Songklanakarin J. Sci. Technol.
41 (2), 483-489, Mar. - Apr. 2019

http://www.sjst.psu.ac.th

Original Article

Spatial variation in early patterns of algal recruitment in a tropical intertidal community

Jaruwan Mayakun

Seaweed and Seagrass Research Unit, Excellence Centre for Biodiversity of Peninsular Thailand,
Department of Biology, Faculty of Science,
Prince of Songkla University, Hat Yai, Songkhla, 90112 Thailand

Received: 14 July 2017; Revised: 13 November 2017; Accepted: 12 December 2017

Abstract

Spatial variation in the patterns of early algal recruitment in a tropical intertidal shore was tested among different degrees of wave exposure and shore elevation levels. Algal recruitment showed a simple pattern. An ephemeral green alga, *Ulva paradoxa* was the early colonist that had high coverage and *Padina* in Vaughaniella stage and *Polysiphonia sphaerocarpa* were late successional algae that had very low coverage. This might be because *Ulva* is an opportunist pioneer species that reproduces all the year round with a large numbers of motile gametes and has a fast colonization, while those two species are slower colonizers. The degree of wave exposure and shore elevation level had no significant effect on the percentage covers of three dominant algae. However, the plots cleared at the exposed shore had the lowest percent cover of three algal species and algal species diversity, because the arrival and settlement of new recruits were influenced by wave action and absence of a stable and suitable substrate.

Keywords: algal recruitment, intertidal community, wave exposure, shore level, spatial variation

1. Introduction

Macroalgal community structure and the processes of recruitment and succession in intertidal zones are spatially and temporally variable because of influences by various disturbances that can produce patches of cleared areas and play roles in the arrival and subsequent survival of new recruits (Connell, 1985; Hutchinson & Williams, 2001; Sousa, 1979a, 1984). Natural disturbances such as wave action can open up a space for new algal recruits that recolonize cleared patches through vegetative regrowth or from spores. Differences in season and location of cleared patches produce different patterns of recruitment and succession (Hutchison & Williams, 2001) determined by the seasonal availability of propagules (Foster, 1975; Kim & DeWreede, 1996), the densities of new recruits in the water column (Hutchinson & Williams, 2001), dispersal, and the life-history traits of the species involved (Benedetti-Cecchi & Cinelli, 1993).

The recruitment and succession of algae have traditionally been investigated by field experiments mostly in coral, rocky intertidal and subtidal algal communities (Anderson & Underwood, 1997; Benedetti-Cecchi & Cinelli, 1996; Connell, 1978; Connell & Anderson, 1999; Foster, 1975; Kim & DeWreede, 1996; Mayakun, Kim, & Prathep, 2010; Sousa, 1979a, 1979b; Sousa, 1980; Underwood, 1998; Underwood, 1999). Numerous studies have shown that the structure of the algal population and community and the successional processes leading to them are influenced by disturbances. In the tropical intertidal zone, space or gaps might be formed as a result of grazing, severe wave action, boat anchors, and log battering that can overturn the boulders. Grazing and season of disturbance can influence algal biomass, their abundance, species competition, recruitment and succession patterns (Belliveau & Paul 2002; Benedetti-Cecchi & Cinelli, 1993; Foster, Nigg, Kiguchi, Hardin, & Pearse, 2003; Hutchinson & Williams, 2001; Kim, 1997; Littler & Littler, 1985; Lotze, Worm, & Sommer, 2000; Lubchenco, 1978; Sousa, 1979b; Mayakun

---

*Corresponding author
Email address: jaruwan.may@psu.ac.th

et al., 2010; McClanahan, 1997). Water motion can also affect algal abundance, distribution (Haring, Dethier, & Williams, 2002; Prathep, Wichachucherd, & Thongroy, 2007) and intertidal macroalgal succession by influencing the arrival and subsequent survival of new recruits and the dispersal range of the algal propagules (Vadas, Johnson, & Norton, 1992). In addition, strong waves have been known to inhibit settlement and recruitment of algal spores by washing new germlings away (Prathep, 2005) and moving potential settlement substrata (personal observation). According to the intermediate disturbance hypothesis, the algal species diversity tends to be greater at a shore where there is a moderate level of disturbance, compared to an undisturbed shore.

There are large spatial and temporal fluctuations in algal abundance, distribution, and succession patterns in intertidal areas (Benedetti-Cecchi & Cinelli, 1994; Foster et al., 20 03). However, studies have mostly concentrated on algal recruitment and succession in the upper intertidal or low intertidal zones rather than comparing between shores or even within shores. In addition, experimental tests of the influence of degree of wave exposure and shore level on algal recruitment and succession patterns in an algal intertidal community is lacking. There have been few quantitative descriptions of spatial variations in early patterns of algal recruitment in a tropical intertidal shore.

