigartina, Gelidium, Rhodoglossum and Laurencia.* In the *late successional stage*, late successional species generally have lower rates of dispersal and colonization, slower growth rates, and were generally larger and longerlived (K-selected species). Late successional stage is often large kelp species (Phaeophyta) in temperate habitats.

Numerous studies have shown that herbivory is a biotic disturbance that has received considerable attention because it is considered to have a major direct and indirect influence on the abundance, functional composition of algae, structure and the organization of marine and algal communities (Sousa, 1979a; Lubchenco and Gaines, 1981; Sammarco, 1983; Jara and Moreno, 1984; Littler and Littler, 1985; Hawkins and Hartnoll, 1985; Vadas, 1985; Farrell, 1991; Hixon and Brostoff, 1996; McClanahan, 1997; Lubchenco, 1978; Hay, 1997; Kim, 1997; Belliveau *et al.*, 2002; Lotze *et al.*, 2000; Williams *et al.*, 2000; Thacker, 2001) including successional processes (Littler and Littler, 1985) in both intertidal and subtidal communities. Herbivory could be a major factor influencing succession, generally defined as a directional change in species dominance through time initiated by the opening of habitat space (Hixon and Brostoff, 1996) and it can increase community diversity by removing dominant competitors (Lubchenco, 1978; Menge and Farrell, 1989 see Thacker 2001 for references), by clearing substrates for new individuals (Menge and Lubchenco, 1981), and by maintaining equilibria between competing species (Gleeson and Wilson, 1986). Herbivory can also decrease community diversity by selectively removing preferred prey (Lubchenco and Gaines, 1981) and altering rates of succession (Hixon and Brostoff 1996; Kim 1997; McClanahan, 1997).

Farrell (1991) and Hixon and Brostoff (1996) have proposed a model and hypotheses that predicts the effect of herbivore on the rate of succession. Farrell (1991) suggested that the qualitative effects of herbivory on the rate of succession can be predicted from two factors: (1) the model of succession, and (2) the successional status of the species whose abundances are reduced by herbivory. His predictions were 1) If herbivores remove mostly later successional species then succession will be slowed compared to succession in the absence of herbivore regardless of the model of succession. 2). Equivalent removal in the inhibition model leads to no clear prediction. In this case, removal of the early colonists would hasten succession by decreasing inhibition, but this would be offset by consumption of later successional species, thereby slowing succession. 3). Equivalent removal in the tolerance model slows the rate of succession since removal of early colonists has no effect and removal of later successional species slows species replacement. 4). Equivalent removal in the facilitation model will greatly slow succession by both decreasing the facilitation provided by early successional species and by removing later successional species. 5). If herbivores remove mostly early successional species the pace of succession is by definition dependent on the model of succession. In this case, consuming early successional species will either hasten succession in the inhibition model, have no effect on the rate of succession in the tolerance model, or slow succession in the facilitation model. The intensity of consumption will influence the magnitude of the change in the rate of succession caused by the activities of herbivores. If herbivores have little influence on any species abundance they will have little effect on the rate of succession regardless of the model of succession and the successional status of the species consumed.

Damselfish also are well known for their effects on benthic organisms, modifying and influencing communities of algae, mesoinvertebrates and corals, as well as the social structure of other herbivores fish (Ferreira *et al.*, 1998). Numerous investigations of the relationships between damselfish and their habitats have advanced knowledge of these fish and their effects on benthic communities (Montgomery, 1980; Hixon and Brostoff, 1996; Sammarco, 1983; Ferreira *et al.*, 1998; Hata and Nishihira, 2002; Hata and Kato, 2003). Their territories are highly productive and have higher biomass and algal diversity than the areas outside territories because damselfish defend their algal gardens from other herbivores. Resident herbivorous damselfish maintain dense stands of filamentous algae (Montgomery, 1980; Sammarco, 1983; Klumpp and Polunin, 1989; Hixon and Brostoff, 1996; Ferreira *et al.*, 1998; Hata and Kato, 2003) known as an algal farm (Hata and Nishihira, 2002). Sammarco (1983) suggested that the damselfish exclude herbivorous fish from its territory, creating undergrazed patches with characteristic "algal lawns" and algal species diversity was relatively high within damselfish territories. Ferreira *et al.*, (1998) also found that damselfish, *Stegastes fuscus*, strongly influences the algal community in its territories, keeping it in an early succession stage and preventing domimance by *Jania* spp., the later succession species. Under natural conditions, nearly monocultural algal communities, or colonial turfs, are formed when algae endure physical stress and moderate grazing pressure (Hay, 1981; Sousa *et al.*, 1981). These turf-forming algal species possess prostrate and upright branches, and exhibit considerable morphological plasticity in response to grazing (Hata and Kato, 2003).

The time or season in which a gap is created by a disturbance is known to determine early successional algal assemblages because of seasonal availability of propagules of certain species (Foster, 1975a; Paine, 1977; Emerson and Zedler, 1978; Hawkins, 1981; Breitburg, 1985; Kennelly, 1987; Kim and DeWreede, 1996). The gaps created in different seasons become dominated by different organisms in later successional stages (Jara and Morenno, 1984; Kim and DeWreede, 1996). Season of clearing affected the algal abundance and succession patterns (Foster *et al.*, 2003). Seasonal progression results from differences in the abundance of settling larvae which in turn is a function of the seasonality of the reproductive cycles of the organisms concerned. Although some species reproduce year-round, others may exhibit marked temporal variability in reproductive cycles as a result of seasonal changes in the physical environment, and the production of larvae is restricted to definitive portions of the year. The abundances and availability, patterns of assemblage development and composition will vary depending on the timing of the availability of surface suitable for colonization (Turner and Todd 1993; Underwood and Anderson, 1994). Kim and DeWreede (1996) suggested that the differences in algal abundance among patches of similar age but produced at different seasons were species-specific. Algal species responded differently to the seasonal effect of disturbance depending on their life histories and reproductive strategies. Season of clearing had more effect on species dispersing by propagules and less on species reproducing by vegetative ingrowth. Also, this study supports the generalization that the abundance of a species is most enhanced by disturbance if a patch is created when the propagules of the species are available for settlement.

In marine systems, most studies of season of clearing and herbivore effects on algal succession have been conducted in temperate rocky intertidal zone (Sousa, 1979a; Lubchenco and Gaines, 1981; Farrell, 1991). In Thailand, the experimental herbivory and season of clearing studies are hardly found and the published research on successional stages in the intertidal and subtidal zones are scant. Hence, a study to determine the effects of herbivory and season of clearing on species composition and algal succession in the intertidal zones are necessary to develop a better understanding of algal successional process as influenced by herbivory and season of clearing in Thailand and tropical waters.

Hypothesis

It was hypothesized that herbivory and seasons of clearing influence the species composition and algal succession, so where there are differences in the number of herbivores and different seasons of clearing, there will also be different species compositions and algal succession patterns.

Objective

The aim of this study is to demonstrate the effects of herbivory and season of clearing on algal species composition and abundance during early succession in a mid-intertidal zone on a tropical reef flat.

Questions

An experiment was designed to address the following questions:

1). Do herbivorous fishes affect the early stage of algal succession?

2). Does season of clearing (i.e. rainy and dry seasons) differentiate the algal assemblage of the tropical intertidal?

2. MATERIALS AND METHODS

Study site

The study site is located in the mid-intertidal zone, Koh Pling, Sirinat Marine National Park (8° 05'N, 98° 17'E), Phuket province, Southern Thailand (Figure 1 and 2). This national park covers an area of 90 square kilometers on the north-western tip of Phuket Island. It was established in 1992 and was previously known as Had Nai Yang national park. The climate of this area is under monsoonal influence. There are two dominant seasons, a rainy season dominated by southwest monsoon (May-October) and a dry season predominated by northeast monsoon (November to April). During this study, maximum water temperature overlying at this site ranged from 27°C in July 2004 to 37 °C in September 2004. In November 2004, maximum salinity was 35 PSU and the minimum salinity was 29.5 PSU in July 2004. The southwest monsoonal winds are extremely forceful from May to October, so the wind speed would be greater during this period. The winds may have a large effect on water movement and sediment in the shallow seaweed beds. This area has various types of marine habitats, such as rocky shores, coral reefs and seagrass beds. The reefs are located about 700 to 1,000 meters away from the shore and at the depth of 4 to 7 meters. It was previously reported that the area is rich in marine organisms (Prathep, 2005) and dominated especially by diverse algal groups such as red algae, brown algae, green algae and blue green algae. Observation found that herbivores in the study site are mainly damselfishes and parrotfishes (Figure 3). The dominant species of this site are *Abudefduf vaigiensis* and *Stegaster nigricans* and *Scarus niger*. Size of damselfish was varied between 2 to 5 cm in length. Damselfishes

(Demoiselles) are a large group of coral reef fishes including approximately 320 species worldwide and about 120 species from Australian seas. Most damselfishes are territorial and zealously defend their small plot against all intruders regardless of size. Damselfishes feed on a wide variety of plants and animals including seaweeds.

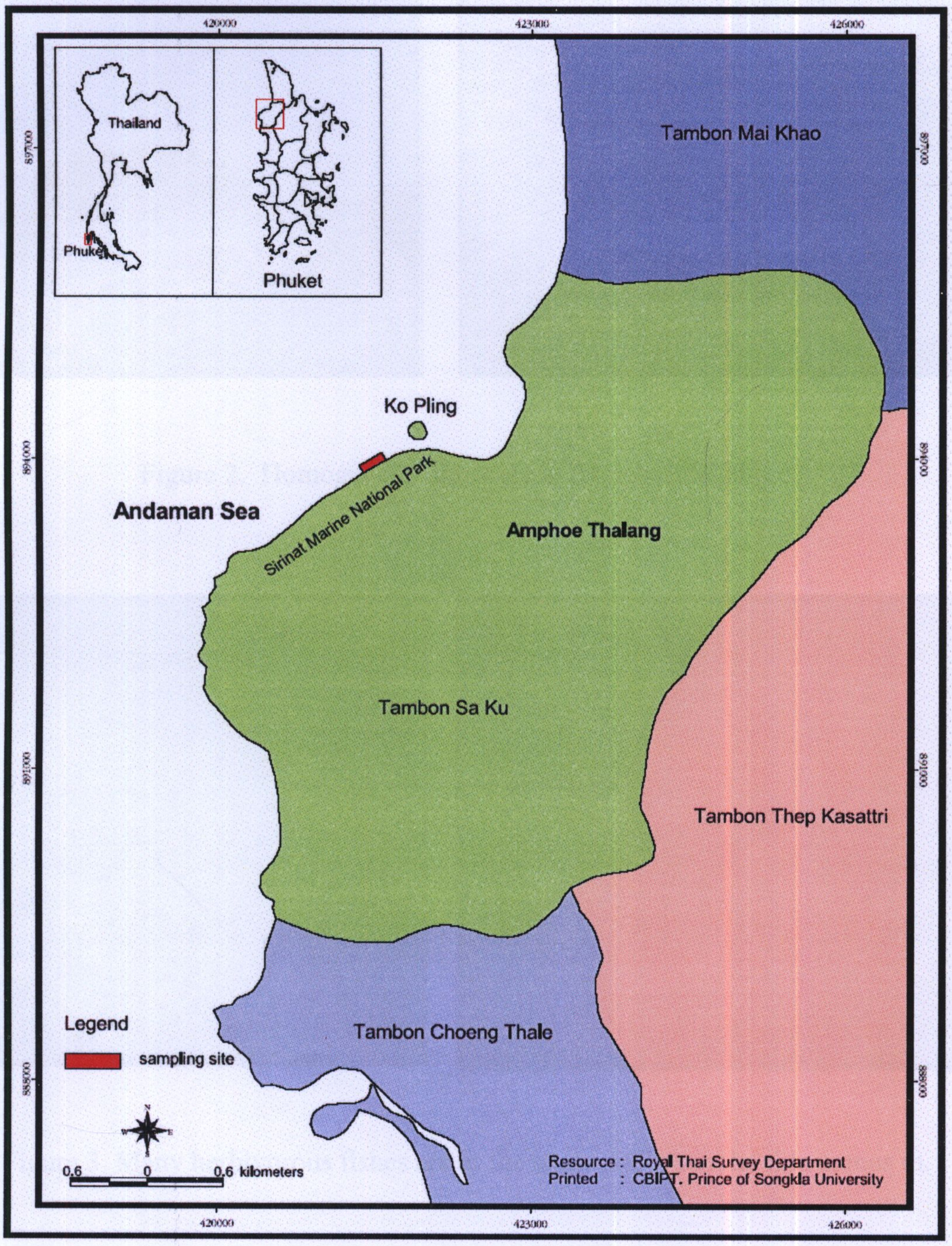


Figure 1. Map of the sampling site at Koh Pling, Phuket Province, Thailand.