In Thailand, spatial variation in the recruitment patterns is rare and the published research on successional stages in the intertidal and subtidal zones is scant. A better understanding of algal succession patterns in Thailand and tropical intertidal communities will enable prediction of the algal intertidal community changes due to environmental changes; and this information, in turn, can be useful for coastal management. The aim of this study was to demonstrate the spatial variation in the early patterns of algal recruitment in a tropical intertidal community. Experiments were designed to assess the following questions: (1) Does the degree of wave exposure and shore level affect early patterns of algal recruitment? (2) What are the pattern(s) of algal recruitment in each spatial zone?

2. Materials and Methods

2.1 Study site

The study site was located at the intertidal zone of Koh Pling, Sirinat Marine National Park (8° 05’ N, 98° 17’ E), Phuket Province, Southern Thailand. The climate of this area is under monsoonal influence. There are two dominant seasons, a rainy season dominated by the southwest monsoon (May-October) and a dry season predominated by the northeast monsoon (November to April). The tide range at Phuket was 0.5-3.6 m (mean sea level was 2.0 m) above mean sea level in 2013. The shore was around 1.5 km long (Prathep, 2005). This area has a variety of marine habitats such as rocky shores, coral reefs and seagrass beds. The study site was a dead coral bed with dead coral fragments. There is a high diversity of marine macroalgae (52 species) (Thongroy, Liao, & Prathep, 2007); *Padina* was the most common species. Three species of seagrasses were also found at this study site, *Thalassia hemprichii* (Ehrenb.) Aschers, *Cymodocea rotundata* Ehrenb. Et Hempr. Ex Aschers. and *Enhalus aco-roides* (L.f) Royle (personal observations).

2.2 Methods

Experiments were carried out among different categories of the shoreline based on different degrees of wave exposure (sheltered, semi-exposed, and exposed shore). The sheltered and the semi-exposed shore were protected by fringing reefs and the exposed shore was directly influenced by wave action. The average water currents at the sheltered, semi-exposed, and exposed shore were 4.36±1.13 m s^{-1}, 6.92± 0.77 m s^{-1}, 8.82±0.97 m s^{-1}, respectively. Three shore levels were recognized; the upper, middle, and lower shore. 0-40 m was designated as the upper shore level, 41-80 m was the middle shore level, and 81-120 m was lower shore level as described in Prathep (2003, 2005) and Thongroy *et al*. (2007).

Dead coral plots of 20 x 20 cm were permanently marked using thread and labeled. All marked plots were cleared by hand chiseling, scraped with a wire brush and then burned with saturated sodium hydroxide to clean and eliminate all organisms. The procedure was adapted from Mayakun *et al*. (2010). Due to dead coral patch availability, dead coral patches could only be cleared and marked in the middle shore level of sheltered, semi-exposed, and exposed shore. Also, only in the semi-exposed shore, the cleared dead coral patches were marked in the upper, middle, and lower shore. There were 15 cleared plots in total (3 cleared plots in each zone) and all plots were monitored every two months from January – October, 2013 during low tide. The percentage cover of each algal species was estimated in hundred 2 cm x 2 cm subplots (adapted from Kim & DeWreede, 1996; Mayakun *et al*., 20 10). All plots were photographed using a digital camera (Nikon COOLPIX AW110, Japan). Unknown specimens were collected, preserved in a 4% formalin-seawater solution, and brought back to the laboratory for identification. The samples were examined for morphology and also internal anatomy using identification guides (Lewmanomont & Ogawa, 1995; Littler & Littler, 2000). All specimens were photographed using a compound microscope (model: BX 51TF Olympus, No.1H20773, Japan fitted with DP 72).

2.3 Statistical analyses

The percentage algal cover was analyzed using a repeated measures analysis of variance (RM-ANOVA). A two-way ANOVA (site x time) with repeated measurements on the time factor was separately applied for each of the three dominant algal species of interest. Mauchly’s test indicated that the assumption of sphericity had been violated; therefore the degrees of freedom were corrected using the Greenhouse-Geisser estimates of sphericity. Homogeneity of variance was determined using the Cochran’s *C*-test. In the case of a violation, arcsine-transformation was made prior to analysis. Species diversity was calculated using Shannon-Wiener index. All data were analyzed using the computer program SPSS for Windows version 16.0.

3. Results

In the control patches, three species, *Cladophora prolifera* (Roth) Kützing, *Padina* in Vaughaniella stage, and *Polysiphonia sphaerocarpa* Børgesen, were found. *Padina* in Vaughaniella stage was the dominant species at the sheltered and exposed shores and its highest percent cover were

90±5.8% and 80±2.9%, respectively. *C. prolifera* was an abundant and common species at all shore levels of the semi-exposed shore. *C. prolifera* had the highest cover at the upper (73.3±6.7%) than at the middle (70±10%), and lower shore levels (56.7±8.8%). *P. sphaerocarpa* was less common at all sites and its highest cover was 16.7±3.3% at the upper, 10% at the middle, and 23.3±3.3% at lower shore levels of the semi-exposed shore. There was greater species diversity in the control plots at the semi-exposed shore (H´=2.79) than those plots at the sheltered (H´=2.41) and exposed shores (H´=2.48). Additionally, the control plots at the middle shore level of the semi-exposed shore had a greater species diversity (H´=2.79) than those plots in the upper (H´=2.37) and the lower shore levels (H´=2.39).

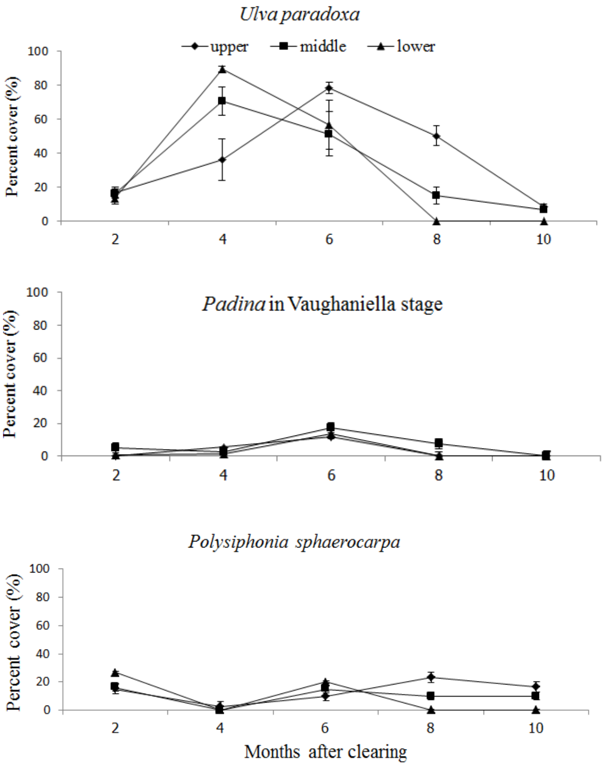
In the cleared patches, there were nine algal species that colonized and recruited, and three dominant species: *Ulva paradoxa* C. Agardh, *Padina* in Vaughaniella stage, and *Polysiphonia sphaerocarpa* Børgesen (Table 1). There was greater species diversity in the plots cleared at the semi-exposed shore (H´=2.76) than those plots cleared at the sheltered (H´=2.24) and exposed shores (H´=2.42). Also, the plots cleared at the middle shore level of the semi-exposed shore showed a greater species diversity (H´=2.76) than those cleared in the upper (H´=2.37) and lower shore levels (H´=2.38).

Table 1. Algal species list and the occurrence on each shore and site. C: common (≥ 10% in at least 1 sample); R: rare (≤ 10%); X: no occurrence.

Taxa	Abundance				
	Sheltered	Semi-exposed			Exposed
	Middle	Upper	Middle	Lower	Middle
Division Chlorophyta					
Boergesenia sp.	R	R	X	X	R
Cladophora prolifera (Roth) Kütz	X	C	C	C	X
Ulva paradoxa C. Agardh	C	C	C	C	X
Valonia aegagropila C. Agardh	C	C	C	X	R
Division Rhodophyta					
Ceramium mazatlanense Dawson	R	C	C	C	C
Chondophycus tronoi	C	X	X	X	C
Gelidiella sp.	R	X	X	X	X
Polysiphonia sphaerocarpa Børgesen	C	C	C	C	X
Class Phaeophyceae					
Padina in Vaughaniella stage	C	C	R	R	C