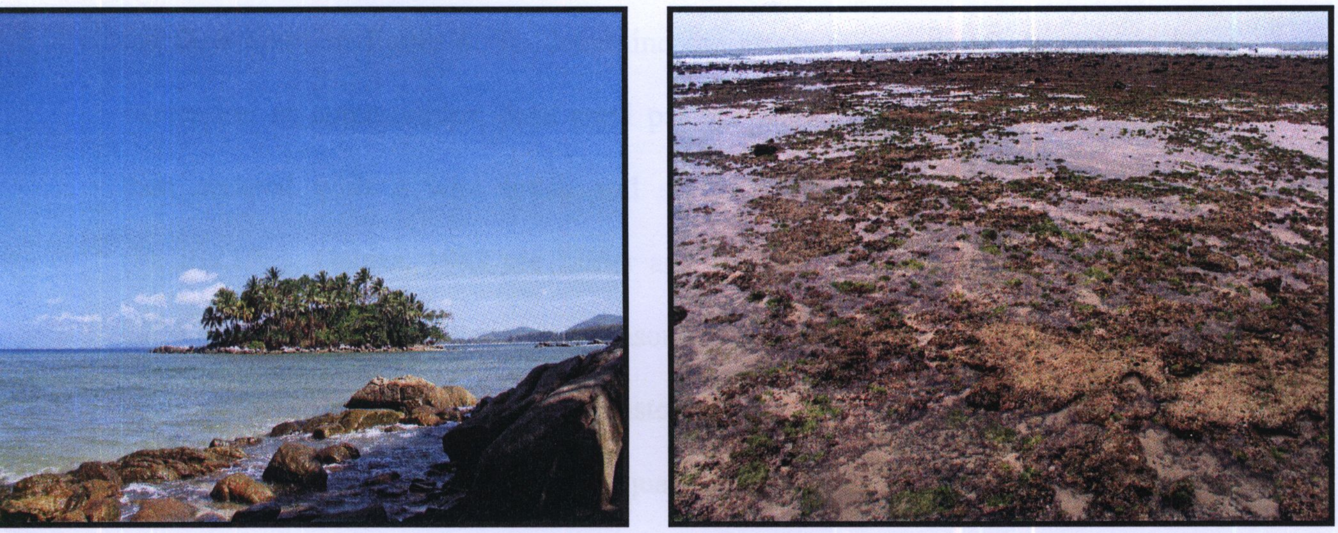


Figure 2. Homogeneity substrate at the intertidal shore

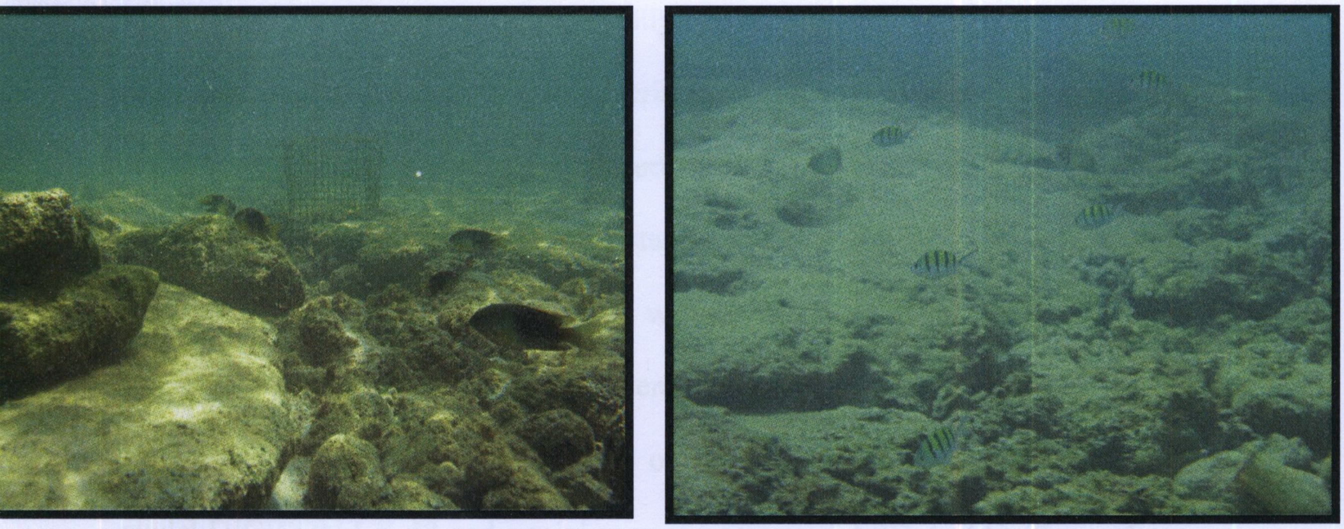


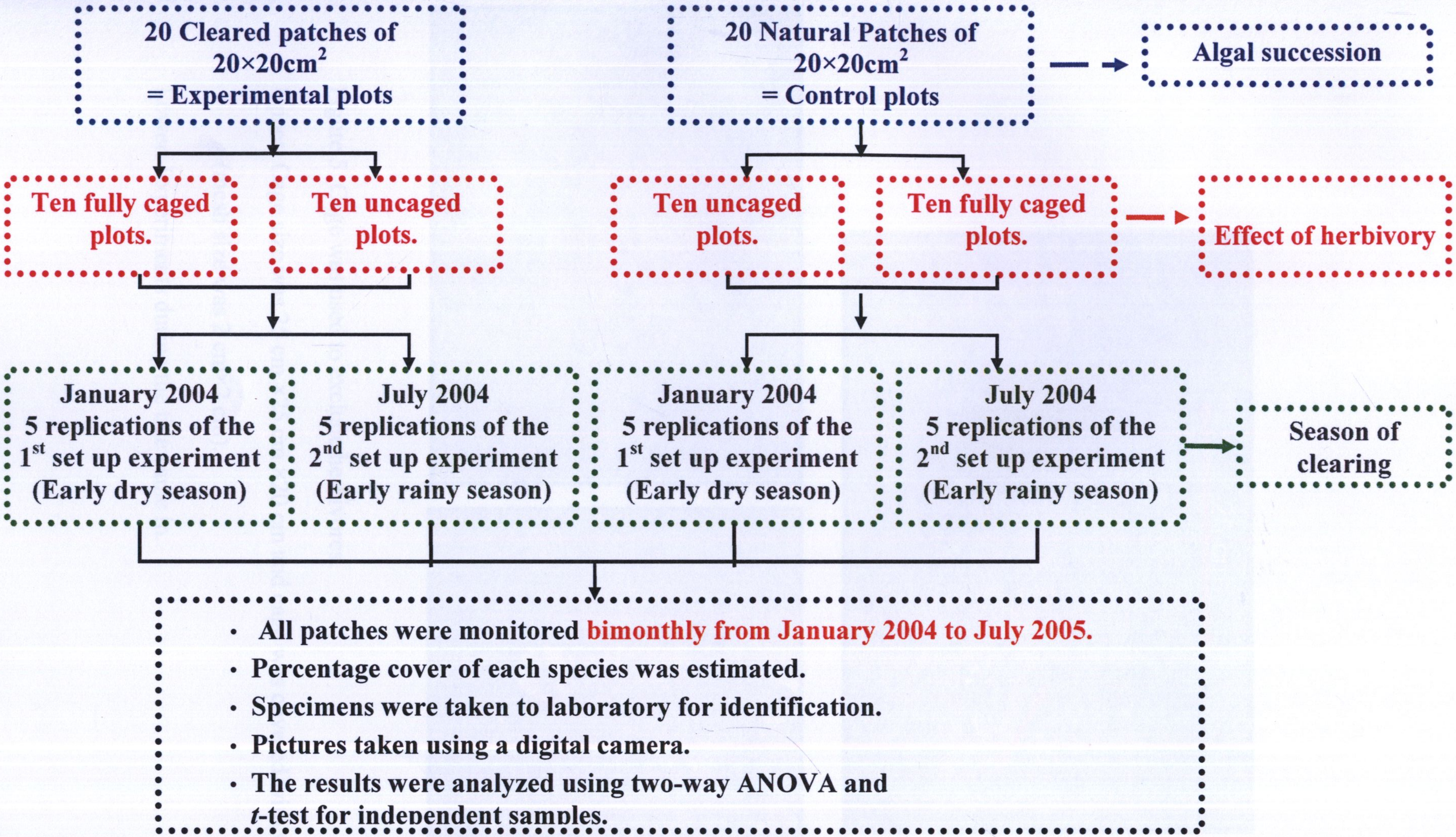
Figure 3. Many herbivorous fishes are at the study site when the tide comes in.

Methods

The effects of herbivory and season of clearing on species composition and algal succession were experimentally tested in the mid-intertidal zone following the flow chart in figure 4. To determine the effect of season of clearing on algal succession or communities, dead coral patches were cleared by hand chiseling and then scraped with a wire brush and scalded with saturated sodium hydroxide (Padilla,1981, Gaines, 1982 see Littler and Littler, 1985 for references) in January 2004 and July 2004 to determine a season effect of clearing. This procedure cleared all organisms (including holdfasts, crustose algae, etc.) and sterilized the substrate. These clear patches were then used to quantify succession of algae. Ten experimental units (20 cm ×20 cm) were marked using thread and labeled, while another ten unmanipulated plots were marked and labeled as control. To determine the effect of herbivory on algal succession, cages were used to exclude herbivores. Herbivory were manipulated into two categories: five fully caged plots both experimental and control plots, and five uncaged plots both experimental and control plots. Cage size was 25 cm ×25 cm ×20 cm (larger than the experimental patches (20 cm×20 cm) to eliminate edge effects). Cages were made of a stainless steel frame covered with wire mesh (mesh size was 2cm×2 cm). All cages were fixed on the dead coral substrate with concrete nails and damaged cages were replaced occasionally (Figure 5). Light intensity and water motion inside and outside cage was measured using luxmeter model DIGICON LX-50 and a mini current meter model SD-4 (4A) (Sensordata a.s., Bergen, Norway). The herbivore exclusion cages used in this study decreased total light intensity by 5.14–14.66% compared to uncaged plots. However, total light intensity was much greater than the level needed for saturation of the photosynthetic rate of a broad variety of algae (Hata and Kato, 2003). The cages also decreased wave motion to 4.77±1.16% less than the uncaged plots. Therefore, we assumed that shading and wave motion decreasing by cages had a minimal influence or non influence to algal succession.

All patches were monitored every two months from January 2004 to July 2005. Monitoring was carried out during low tide when most of the patches were exposed to the air and direct sunlight. Data collection of the 1st set experiment was done from January 2004 (early dry season) to January 2005 and the 2nd set experiment was conducted from July 2004 (early rainy season) to July 2005. The two sets of experiments were designed to test for the effect of different clearing season on species composition and algal succession. Quadrates of the same size as the experimental plots, with 2 cm×2 cm subplots adapted from Kim and DeWreede (1996) marked off within the quadrate frame (100 subplots for 20 cm×20 cm) were used for measuring the abundance of organisms. Percent cover of each species was estimated by counting the number of subplots in which a species occupied. The accuracy and repeatability of this technique has been tested by Dethier *et al.*, (1993) and they reported that this method is generally more accurate than the random-point-quadrate method. Algal covers included only those thalli whose holdfasts were in the plot.

All patches were photographed by using a digital camera. Specimens were collected and taken to the laboratory and identified using various taxonomical identification guides, *e.g.* Common Seaweeds and Seagrasses of Thailand (Lewmanomont and Ogawa, 1995), Seaweeds of Queensland (Cribb, 1996), Caribbean Reef Plants (Littler and Littler, 2000), Plant Resources of South-East Asia No 15 (1) and Cryptograms: Alga (Prud'homme van Reine and Trono, 2001). Algal samples were preserved with 4% formaldehyde and were photographed. Samples for sediment were collected bimonthly from March 2004 to May 2005. Samples were taken in three shore levels, upper, middle and lower shore level for comparing the amount of sediment between shore levels. Three samples were placed randomly at each shore level during the low tide and the patches were left 24 hours. After that the samples were placed in plastic bags and transferred to the laboratory and then the samples were dried at 60 °c. The dried sediment samples of same weight were then sieved using a shaker classified into seven size fractions: > 2.00 mm, 1.00-2.00 mm, 500 µm-1.00 mm, 250-500 µm, 125-250 µm, 63-125 µm and < 63 µm, and then each fraction was weighed.



- All patches were monitored bimonthly from January 2004 to July 2005.
- Percentage cover of each species was estimated.
- Specimens were taken to laboratory for identification.
- Pictures taken using a digital camera.
- The results were analyzed using two-way ANOVA and *t*-test for independent samples.

Figure 4. Flow chart of experimental design.