In this succession process, an ephemeral green alga, *U. paradoxa* was the earliest colonizer that recruited and colonized in the cleared plots. The early patterns of algal succession in this intertidal community were variable in time. *U. paradoxa* was the dominant species at all shore levels and had the highest percentage cover at the lower (89.3±1.5%) than at the middle (70.5±8.1%) and upper shore levels (36±11.1%) within the first four months after clearing. However, cover by *U. paradoxa* at the upper shore level increased in 6 and 8 months after clearing (78.3±3.3% and 50±5.8%, respectively) and its cover decreased afterwards (Figure 1). The late successional algae, *Padina* in Vaughaniella stage, and *P. sphaerocarpa* were rare and had a very low cover throughout the study. Their highest percent cover was 17.5±4.8% and 26.7±6.3%, respectively. However, the different shore levels did not significantly affect the percentage cover of these three algal species (*P* = 0.180, 0.408, 0.297, respectively; Table 2), but their cover varied through time. In addition, there was only a significant interaction between the shore level and time on the percentage cover of *U. paradoxa* (*P* = 0.000; Table 2).

The percentage cover of all algae was not significantly affected by the degree of wave exposure (Table 3). *U. paradoxa* had the greatest percentage cover at the semi-exposed shore (70.5±8.1%) and was not found at the exposed shore. *Padina* in Vaughaniella stage colonized and covered at both the sheltered and semi-exposed shores within 10 months after clearing. *Padina* was more abundant at the sheltered


Ulva paradoxa

Padina in Vaughaniella stage

Polysiphonia sphaerocarpa

Figure 1. Percentage cover of the 3 dominant algal species; *Ulva paradoxa*, *Padina* in Vaughaniella stage, *Polysiphonia sphaerocarpa*, in cleared patches in the upper, middle, and lower shore levels of the semi-exposed shore. Data are mean values ± SE of three replicates for each sampling time.

Table 2. Effects of time and the shore elevation level (the upper, middle, and lower shore levels) on the percentage cover of the 3 dominant algae, *Ulva paradoxa*, *Padina* in Vaughaniella stage and *Polysiphonia sphaerocarpa*. A repeated measure ANOVA was applied to 10 months of data. * P <0.05; ** P <0.01; *** P <0.001; ns not significant.

Source of variation	*Ulva paradoxa*			*Padina* in Vaughaniella stage			*Polysiphonia sphaerocarpa*		
	df	MS	*F*	df	MS	*F*	df	MS	*F*
Between subjects									
Shore level	2	194.939	2.313 ns	2	68.814	1.043 ns	2	167.089	1.495 ns
Error	6	84.272		6	65.958		6	111.756	
Within subject									
Time	4	5764.604	30.552 ***	4	216.197	3.767 ns	4	476.978	3.643 *
Time x Shore level	8	1087.126	5.762 ***	8	18.800	0.328 ns	8	167.644	1.280 ns
Error	24	188.682		24	57.389		24	130.922	
Multivariate repeated measures analysis									
Effect	Wilks'lambda	*F*		Wilks'lambda	*F*		Wilks'lambda	*F*	
Time	0.007	113.793 **		0.161	3.915 ns		0.062	11.376 *	
Time x Shore level	0.050	2.596 ns		0.172	1.056 ns		0.121	1.407 ns	

Table 3. Effects of time and the degree of wave exposure (sheltered, semi-exposed, and exposed shores) on the percentage cover of the 3 dominant algae, *Ulva paradoxa*, *Padina* in Vaughaniella stage and *Polysiphonia sphaerocarpa*. A repeated measure ANOVA was applied to 10 months of data. * P <0.05; ** P <0.01; *** P <0.001; ns not significant.

Source of variation	*Ulva paradoxa*			*Padina* in Vaughaniella stage			*Polysiphonia sphaerocarpa*		
	df	MS	*F*	df	MS	*F*	df	MS	*F*
Between subjects									
Wave exposure	2	1611.014	2.574 ns	2	2535.139	3.089 ns	2	167.089	1.495 ns
Error	6	625.892		6	820.717		6	111.756	
Within subject									
Time	4	1233.908	2.347 ns	4	880.279	2.264 ns	4	76.354	0.726 ns
Time x Wave exposure	8	341.326	0.649 ns	8	307.153	0.790 ns	8	63.819	0.607 ns
Error	24	525.788		24	388.842		24	105.208	
Multivariate repeated measures analysis									
Effect	Wilks'lambda	*F*		Wilks'lambda	*F*		Wilks'lambda	*F*	
Time	0.303	1.728 ns		0.241	2.359 ns		0.300	1.749 ns	
Time x Wave exposure	0.223	0.839 ns		0.233	0.572 ns		0.285	0.654 ns	

shore (45±15.1%) than at the semi-exposed shore (17.5± 4.8%). However, *Padina* was found at the exposed shore with the highest cover; 57.5±8.3%, within the first 2 months, after which its cover dropped, and it disappeared by the first 4 months until the end of the study. *P. sphaerocarpa* had a very low cover at all sites and its highest cover was found at the sheltered shore; 16.7±7.7%. *P. sphaerocarpa* did not colonize at the exposed shore (Figure 2).