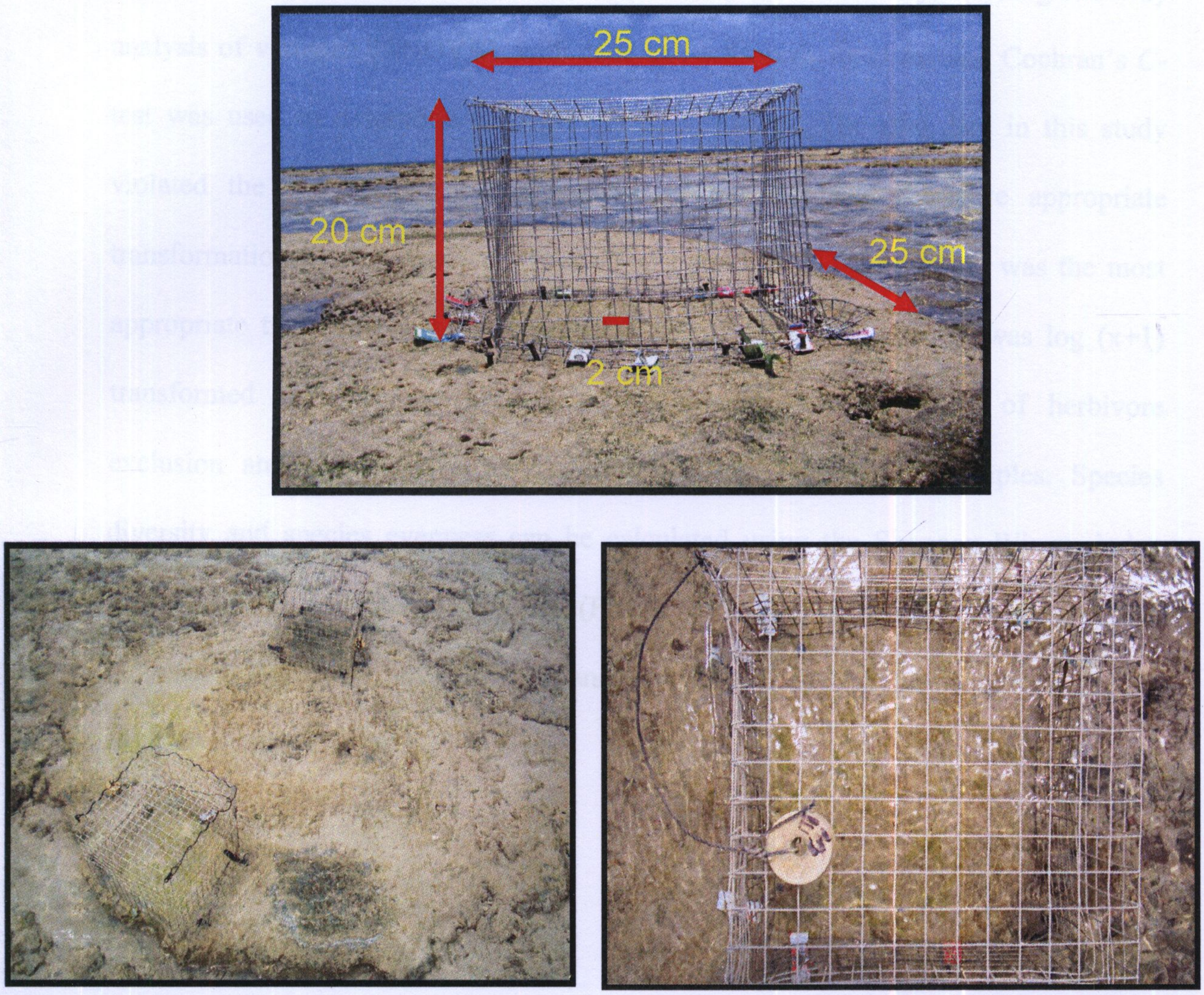


Figure 5. Cage was used to exclude herbivores.

Upper: Cage size was 25 cm ×25 cm ×20 cm and cage was covered with wire mesh (mesh size was 2 cm×2 cm).

Lower: Experiments during the tide came in.

Statistical analyses

The effects of herbivory, season of clearing and their interaction on change in percent cover of algae in manipulated plots were analyzed using two-way analysis of variance (ANOVA), with cage and season as fixed factors. Cochran's *C*-test was used to determine homogeneity of variances. The raw data in this study violated the assumption of homogeneity of variance and therefore appropriate transformations of the data were tests (Underwood, 1981). Log (x+1) was the most appropriate transformation. The percent cover of each algal species was log (x+1) transformed prior to analysis. Differences between mean effects of herbivore exclusion and season were tested with *t*-test for independent samples. Species diversity and species evenness can be calculated using the Shannon-Wiener index (Pielou, 1977) and Simpson index (Pielou, 1977) at different seasons and two densities of herbivory. All data were analyzed using the computer program SPSS for Windows version 10.0.

3. RESULTS

Unmanipulated plots

There were no significant differences in species composition between the two clearing times. *Cladophora prolifera* and *Polysiphonia sphaerocarpa* were the most conspicuous species in unmanipulated plots, 73% ± 3.74 (mean ± SE) and 52.2% ± 8.94 respectively for the dry season (Figure 6) and 72% ± 5.15 and 39% ± 18.80, respectively for the rainy season (Figure 7). In the dry season, *Dictyerpa* stage of *Padina* was relatively abundant in the first 6 months of this study, but its abundance was lower after that; it became less abundant during the raining season. The ephemeral alga, *Ulva paradoxa*, was less abundant in unmanipulated plots. The highest percent cover was only 16% in the dry season and only 8% in the rainy season. These findings are different to that found in surveys at Samui Island which is in the Gulf of Thailand and not in the Andaman Sea (Mayakun and Prathep, 2005). Seasonal changes in algal abundance were greater for both *C. prolifera* and *P. sphaerocarpa* compared to *Dictyerpa* stage of *Padina* (Figure 6 and 7).

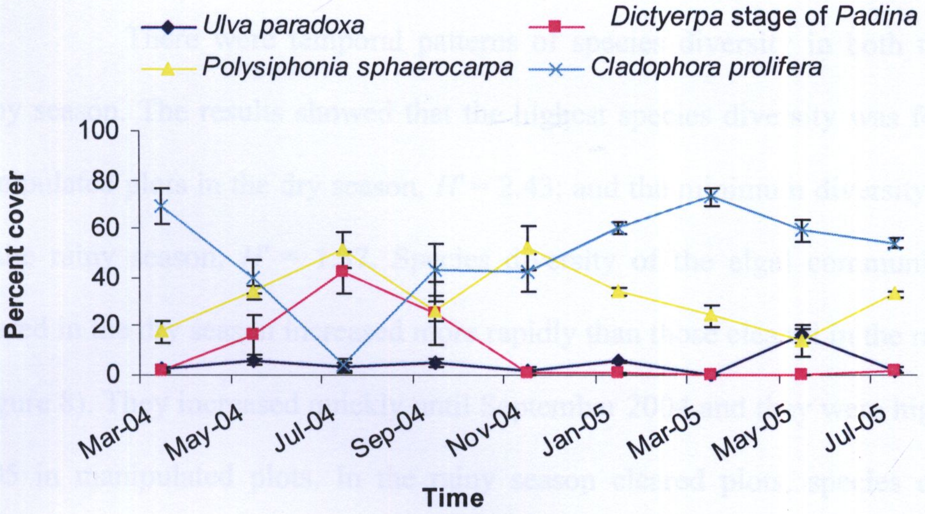


Figure 6. The percent cover of algal species in unmanipulated plots without cage over 18 months. Data shown are from plots cleared in the dry season (January 2004). Data are the mean ± SE of 5 replicates.

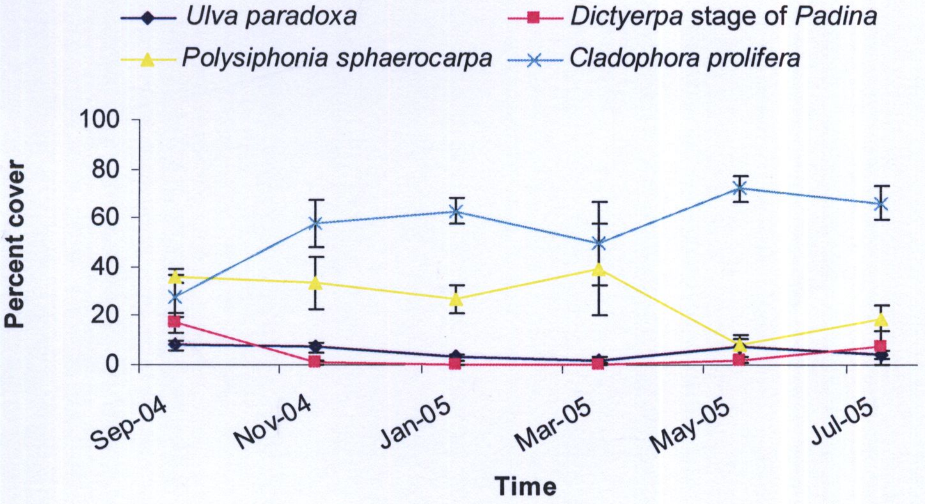


Figure 7. The percent cover of algal species in unmanipulated plots without cage over 12 months. Data shown are from plots cleared in the rainy season (July 2004). Data are the mean ± SE of 5 replicates.

Effects of clearing season

There were temporal patterns of species diversity in both the dry and rainy season. The results showed that the highest species diversity was found in the manipulated plots in the dry season, $H' = 2.43$; and the minimum diversity was found in the rainy season, $H' = 1.37$. Species diversity of the algal community in plots cleared in the dry season increased more rapidly than those cleared in the rainy season (Figure 8). They increased quickly until September 2004 and they were higher in July 2005 in manipulated plots. In the rainy season cleared plots, species diversity of control plots decreased initially until March 2005. Diversity increased slowly in manipulated plots and highest species diversity was reached in July 2005. The result showed that the same four dominant species occupied cleared sites in areas cleared during both the rainy and dry seasons.

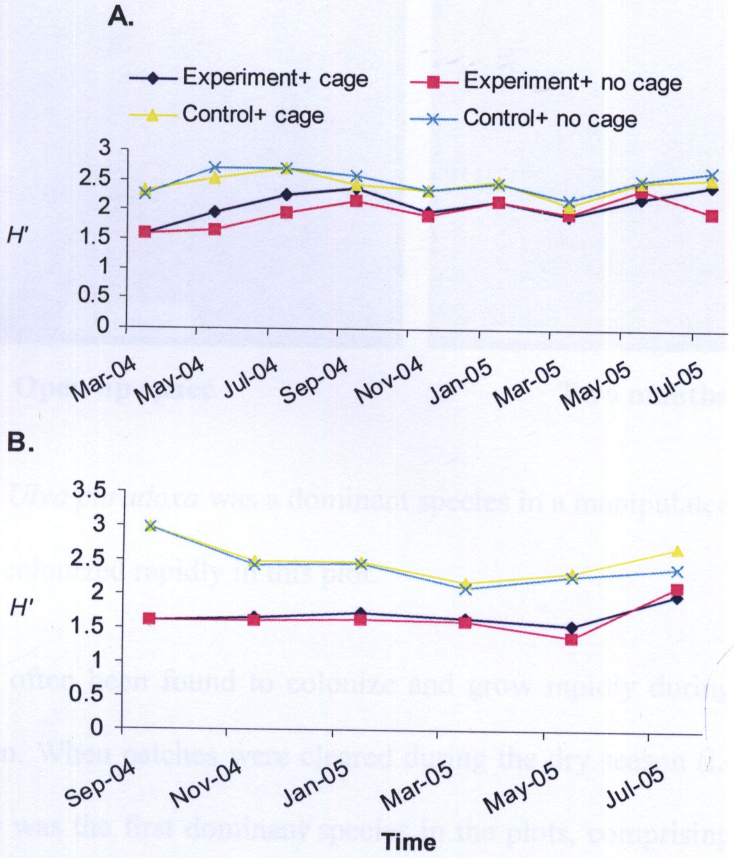


Figure 8. Temporal patterns of species diversity of A) Dry and B) Rainy season

In total, 10 algal species occurred in the manipulated plots (Table 1). Species composition of colonists was not different between the plots that were cleared at the two different times (January and July 2004). However, algal abundance was different depending on the clearing time (Table 2 and 3). Two months after clearing, there was a high initial cover of ephemeral algal species, *U. paradoxa*, in both clearing times (Figure 9).

Open up space **Two months after clearing**

Figure 9. *Ulva paradoxa* was a dominant species in a manipulated plot and it colonized rapidly in this plot.

Ulva has often been found to colonize and grow rapidly during the early stages of succession. When patches were cleared during the dry season (i.e. January 2004), *U. paradoxa* was the first dominant species in the plots, comprising 86% of the ground cover in May 2004. After 4 months elapsed, *U. paradoxa* declined until March 2005 and was displaced by a filamentous rhodophyte, *P. sphaerocarpa*. *P. sphaerocarpa* had a high percentage cover with 23% in July 2005 and *Dictyerpa* stage of *Padina* had a low cover in these cleared plots (Figure 10). However, *C. prolifera* was not found in plots cleared during the dry season. When the areas were cleared in the rainy season, the percent cover of *U. paradoxa* was 99% in September 2004 (Figure 11) and was found to colonize more rapidly in the rainy season than during the dry season. *Dictyerpa* stage of *Padina* and *P. sphaerocarpa* had a very low cover in the plots that were cleared in the rainy season while *C. prolifera* also was not found in these plots when compared with plots that were cleared in the dry season.

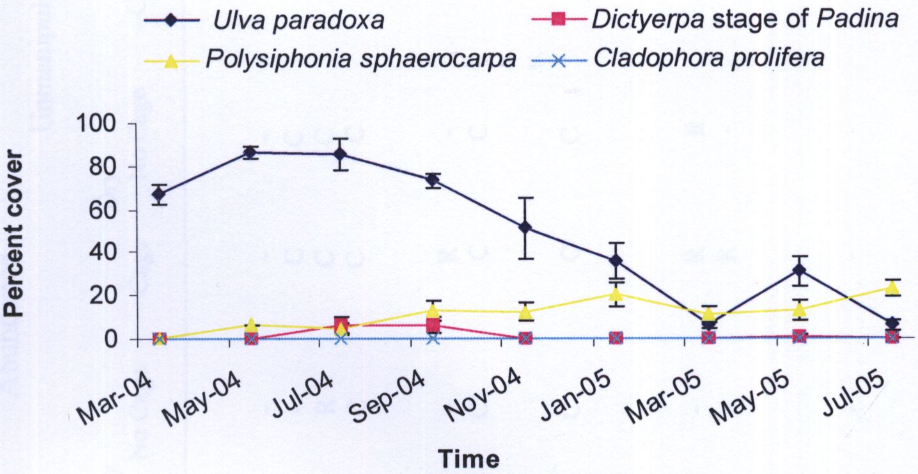


Figure 10. The cover of abundant algae in manipulated plots without cages over 18 months. Data shown are from plots cleared in the dry season (January 2004). Data are the mean ± SE of 5 replicates.

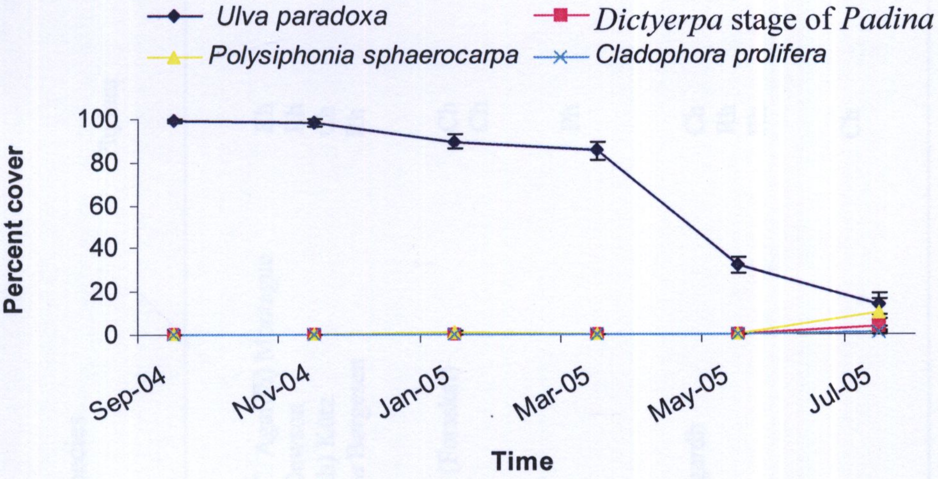


Figure 11. The cover of abundant algae in manipulated plots without cages over 12 months. Data shown are from plots cleared in the rainy season (July 2004). Data are the mean ± SE of 5 replicates.

Table 1. List of algal species and their abundance in the each experiment between dry and rainy seasons. Ch: Chlorophyta; Ph: Phaeophyta; Rh: Rhodophyta. C: common occurrence more than 10% in percentage cover at least 1 sample; R: rare occurrence less than 10%; -: no occurrence.

Functional groups / Species	Phylum	Abundance							
		Experimental plots				Unmanipulated plots			
		Dry		Rainy		Dry		Rainy	
		Cage	No Cage	Cage	No Cage	Cage	No Cage	Cage	No Cage
Filamentous algae									
Centroceras clavulatum (C. Agardh) Montague	Rh	-	-	-	-	-	-	R	R
Ceramium mazatlanense Dawson	Rh	C	C	R	-	C	C	C	C
Cladophora prolifera (Roth) Kütz	Ch	-	-	-	R	C	C	C	C
Polysiphonia sphaerocarpa Børgesen	Rh	C	C	C	C	C	C	C	C
Foliose algae									
Dictyosphaeria cavernosa (Forsskal)	Ch	R	-	-	-	R	-	R	R
Ulva paradoxa C. Agardh	Ch	C	C	C	C	C	C	C	C
Corticated macrophytes									
Dictyerpa stage of *Padina*	Ph	C	C	C	C	C	C	C	C
Leathery macrophytes									
Valonia aegagropila C. Agardh	Ch	-	-	-	-	R	R	C	C
Laurencia sp.	Rh	R	-	-	-	R	-	C	-
Gelidium sp.	Rh	-	R	-	-	-	-	-	-
Calcareous algae									
Acetabularia sp. *	Ch	-	-	R	-	-	-	-	-
* (15 thallus)									

Table 2. Effects of herbivory and season of clearing on recolonization of total algae from each season.

Source of variation	**df**	Dry **MS**	***F***	**P**	**df**	Rainy **MS**	***F***	**P**
Month	5	0.101	6.814	0.000	5	0.421	5.238	0.000
Caged	1	4.259E-04	0.029	0.866	1	2.027E-03	0.025	0.874
Season *Caged	5	3.485E-03	0.235	0.946	5	1.603E-02	0.199	0.962
Error	108	1.484E-02			108	8.033E-02		

Season of clearing affected the relative abundance patterns of *Dictyerpa* stage of *Padina* and *P. sphaerocarpa* (season effect: *p*= 0.013 and *p*= 0.000, respectively; Table 3, Figure 12 and 13). However, differences in percent cover of *C. prolifera* and *U. paradoxa* between dry and rainy clearing were not significantly different (*p*= 0.606 and *p*= 0.922, respectively). Thus, there were seasonal changes in the dominant species between seasons.

Table 3. Effects of herbivore and season of clearing on recolonization of 4 dominant algae, *Cladophora prolifera*, *Ulva paradoxa*, *Dictyerpa* stage of *Padina* and *Polysiphonia sphaerocarpa*.

	Cladophora prolifera				***Ulva paradoxa***				***Dictyerpa* stage of *Padina***				***Polysiphonia sphaerocarpa***			
Source of variation	**df**	**MS**	***F***	**P**	**df**	**MS**	***F***	**P**	**df**	**MS**	***F***	**P**	**df**	**MS**	***F***	**P**
Between subjects																
Season	1	8.453E-03	0.267	0.606	1	1.179E-03	0.010	0.922	1	1.060	6.312	0.013	1	8.973	35.338	0.000
Cage	1	8.453E-03	0.267	0.606	1	2.059E-02	0.167	0.684	1	0.408	2.433	0.122	1	4.80	1.889	0.172
Season *Cage	1	5.476E-02	1.733	0.191	1	7.781E-02	0.631	0.429	1	6.408 E-02	0.382	0.538	1	0.262	1.033	0.312
Error	116	3.161E-02			116	0.123			116	0.168			116	0.254		

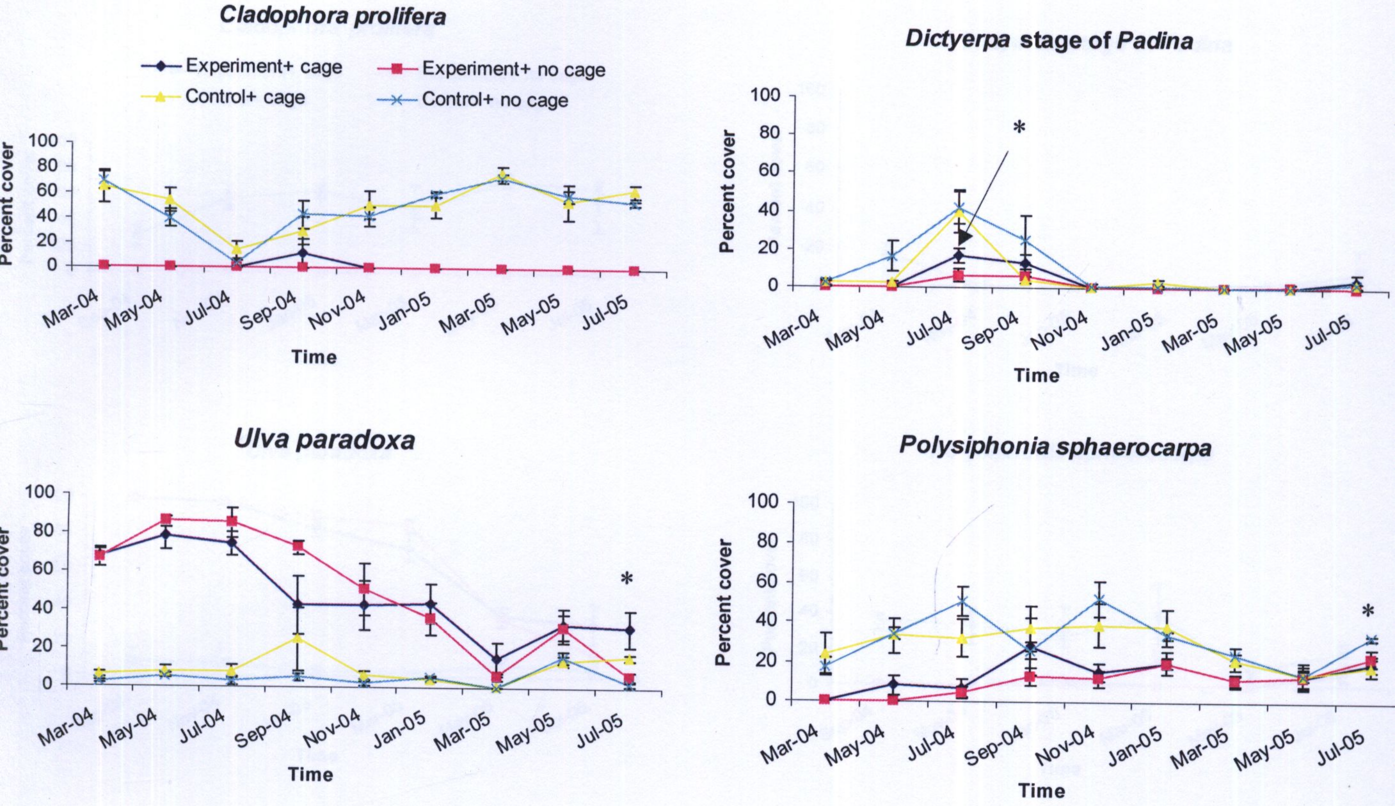


Figure 12. Seasonal changes of alga percent cover, *Cladophora prolifera*, *Ulva paradoxa*, *Dictyerpa* stage of *Padina* and *Polysiphonia sphaerocarpa* in 20×20 cm of clearing. Data shown are from dry season (January 2004) plots. Data are the mean ± SE of 5 replicates for each experiment. Comparisons between cages were made using independent *t*-test: * $0.05 \geq p > 0.01$; ** $0.01 \geq p > 0.001$; *** $p < 0.001$.

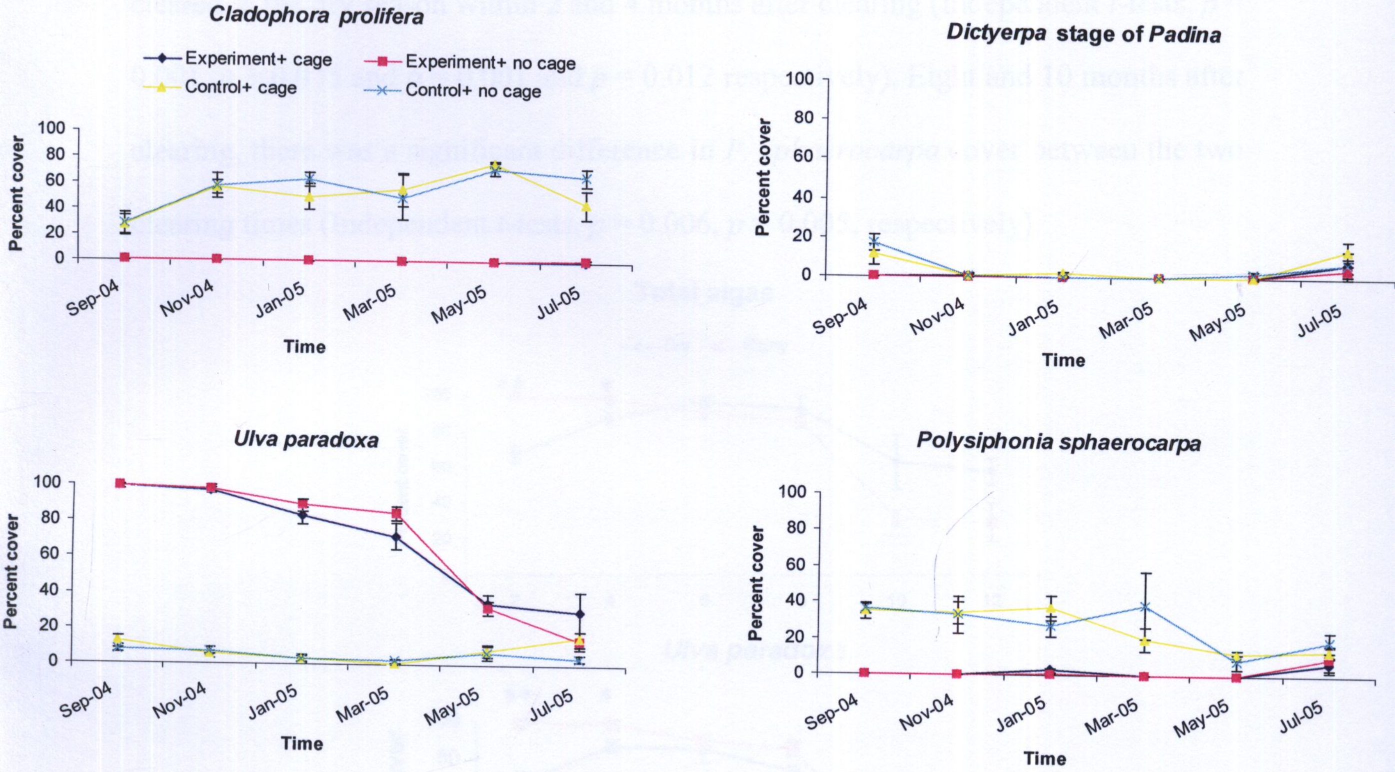


Figure 13. Seasonal changes of algal percent cover, *Cladophora prolifera*, *Ulva paradoxa*, *Dictyerpa* stage of *Padina* and *Polysiphonia sphaerocarpa* in 20×20 cm of clearing. Data shown are from rainy season (July 2004) plots. Data are the mean ± SE of 5 replicates for each experiment. Comparisons between cages were made using independent *t*-test: * $0.05 \geq p > 0.01$; ** $0.01 \geq p > 0.001$; *** $p < 0.001$.

The effect of clearing time on total algal cover and two dominant species in manipulated plots without caging is shown in Figure 14. Plots cleared in the rainy season had a greater percent cover of total algae and *U. paradoxa* than in plots cleared in the dry season within 2 and 4 months after clearing (Independent *t*-tests, $p = 0.001$, $p = 0.035$ and $p = 0.001$ and $p = 0.012$ respectively). Eight and 10 months after clearing, there was a significant difference in *P. sphaerocarpa* cover between the two clearing times (Independent *t*-tests, $p = 0.006$, $p = 0.005$, respectively).

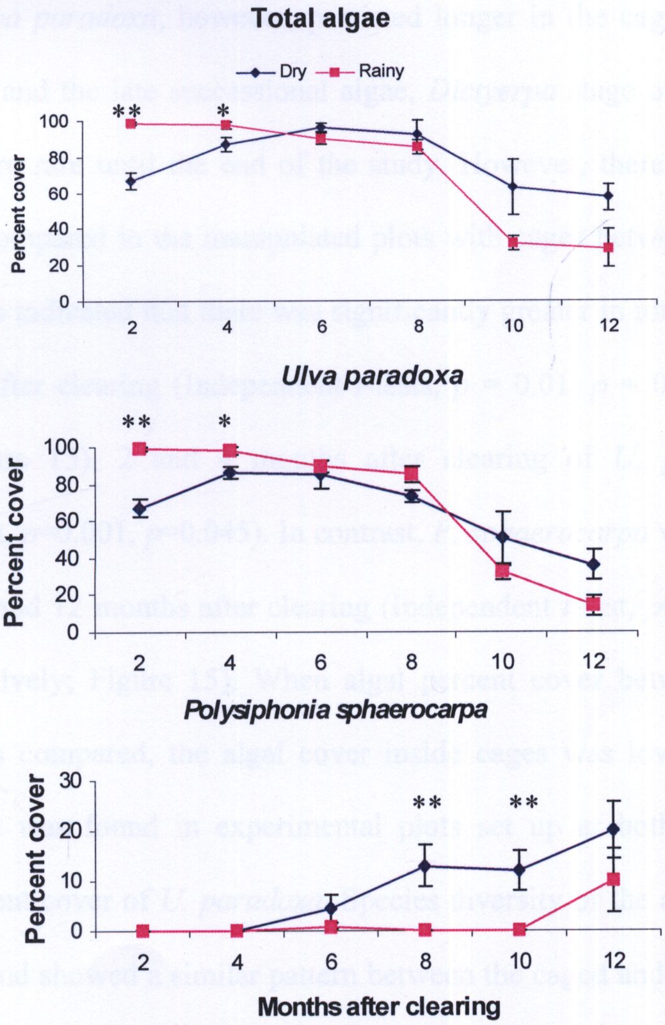


Figure 14. Effects of clearing time on total algae and two dominant species, *Ulva paradoxa* and *Polysiphonia sphaerocarpa*, in manipulated plots without cage. Comparisons between clearing time were made using independent *t*-test: * $0.05 \geq p > 0.01$; ** $0.01 \geq p > 0.001$; *** $p < 0.001$.

Herbivory effects

Cage controls were conducted on both experimental and unmanipulated plots to determine the effect of herbivory on algal abundance and succession patterns.

Abundance of 4 dominant algal species was not significantly different between the caged and uncaged plots (Table 3; Figure 12 and 13). Both in the absence of fish grazing within cages and inside damselfish territories without cages, plots were first dominated by green alga, *Ulva paradoxa*, followed by *Polysiphonia sphaerocarpa. Ulva paradoxa*, however, persisted longer in the caged plots than in the uncaged plots and the late successional algae, *Dictyerpa* stage of *Padina* and *P. sphaerocarpa*, were rare until the end of the study. However, there was significant difference when compared in the manipulated plots with cages between two clearing season. The results indicated that there was significantly greater in total algal cover 2, 6 and 8 months after clearing (Independent *t*-tests, $p = 0.01$, $p = 0.037$, $p = 0.024$ respectively; Figure 15), 2 and 4 months after clearing of *U. paradoxa* cover (Independent *t*-test, p=0.001, p=0.045). In contrast, *P. sphaerocarpa* was significantly different in 8, 10 and 12 months after clearing (Independent *t*-test, p=0.000, p=0.000 and 0.034 respectively; Figure 15). When algal percent cover between inside and outside cages was compared, the algal cover inside cages was lower than outside cages. This result was found in experimental plots set up at both clearing times especially in percent cover of *U. paradoxa.* Species diversity of the algal community was no different and showed a similar pattern between the caged and non-caged plots (Figure 8).

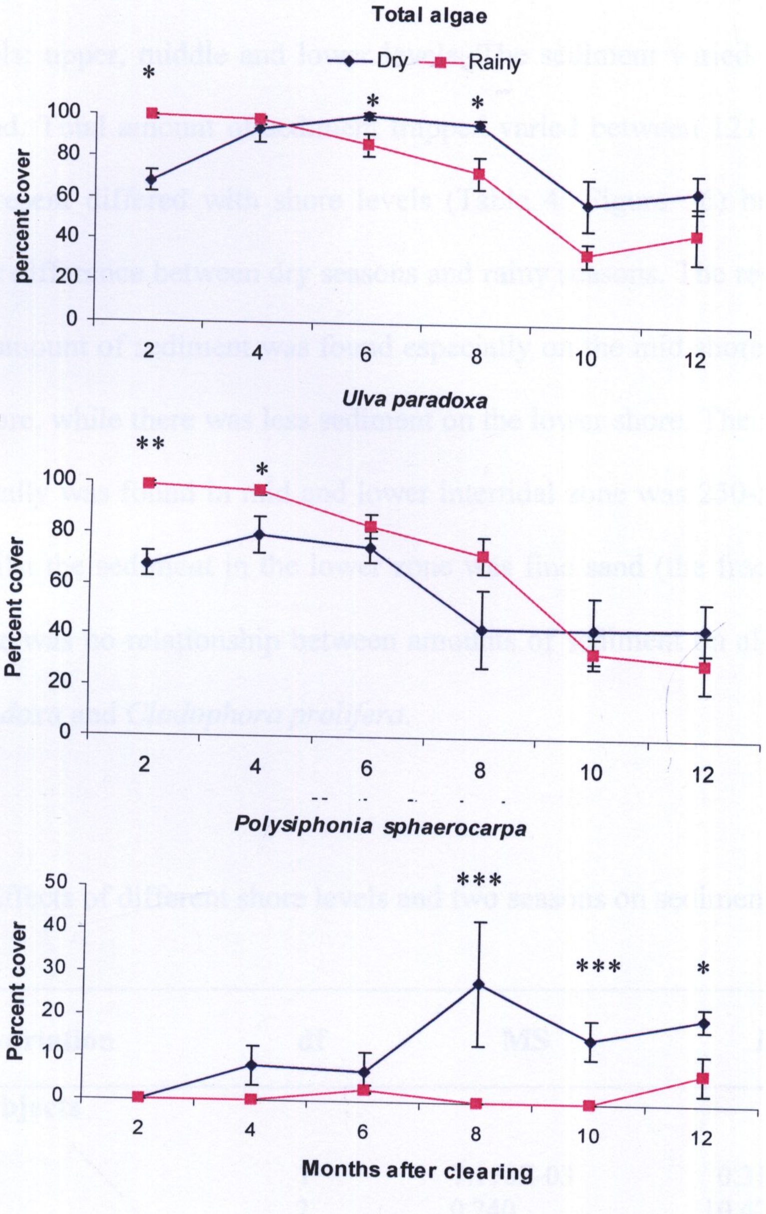


Figure 15. Effects of clearing time on total algae and two dominant species, *Ulva paradoxa* and *Polysiphonia sphaerocarpa* in manipulated plots with cages. Comparisons between clearing time were made using independent *t*-test: * $0.05 \geq p > 0.01$; ** $0.01 \geq p > 0.001$; *** $p < 0.001$.

Effect of sediment

This study investigated the amount and grain size of sediment at three shore levels: upper, middle and lower levels. The sediment varied from silt to very coarse sand. Total amount of sediment trapped varied between 121-2,340 g/m^2. The amount present differed with shore levels (Table 4; Figure 16) but there were no significant difference between dry seasons and rainy seasons. The results showed that a greater amount of sediment was found especially on the mid shore level and higher on this shore, while there was less sediment on the lower shore. The sediment fraction which usually was found in mid and lower intertidal zone was 250-500 µm (Medium sand), whilst the sediment in the lower zone was fine sand (the fraction was125-250 µm). There was no relationship between amounts of sediment on algal abundance of *Ulva paradoxa* and *Cladophora prolifera.*

Table 4. Effects of different shore levels and two seasons on sediment.

Source of variation	**df**	**MS**	***F***	**P**
Between subjects				
Season	1	7.158E-03	0.311	0.587
Shore level	2	0.240	10.428	0.002
Season *Shore level	2	2.317E-02	1.007	0.394
Error	12	2.301E-02		

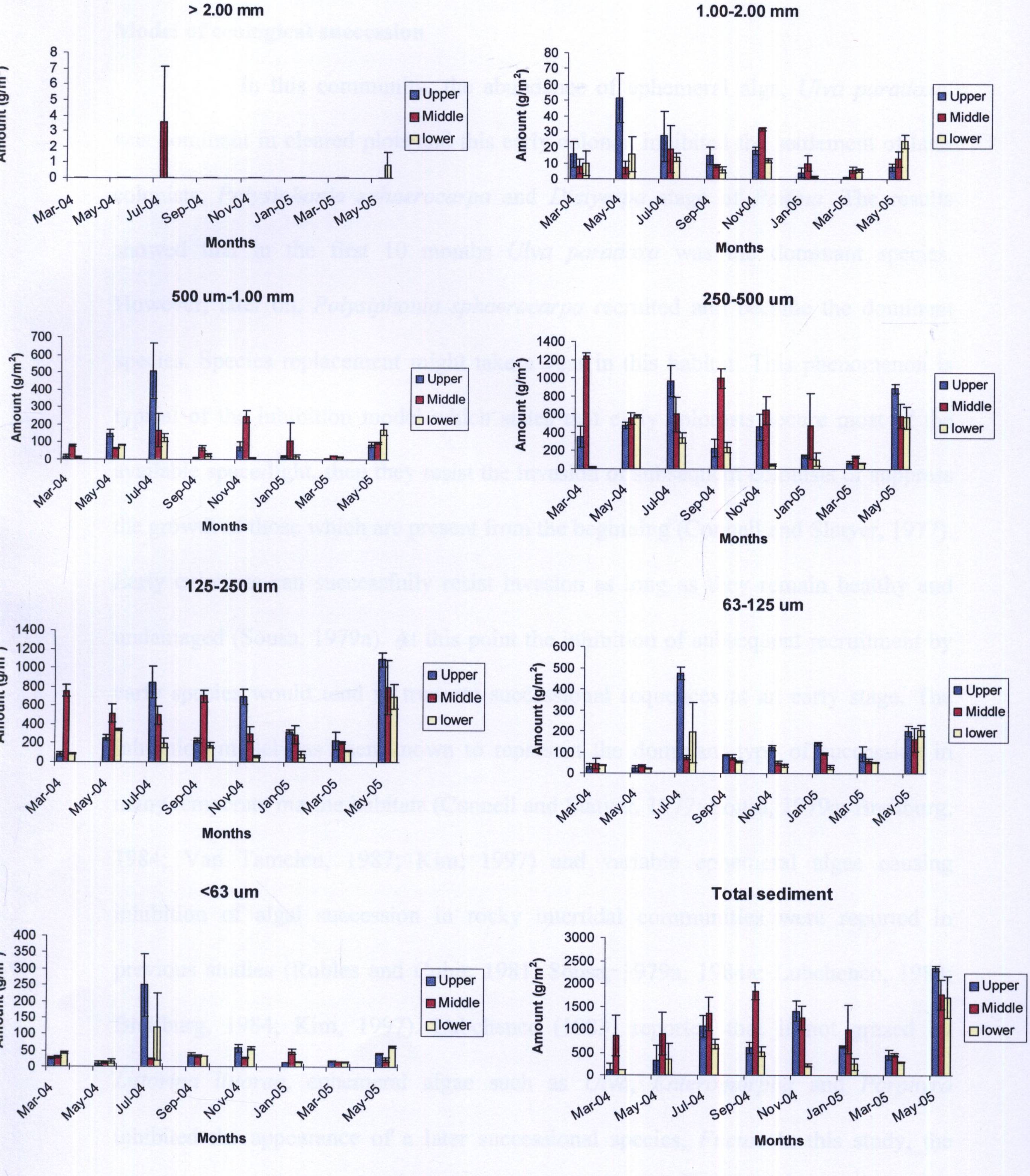


Figure 16. Total amount of sediment were trapped during the experiment.

4. DISCUSSION

Model of ecological succession

In this community, the abundance of ephemeral alga, *Ulva paradoxa*, was dominant in cleared plots and this early colonist inhibited the settlement of later colonists, *Polysiphonia sphaerocarpa* and *Dictyerpa* stage of *Padina.* The results showed that in the first 10 months *Ulva paradoxa* was the dominant species. However, later on, *Polysiphonia sphaerocarpa* recruited and became the dominant species. Species replacement might take a year in this habitat. This phenomenon is typical of the inhibition model which states that early colonists secure most of the available space/light, then they resist the invasion of subsequent colonists or suppress the growth of those which are present from the beginning (Connell and Slatyer, 1977). Early colonists can successfully resist invasion as long as they remain healthy and undamaged (Sousa, 1979a). At this point the inhibition of subsequent recruitment by early species would tend to truncate successional sequences at an early stage. The inhibition model has been known to represent the dominant type of succession in many temperate marine habitats (Connell and Slatyer, 1977; Sousa, 1979a; Breitburg, 1984; Van Tamelen, 1987; Kim, 1997) and variable ephemeral algae causing inhibition of algal succession in rocky intertidal communities were reported in previous studies (Robles and Cubit, 1981; Sousa, 1979a, 1984a; Lubchenco, 1983; Breitburg, 1984; Kim, 1997). Lubchenco (1983) reported that if not grazed by *Littorina littorea*, ephemeral algae such as *Ulva*, *Enteromorpha* and *Porphyra* inhibited the appearance of a later successional species, *Fucus*. In this study, the pattern of algal community in tropical intertidal zone development during succession seemed to follow a typical inhibition model similar to that shown in many temperate shores where ephemeral algae often caused inhibition of colonization by late successional species (Connell and Slatyer, 1977).

Effect of Sediment

In this study, the percent cover of two major species, *Ulva* and *Cladophora* appeared to show no significant response to the sediment. The results showed that their percentage covers were not related to the amount of sediment; and their cover appeared throughout the year whether there was increasing or decreasing of sediment. *U. paradoxa* has a life history with continuous spore production and colonized the cleared plots with large cohorts early in the succession (Eriksson, 2002) while *C. prolifera* dispersed by vegetative propagation and this seemed to be a successful strategy to tolerate sedimentation. This result is in accordance with that of Eriksson (2002); *Ulva* and *Cladophora* seem highly adapted to exploit temporarily favorable sediment conditions. Also *Ulva* species have a small button-like stage called the collinsiella-stage that it is often found on rocks that are seasonally covered by sand on beaches. The collinsiella stage acts as a dormant stage which rapidly grows new *Ulva* filaments when the sand cover is washed off (Bold and Wynne, 1978). In general, regeneration has been suggested to confer tolerance to high sedimentation by releasing the alga from the dependence of spore attachment to substrata that are often buried (Stewart, 1983; Eriksson, 2002). Long continuous spore production should be advantageous in temporally unstable sediment environments since establishment success will not be dependent on sediment conditions during a short period of time. In addition, the physical factors were observed during the dry and rainy season in this study site. Thongroy (2006) reported that the physical factors (Salinity, water and air temperature, phosphate (PO_4^{3-}) and nitrate (NO_3^-)) were significant difference between dry and rainy season. Fluctuation of salinity, water and air temperature were low while the concentration of phosphate and nitrate were high but those conditions are suitable for growth and reproduction of macroalgae.

More experiments would be, however, required to address the effects of sediment on algal succession in this habitat.

Effect of season of clearing

There were differences in algal abundance in the plots cleared at different seasons (Table 2). When the areas were cleared in the rainy season, *Ulva paradoxa* had greater percent cover than in plots cleared in the dry season. Whereas, the *Dictyerpa* stage of *Padina* and *Polysiphonia sphaerocarpa* were found and were more abundant in the cleared plots in the dry season than those cleared in the rainy season. In this study, time of patch creation was an important determinant of algal abundance than of species composition, as also shown in other studies (Foster *et al.*, 2003). Abundance and species composition of species can be increased by disturbance if a patch is cleared when reproduction and propagule release of the species occurred (Denley and Underwood, 1979; Sousa, 1979a; Hawkins, 1981; Turner, 1983; Dayton *et al.*, 1984; Jara and Moreno, 1984; Sousa, 1984a, b; Benedetti-Cecchi and Cinelli, 1993, 1994; Kim and DeWreede, 1996; Foster *et al.*, 2003). Dispersive properties of spores of different species affect their ability to colonize the areas (Hutchins, 1952; Foster, 1975a see Denley and Dayton, 1985). Therefore, the algal abundance is most enhanced by disturbance if a patch is created when the propagules of algae are available for settlement (Kim and DeWreede, 1996).

Plots from both clearing seasons were all dominated by the green alga, *Ulva paradoxa,* in this early-successional stage. In addition, this showed that *U. paradoxa* reproduced and recruited throughout the year (Lubchenco, 1978; Sousa, 1979a; Begon *et al*., 1996). Species of *Ulva* have been known as a first colonizer in many rocky communities from temperate regions (Luchenco, 1978; Sousa, 1979a). It is well known that species of *Ulva* are the first dominant species to colonize rapidly because of evolved life history characteristics such as the production of large numbers of small motile propagules with a high degree of dispersal, which grow rapidly to maturity (r-selected species) and it reproduces throughout the year (Lubchenco, 1978; Sousa, 1979a; Begon *et al*., 1996). Other algal species responded to the seasonal effect of disturbance depending on their life histories and reproductive strategies (Kim and DeWreede, 1996).

In the present study, *Ulva paradoxa* dominated the patches within 2 months after clearing and it was found to colonize and grow rapidly particularly in the plots cleared in the rainy season (Figure 10and 11). It might be a result of timing of clearing and their ability to colonize of *Ulva paradoxa* in this area. The new cleared plots might receive numbers of *Ulva paradoxa* propagules with no interference from previously settled species such as *Cladophora prolifera* and *P. sphaerocarpa.* The *Dictyerpa* stage of *Padina* and *P. sphaerocarpa* were not abundant in the cleared plots for the first 12 months, indicating that this brown and red alga were slow colonizers and had slower growth as suggested in many studies (Sousa, 1979a). *Ulva paradoxa* might inhibit the successive invasion of these slow colonizers during the early stage of succession by preventing the settlement of spores with its wide fronds and great percentage cover.

On the other hand, *Cladophora prolifera* was not affected by the season of clearing. The result showed that this species was not found in cleared plots made at both clearing times but was often found in unmanipulated plots. It might be a result of the spore of *C. prolifera* not being able to colonize or compete with *U. paradoxa* in the early succession stage. In addition, *Ulva* is the best competitor for the space and quickly becomes established on newly cleared plots. This is also found in other algae studies, when *Ulva* was first colonized (Sousa, 1979a).

In addition, there was greater species diversity in cleared plots during the dry season than the rainy season. This might be a result of less disturbances from wave action in the dry season. Prathep (2005) reported that waves of two-to-three meter heights were observed during the rainy season in this study site; these strong waves might wash away seaweeds as well as new germlings from the plots or remove them by abrasion. Also, wave action is known to inhibit spore settling and recruitment of algae (Hurby and Norton, 1979; Lobban and Harrison, 1994). Therefore, the calmer wave conditions during the dry season would cause less disturbances and allow a stable community with many species could settle and develop.

Effect of herbivores

The herbivore exclusion cages in this study decreased light intensity by only 5.14-14.66% which allowed sufficient light for photosynthesis in these algae (Hata and Kato, 2003). The cages also decreased wave motion by only 4.77±1.16% which was less than the uncaged plots but there was no significant difference of water current between inside and outside the cages. Therefore, we assumed that shading and wave motion had a minimal influence on algal succession.

The abundance of 4 dominant species was not significantly different between the caged and uncaged plots (Table 3). Both in the absence of fish grazing within cages and inside damselfish territories without cages, plots were first dominated by green alga, *Ulva paradoxa* and *Ulva* persisted longer in the caged plots than in the uncaged plots and the late successional algae, *Dictyerpa* stage of *Padina* and *P. sphaerocarpa*, were rare until the end of the study. A possible explanation could be that herbivores are likely to be less important in eliminating early species in the initial stage of succession, or they prefer the late successional seaweeds. A similar pattern has been shown in previous studies. Sousa *et al.*, (1981) reported that sea urchins of southern California preferred late successional seaweeds, and consequently early successional species persisted longer in areas where urchins were abundant. Recently, Hixon and Brostoff (1996) reported that inside damselfish territories, succession was decelerated. Early dominance by green and brown filaments, *Enteromorpha rhizoidea* and *Ectocarpus indicus* were protracted and still dominated over 230 days into the experiment. In the patches exposed to herbivores, in theory, herbivores could facilitate the establishment of later species (Benedetti-Cecchi and and Cinelli, 1993). In contrast to this study, algal abundance in the patches exposed to herbivores was not influenced by grazing animals and algal abundance was not significantly different between the caged and non-caged plots. It might be the results of resident herbivorous damselfishes excluding other herbivores from their territories and maintain algal lawns and dense stands of filamentous algae (Montgomery, 1980; Wilkinson and Sammarco, 1983; Sammarco, 1983; Russ, 1987; Klumpp and Polunin, 1989; McClanahan, 1997; Ferreira *et al.*, 1998; Ceccarelli *et al.*, 2001; Hata *et al.*, 2002; Hata and Kato, 2002, 2003). Ferreira *et al.*, (1998) indicated that herbivory by *Stegastes fuscus* exerted a strong influence upon the epilithic algal community of territories. Herbivorous damselfishes apparently act by preventing any algae from being competitively excluded by others. This might be a dietary preference. In their case study, *S. fuscus* strongly influences the algal community in its territories, preventing dominance by *Jania* spp. Hata and Kato (2003) also found that resident herbivorous damselfishes, *Stegastes nigricans,* excluded other herbivores from their territories and this species is unique in maintaining monocultural algal farms of the filamentous rhodophyte *Polysiphonia* sp.

In this study, when comparing algal percent cover between inside and outside cages, the algal cover inside cages was lower than outside cages, probably because there might have been some smaller fishes or small grazers which entered into the cages and graze the algae. Higher standing crop of filamentous algae may provide a shelter and thus enhance density of invertebrate micrograzers (Kennelly, 1983; Lobel, 1980 see Russ, 1987 for other references). Brawley and Adey (1981) noted that amphipods reduced algal cover when predators such as carnivorous fish were excluded and Kennelly (1983) suggested that the caging led to an increase in the abundance of small invertebrate grazer which caused a reduction of algal abundance inside cages.

The abundance of *Dictyerpa* stage of *Padina* increased quickly during the first 6 months of the experiment in all plots especially in the dry clearing season and then decreased quickly after that, which might be the result of a certain unpalatable characteristic of *Dictyerpa* stage of *Padina* by calcium accumulation which would not be preferred by herbivores. Damselfish also maintain algal farms by selective weeding of indigestible algae and late-colonizing algae to maintain highly digestible algae (Hata and Kato, 2003).

In conclusion, there was no significant difference on herbivory effect on algal abundance between the absence of fish grazing within cages and inside damselfish territories without cage. This result contrasted with other studies which have tested on the effect of herbivores especially damselfishes in the tropical areas. Those studies showed that damselfishes were well known for their effects on algal communities and they were capable of maintaining the high abundance and species diversity of tropical benthic algae inside their territories (Hixon and Brostoff, 1996; Ferreira *et al.*, 1998). The results can be explained by the following cases 1) cages with this mesh size would exclude fishes larger than 2 cm high but would allow smaller fishes or small invertebrate grazers to the cages. In the cages, micrograzers were protected from fishes or other predators and then they could graze the algae. 2) the epilithic algal communities provided shelter and food to various micrograzers or mesoinvertebrates which contribute to greater grazing. The last possible explanation was that the existing algae were not the preferred food for the fishes. Further experiments to test the above possibilities would be necessary to address herbivore's role (smaller fisher and small grazers such as isopods and amphipods) in algal succession in this habitat type and other aspects of disturbances such as frequency, size, and location on algal succession should be investigated.

REFERENCES

Airoldi, L. and Cinelli, F. 1997. Effects of sedimentation on subtidal macroalgal assemblages: an experimental study from a Mediterranean rock shore. *J. Exp. Mar. Biol.Ecol.* 215: 269-288.

Anderson, M. J. and Underwood, A. J. 1997. Effects of gastropod grazers on recruitment and succession of an estuarine assemblage : a multivariate and univariate approach. *Oecologia.* 109. 442-453.

Begon, M., Harper, J. L. and Townsend, C. R. 1996. *Ecology: Individuals, Populations and Communities.* 3 nd edition. Blackwell Scientific publications. Oxford, 1068 pp.

Benedetti-Cecchi, L. and Cinelli, F. 1993. Early patterns of algal succession in a midlittoral community of the Mediterranean sea: a multifactorial experiment. *J. Exp. Mar. Bio. Ecol.* 169: 15-31.

Benedetti-Cecchi, L. and Cinelli, F. 1996. Patterns of disturbance and recovery in littoral rock pools: nonhierarchical competition and spatial variability in secondary succession. *Mar. Ecol. Prog. Ser.* 135: 145-161.

Belliveau, S. A. and Paul, V, J. 2002. Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. *Mar. Ecol. Prog. Ser.* 232: 105-114.

Brawley, S. H. and Adey, W. H. 1981. The effect of micrograzers on algal community structure in a coral reef microcosm. *Mar. Biol.* 61: 167-177.

Breitburg, D. L. 1984. Residual effects of grazing: inhibition of competitor recruitment by encrusting coralline algae. *Ecology.* 65: 1136-1143.

Breitburg, D. L. 1985. Development of a subtidal epibenthic community: factors affecting species composition and the mechanisms of succession. *Oecologia* 65: 173-184.

Bold, H. C. and Wynne, M. J. 1978. *Introduction to the Algae*. Prentice Hall, Inc. Englewood Cliffs, New Jersey.

Carpenter, R. C. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecol. Monogr.* 56, 345-363.

Ceccarelli, D. M., Jones, G. P. and McCook, L. J. 2001. Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. *Oceanogr. Mar. Biol. Annu. Rev.* 39: 355-389.

Connell, J. H. 1961.The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*. 42: 710-723.

Connell, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecol. Monogr.* 40: 49-78.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science.* 199: 1302-1310.

Connell, S. D. and Anderson, M. J. 1999. Predation by fish on assemblages of intertidal epibiota: effects of predator size and patch size. *J. Exp. Mar. Biol. Ecol.* 241, 15-29.

Connell, J. H., Slatyer, R. O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111: 1119-1144.

Cribb, A. B. 1996. *Seaweeds of Queensland a naturalist's guide.* Kingswood Press, Underwood, Qld, 130.

Dayton, P. K. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351-389.

Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* 45: 137-159.

Dayton,P. K., Curriee, V., Gerrodette, T. Keller, B.D., Rosenthal, R. and Tresca, D. V. 1984. Patch dynamics and stability of some California kelp communities. *Ecol. Monogr.* 54: 253-289.

Dean, R. L. and Connell, J. H. 1987a. Marine invertebrates in an algal succession I. Variations in Abundance and diversity with succession. *J. Exp. Mar. Biol. Ecol.* 109: 195-215.

Dean, R. L. and Connell, J. H. 1987b. Marine invertebrates in an algal succession II. Tests of hypotheses to explain changes in diversity with succession. *J. Exp. Mar. Bio. Ecol.* 109: 217-247.

Denley, E. J. and Dayton, P. K. 1985. Competition among macroalgae. In Littler, M. M. and Littler, D. S. (eds.), *Handbook of Phycological Methods:Ecological Field Methods : Macroalgae.* pp. 511-530. Cambridge University Press. New York.

Denley, E. J. and Underwood, A. J. 1979. Experiments on factors influencing settlement, survivorship and growth of two species of barnacles in New South Wales. *J. Exp. Mar. Biol. Ecol.* 36: 269-293.

Dethier, M. N. 1984. Disturbance and recovery in intertidal pools: maintenance of mosaic patterns. *Ecol. Monogr.* 54: 99-118.

Dethier, M. N. Graham E. S., Cohen, S. and Tear, L. M. 1993. Visual versus random-point percent cover estimation : 'objective' is not always better. *Mar. Ecol. Prog. Ser.* 96: 93-100.

Eggeling, W. J. 1947. Observations on the ecology of the Budogo rain forest, Uganda. *J. Ecol.* 34: 20-87.

Emerson, S. E. and Zedler, J. B. 1978. Recolonization of intertidal algae: an experimental study. *Mar. Biol.* 44: 315-324.

Eriksson, B. K. 2002. *Long-term changes in macroalgal vegetation on the Swedish coast. An evaluation of eutrophication effects with special emphasis on increased organic sedimentation.* Ph.D. Dissertation, Uppsala University, Sweden. 34 pp.

Farrell, T. M. 1991. Models and mechanisms of succession: An example from a rocky intertidal community. *Ecol. Monogr.* 61: 95-113.

Ferreira, C. E., Goncalves, J. E., Coutinho, R. and Peter, A. C. 1998. Herbivory by the dusky damselfish *Stegasters fuscus* (Cuvier, 1830) in a tropical rocky shore: effects on the benthic community. *J. Exp. Mar. Biol. Ecol.* 229: 241-264.

Foster, M. S. 1975a. Algal succession in a *Macrocystis pyrifera* Forest. *Mar. Biol.* 32, 313-329.

Foster, M. S. 1975b. Regulation of algal community development in a *Macrocystis pyrifera* forest. *Mar. Biol.* 32: 331-342.

Foster, M. S. and Sousa, W. P. 1985. Succession. In Littler, M. M. and Littler, D. S. (eds.), *Handbook of Phycological Methods:Ecological Field Methods : Macroalgae*. pp. 269-290. Cambridge University Press. New York

Foster, M. S., Nigg, E. W., Kiguchi, L. M., Hardin, D. D. and Pearse, J. S. 2003. Temporal variation and succession in an algal-dominated high intertidal assemblage. *J. Exp. Mar. Biol. Ecol.* 289: 15-39.

Gaines, S. D. 1982. *"The Role of Consumer Guild Structure in Community Organization: Tests in Temperate and Tropical Intertidal Communities."* Ph.D. Dissertation, Oregon State University, Corvallis. 131 pp.

Gleeson, S. K. and Wilson, D. S. 1986. Equilibrium diet: optimal foraging and prey coexistence. *Oikos.* 46: 139-144.

Glynn, P. W. 1976. Some physical and biological determinants of coral community structure in the eastern Pacific. *Ecol. Monogr.* 46: 431-456.

Harlin, M. M. and Lindbergh, J. M. 1977. Selection of substrata by seaweeds: optimal surface relief. *Mar. Biol.* 40: 33-40.

Hata, H. and Kato, M. 2002. Weeding by the herbivorous damselfish *Stegastes nigricans* in nearly monocultural algae farms. Mar. Ecol. Prog. Ser. 237: 227-231.

Hata, H. and Nishihira, M. 2002. Territorial damselfish enhances multi-species co-existence of foraminifera mediated by biotic habitat structuring. *J. Exp. Mar. Biol.Ecol.* 270: 215-240.

Hata, H., Nishihira, M. and Kamura, S. 2002. Effects of habitat-conditioning by the damselfish *Stegastes nigricans* (Lacepède) on the community structure of benthic algae. *J. Exp. Mar. Biol. Ecol.* 280: 95-116.

Hata, H. and Kato, M. 2003. Demise of monocultural algal farms by exclusion of territorial damselfish. *Mar. Ecol. Prog. Ser.* 263: 159-167.

Hawkins, S. J. 1981. The influence of season and barnacles on the algal colonization of *Patella vulgata* ecclusion areas. *J. Mar. Biol. Ass. UK* 61:1-15.

Hawkins, S. J. and Hartnoll, R. G. 1985. Grazing of intertidal algae by marine invertebrates. Oceanography and Marine Biology: Annual Review. 21: 195-282.

Hay, M. E. 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology.* 62: 739-750.

Hay, M. E. 1997. The ecology and evolution of seaweed-herbivore interactions on coral reefs. *Coral Reefs.* 16:S67-S76.

Hixon, M. A. and Brostoff, W. N. 1996. Succession and Herbivory: Effects of Differential Fish Grazing on Hawaiian Coral-Reef Algae. *Ecol. Monogr.* 66. 67-90.

Hurby, T. and Norton, T. A. 1979. Algal colonization on rocky shores in the Firth of Clyde. *J. Ecol.* 67: 65-77.

Huston, M. and Smith, T. 1987. Plant succession: life history and competition. *Am. Nat.* 130: 168-198.

Hutchins, L. W. 1952. Relations to local environment. In Marine Fouling and Its Prevention , 102-117, U.S. Naval Institute, Annapolis, Md.

Jara, H. F. and Moreno, C.A. 1984. Herbivory and structure in a midlittoral rocky community: a case in southern Chile. *Ecology.* 65: 28-38.

Keever, C. 1950. Causes of Succession on old Fields of the Piedmont, North Carolina. *Ecol. Monogr.* 20: 229-250.

Kenelly, S. J. 1983. An experimental approach to the study of factors affecting algal colonization in a sublittoral kelp forest. *J. Exp. Mar. Biol. Ecol.* 68: 257-276.

Kennelly, S. J. 1987. Physical disturbances in an Australian kelp community. I. Temporal effects. *Mar. Ecol. Prog. Ser.* 40:145-153.

Kim, J. H. and DeWreede, R. E. 1996. Effects of size and season of disturbance on algal patch recovery in a rocky intertidal community. *Mar. Ecol. Prog. Ser.* 133: 217-228.

Kim, J. H. 1997. The role of herbivory, and direct and indirect interactions, in algal succession. *J. Exp. Mar. Biol. Ecol.* 217:119-135.

Kim, Y. H., J. S. Yoo and J. H. Kim. 1992. Marine algal succession in a perturbated intertidal community. *Kor. J. Phycol.* 7: 131-137.

Kitching, J. A. 1937. Studies in sublittoral ecology. II. Recolonization at upper margin of the sublittoral region, with a note on the denudation of *Laminaria* forest by storms. *J. Ecol.* 25: 482-495.

Klumpp, D. W. and Polunin, N. V. C. 1989. Partitioning among grazers of food resources within damselfish territories on a coral reef. *J. Exp. Mar. Biol. Ecol.* 125: 145-170.

Lewis, S. M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol. Monogr.* 56: 183-200.

Lewmanomont, K. and Ogawa, H. 1995. *Common seaweeds and seagrasses of Thailand.* 164 pp. Integrated Promotion Technology Co. Ltd., Bangkok, Thailand.

Littler, M. M. and Littler, D.S. 1985. *Handbook of Phycological Methods:Ecological Field Methods : Macroalgae.* 617 pp. New York: Cambridge University

Press.

Littler, D. S. and Littler, M. M. 2000. *Caribbean Reef Plants.* Offshore Graphics, Inc. United States of America.

Lobban, C. and Harrison, P. J. 1994. *Seaweed Ecology and Physiology.* 380 pp. Cambridge University Press, New York.

Lobel, P. S. 1980. Herbivory by damselfishes and their role in coral reef community ecology. *Bull. Mar. Sci.* 30: 273-289.

Lonya, Y. 1976. Recolonization of Red Sea corals affected by natural catastrophes and man-man perturbations. *Ecology.* 57: 278-289.

Lotze, H. K., Worm, B. and Sommer, U. 2000. Progagule banks, herbivory and nutrient supply control population development and dominance patterns in macroglagal blooms. *Oikos.* 89: 46-58.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am. Nat.* 112: 23-39.

Lubchenco, J. 1982. Effects of Grazers and algal competitors on fucoid colonization in tide pools. *J. Phycol.* 18: 544-550.

Lubchenco, J. 1983. *Littorina* and *Fucus*: Effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology.* 64: 1116-1123.

Lubchenco, J. and Gaines, S. D. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Ann. Rev. Ecol. Syst.* 12: 405-437.

Lubchenco, J. and Menge, B. A. 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.* 48: 67-94.

Mayakun, J. and Prathep, A. 2005. Seasonal variations in diversity and abundance of macroalgae at Samui Island, Surat Thani Province, Thailand. Songklanakarin J. Sci. Technol. 27: 653-663.

McClanahan, T. R. 1997. Primary succession of coral-reef algae: Differing patterns on fished versus unfished reefs. *J. Exp. Mar. Biol. Ecol.* 218: 77-102.

McClanahan, T. R., Nugues, M., Mwachireya, S. 1994. Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: The role of reef management. *J. Exp. Mar. Biol. Ecol.* 184: 237-254.

Menge, B. A. and Farrell, T. M. 1989. Community structure and interaction webs in shallow marine hard-bottom communities: tests of an environmental stress model. *Adv. Ecol. Res.* 19: 189-262.

Menge, B. A. and Lubchenco, J. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecol. Monogr.* 51: 429-450.

Miller, T. E. 1982. Community diversity and interactions between the size and frequency of disturbance. *Am. Nat.* 120: 533-536.

Montgomery, W. L. 1980. Comparative feeding ecology of two herbivorous damselfishes (Pomacentridae: Teleostei) from the Gulf of California, Mexico. *J. Exp. Mar. Biol. Ecol.* 47: 9-24.

Niell, F. X. 1979. Structure and succession in rocky algal community of temperature intertidal system. *J. Exp. Mar. Biol. Ecol.* 36: 185-200.

Northcraft, R. D., 1948. Marine algal colonization on the Monterey Peninsula. *Amer. J. Bot.* 35: 396-404.

Olson, A. M. 1985. *"Early succession in Beds of the Red Alga, Iridaea cornucopiae Post. & Rupr. (Gigartinaceae): Alternate Pathways".* Master's thesis, Oregon State University. 86 pp.

Osman, R. 1977. The establishment and development of a marine epifaunal community. *Ecol. Monogr.* 47: 37-63.

Padilla, D. 1981. *"Selective Agents Influencing the Morphology of Coralline Algae."* Master's thesis, Oregon State University, Corvallis. 80 pp.

Paine, R. T. 1966. Food web complexity and species diversity. *Amer. Nat.* 100: 65-75.

Paine, R. T. 1976. Size-limited predation: An observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology.* 57: 858-873.

Paine, R. T. 1977. Controlled manipulations in the marine intertidal zone and their contributions to ecological theory. *Spec. Publ. Acad. Nat. Sci Philadelphia* 12 : 245-270.

Paine, R. T. and Levin, S. A. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.* 51: 145-178.

Peer, R. L. 1986. The effects of microcrustaceans on succession and diversity of an algal microcosm community. *Oecologia.* 68: 308-314.

Prathep, A. 2005. Spatial and temporal variations in diversity and percentage cover of macroalgae at Sirinat Marine National park, Phuket province, Thailand. *ScienceAsia.* 31: 225-233.

Prathep, A., Marrs, R. H. and Norton, T. A. 2003. Spatial and temporal variations in sediment accumulation in an algal turf and their impact on associated fauna. *Mar. Biol.* 142: 381-390.

Pielou, E. C. 1977. *Mathematical Ecology.* John Wiley & Sons, New York, 385 pp.

Prud'homme van Reine W, F and Trono, Jr., G.C. 2001. *Plant Resources of South-East Asia No. 15 (1). Cryptograms: Algae.* 318 pp. Backhuys Publishers, Leiden.

Rees, T. K. 1940. Algal colonization at Mumbles Head. *J. Eol.* 28: 403-437.

Russ, G. R. 1987. Is rate of removal of algae by grazers reduced inside territories of tropical damselfishes? *J. Exp. Mar. Biol. Ecol.* 110: 1-17.

Robles, C. D. and Cubit, J. D. 1981. Influence of biotic factors in an upper intertidal community: dipteran larvae grazing on algae. *Ecology.* 62. 1536-1547.

Saito, Y., S. Naganawa and H. Miyasaka. 1977. The climax phase and its recognition in intertidal algal vegetation. *Jap. J. Ecol.* 27: 33-43.

Saito, Y., H. Sasaki and Watanabe. K. 1976. Succession of algal communities on the vertical substratum faces of breakwaters in Japan. *Phycologia.* 15: 93-100.

Sammarco, P. W. 1983. Effects of fish grazing and damselfish territoriality on coral reef algae. I. Algal community structure. *Mar. Ecol. Prog. Ser.* 13: 1-14.

Serisawa, Y. and Ohno, M. 1995a. Succession of seaweed communities on artificial reefs in Tei, Tosa Bay, Japan. *Nippon Suisan Gakkaishi.* 61: 854-859.

Serisawa, Y. and Ohno, M. 1995b. Succession of seaweed communities on artificial reefs in the inlet of Tosa Bay, Japan. *Suisanzoshoku.* 43: 437-443.

Serisawa, Y., Taino, S., Ohno. M. and Arugn. Y. 1998. Succession of seaweed on the experimental plates immersed during seasons in Tosa Bay. Japan. *Bot. Mar.* 41, 321-328.

Smith, R. L. and Smith, T. M. 2001. *Ecology & Field Biology.* 6 th edition. 771 pp. Lehigh Press.

Somsueb, S., Ohno, M. and Kimura, H. 2001. Development of seaweed communities on suspended substrata with three slope angles. *J. Appl. Phycol.* 13, 109-115.

Sousa, W. P. 1979a. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecol Monogr.* 49: 227-254.

Sousa, W. P. 1979b. Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity. *Ecology.* 60: 1225-1239.

Sousa, W. P. 1980. The responses of a community to disturbance: the importance of successional age and species' life histories. *Oecologia.* 45: 72-81.

Sousa. W. P. 1984a. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. *Ecology.* 65: 1918-1935.

Sousa, W. P. 1984b. The role of disturbance in natural communities. *Ann. Rev. Ecol. Syst.* 15: 353-391.

Sousa, W. P. and Schroeter, S. C. and Gaines, S. D. 1981. Latitudinal Variation in Intertidal Algal Community Structure: the Influence of Grazing and Vegetative Propagation. *Oecologia.* 48: 297-307.

Stewart, J. G. 1983. Fluctuations in the quantity of sediment trapped among algal thalli on intertidal rock platforms in southern California. *J. Exp. Mar. Biol. Ecol.* 73: 205-211.

Thacker, R. W., Ginsburg, D. W. and Paul, V. J. 2001. Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. *Coral Reefs.* 19: 318-329.

Thongroy, P. 2006. " *Spatial and Temporal Variations in Diversity, Abundance and Distribution of Macroalgae at Sirinat Marine Park, Phuket Province, Thailand*" Master's thesis, Prince of Songkla University, Hat Yai. 145 pp.

Tilman, D. 1985. The resource ratio hypothesis of succession. *Am. Nat.* 125: 827-852.

Tuner, T. 1983. Complexity of early and middle successional stages in a rocky intertidal surfgrass community. *Oecologia.* 60: 56-65.

Turner, S. and Todd, C. D. 1993. The early development of epifaunal assemblages on artificial substrata at two intertidal sites on an exposed rocky shore in St. Andrews Bay, N. E. Scotland. *J. Exp. Mar. Biol. Ecol.* 166: 251-272.

Underwood, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol. Ann. Rev.* 19: 513-605.

Underwood, A. J. and Anderson, M. J. 1994. Seasonal and temporal aspects of recruitment and succession in an intertidal estuarine fouling assemblage. *J. Mar. Biol. Ass. UK.* 74: 563-584.

Underwood, A. J. 1998. Grazing and disturbance: an experimental analysis of patchiness in recovery from a severe storm by the intertidal alga *Hormosira banksii* on rocky shores in New South Wales. *J. Exp. Mar. Biol. Ecol.* 231: 291-306.

Underwood, A. J. 1999. Physical disturbances and their direct effect on an indirect effect: responses of an intertidal assemblage to a severe storm. *J. Exp. Mar. Biol. Ecol.* 232: 125-140.

Vadas, R. L. 1985. Herbivory. In Littler, M. M., and Littler, D. S. (eds). *Handbook of phycological methods. Ecological field methods: macroalgae.* pp. 531–572 Cambridge University Press, Cambridge, England.

Van Tamelen, P. G. 1987. Early successional mechanisms in the rocky intertidal: the role of direct and indirect interactions. *J. Exp. Mar. Biol. Ecol.* 112: 39-48.

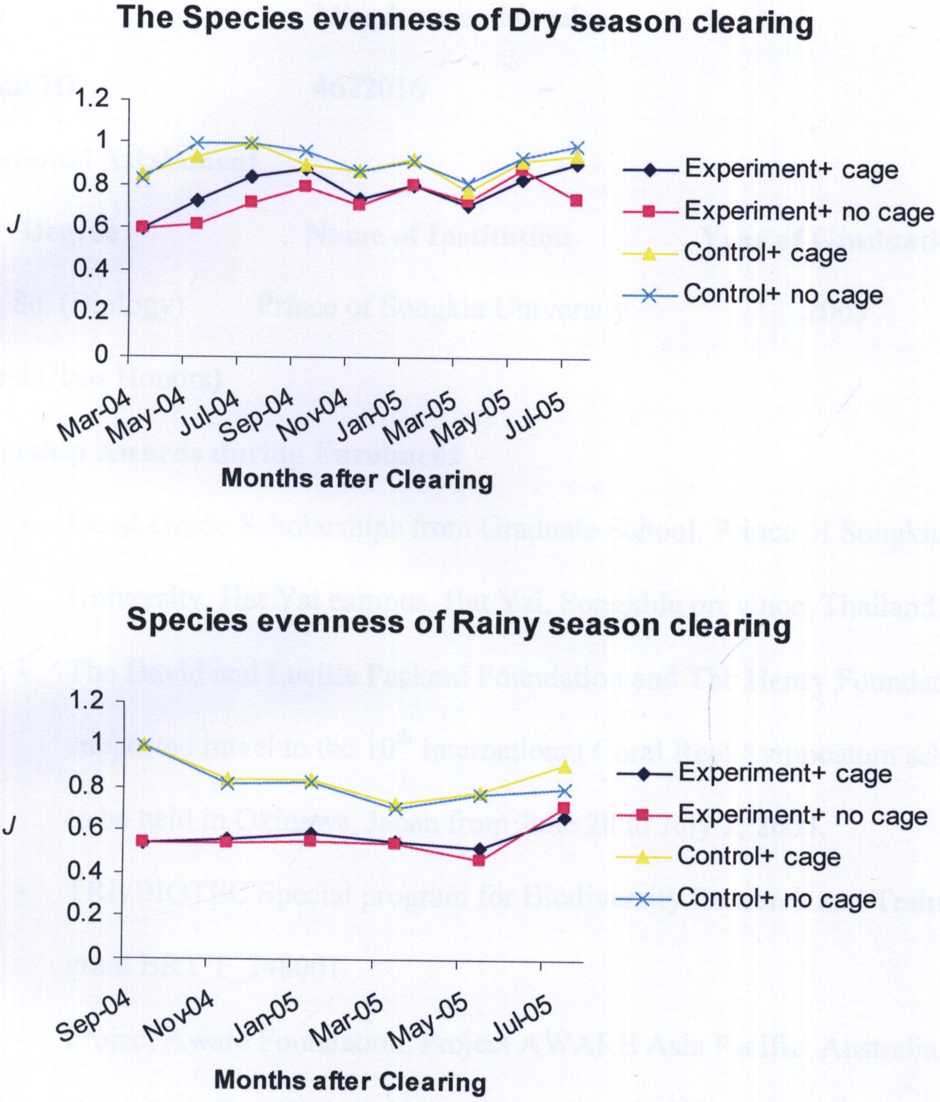
Williams, G. A., Davies, M. S. and Nagarkar, S. 2000. Primary succession on a seasonal tropical rocky shore: the relative roles of spatial heterogeneity and herbivory. *Mar. Ecol. Prog. Ser.* 203: 81-94.

Wilkinson, C. R., and Sammarco, P. W. 1983. Effects of fish grazing and damselfish territoriality on coral reef algae. II. Nitrogen fixation. *Mar. Ecol. Prog. Ser.* 13: 15-19.

Wilson, O. T. 1925. Some experimental observations of marine algal succession. *Ecology*. 6: 303-311.

Wootton, J. T. 2002. Mechanisms of successional dynamics: Consumers and the rise and fall of species dominance. *Ecol. Res.* 17: 249-260.

APPENDIX



Appendix 1. Temporal patterns of species evenness of A) Dry season and B) Rainy season.

VITAE

Name	Miss Jaruwan Mayakun
Student ID	4622016

Educational Attainment

Degree	Name of Institution	Year of Graduation
B. Sc. (Biology) (Second Class Honors)	Prince of Songkla University	2003

Scholarship Awards during Enrolment

- Good-Grade Scholarships from Graduate School, Prince of Songkla University, Hat Yai campus, Hat Yai, Songkhla province, Thailand.
- The David and Lucille Packard Foundation and The Henry Foundation supported travel to the 10th International Coral Reef Symposium scheduled to be held in Okinawa, Japan from June 28 to July 2, 2004.
- TRF/BIOTEC Special program for Biodiversity Research and Training grant BRT T_348001.
- Project Aware Foundation, Project AWARE Asia Pacific, Australia.
- Grant from Faculty of Science, Prince of Songkla University, Hat Yai campus, Hat Yai, Songkhla province, Thailand to support traveling to Department of Biological Science, Sungkyunkwan University, Suwan, South Korea from July 24- October 21, 2005.
- Support grant from the World Agency for Planetary Monitoring and Earthquake Risk Reduction (WAPMERR) for participation in International Workshop *"Post-Disaster Assessment and Monitoring of Changes in*

Coastal, Ocean, and Human Systems in the Indian Ocean and Asian Waters" that organized by UNESCO-IOC/WESTPAC and the Department of Marine and Coastal Resources (DMCR) of the Ministry of Environment and Natural Resources of Thailand, Royal Phuket City Hotel, Phuket, Thailand from 20-24 February 2006.

List of Publication and Proceeding

- Mayakun, J. and Prathep, A. 2005. Seasonal variations in diversity and abundance of macroalgae at Samui Island, Surat Thani Province, Thailand. Songklanakarin J. Sci. Technol. 27: 653-663.
- Mayakun, J., Kim, J. H. and Prathep, A. Effects of Herbivory and Season of Clearing on Species Composition and Algal Succession in a tropical intertidal shore, Phuket, Thailand. (In preparation)