4. Discussion

In this study, algal recruitment showed the first stage of colonization. The early pattern of algal recruitment in this intertidal community varied over time. During this recruitment process, an ephemeral green alga, *U. paradoxa* was the pioneer species that recruited the cleared plots at the upper, middle, and lower shore levels of the semi-exposed

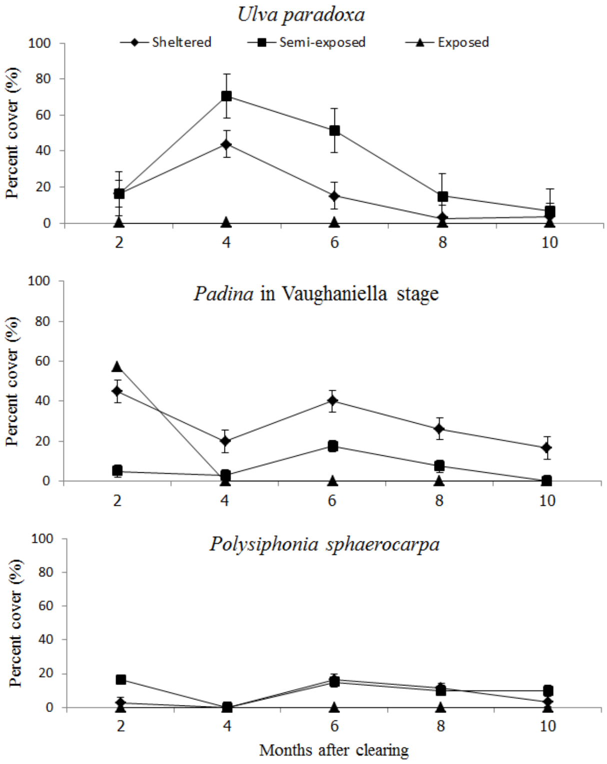


Figure 2. Percentage covers of the 3 dominant algal species; *Ulva paradoxa*, *Padina* in Vaughaniella stage, *Polysiphonia sphaerocarpa*, in the cleared patches in the sheltered, semi-exposed, and exposed shores. Data are mean values ± SE of three replicates for each sampling time.

shore. Additionally, *Ulva* was the earliest colonizer only at the sheltered and semi-exposed shores. *Ulva* covered the cleared plots within the first four months and remained until the end of the study. Then, *U. paradoxa* was replaced by *Padina* in Vaughaniella stage and *P. sphaerocarpa*. This is a similar result to the study of Mayakun *et al*. (2010), showing a simple pattern of algal succession and it took a year from *Ulva* stage to the late *Polysiphonia* stage.

For species diversity, our results showed that the plots cleared at the middle shore level and the semi-exposed shore had greater species diversity than at the other shores. It can be a result of the middle shore level and the semi-exposed shore would have a moderate wave disturbance. According to the intermediate disturbance hypothesis, more species would be found at the sites where exposed to the intermediate disturbance. Then, there would be more species diversity at the middle shore level and the semi-exposed shore. Cleared plots at the lower shore level of the semi-exposed shore and the exposed shore have been colonized by fewer because algae may have been washed away or overturned by the strong wave action. In addition, wave action can inhibit algal spore settling and recruitment (Prathep, 2005; Thongroy *et al*., 2007).

U. paradoxa was the dominant species in this study because it can reproduce large numbers of small and motile propagules throughout the year (Hoffmann & Ugarte, 1985). When spores have been released, *Ulva* zoospores have a swimming speed of around 0.2 mm s^{-1} and can settle quickly within minutes up to eight days under calm conditions (Callow, Callow, & Pickett-Heaps, 1997; Granhag, Larsson, & Jonsson, 2007). Also, *Ulva* has a high tolerance of the environment such as surviving a wide range of temperatures and salinities (Baamonde López, Baspino Fernández, Barreiro Lozano, & Cremades Ugarte, 2007; Mayakun *et al*., 2010; Sousa, 1979a). While, the other two species, *Padina* in Vaughaniella stage and *P. sphaerocarpa*, are slower colonizers, not good competitors, and have slower growth rates (Mayakun *et al*., 2010).

Statistical analyses showed that the shore elevation level and the degree of wave exposure do not appear to significantly affect algal percentage covers since shore elevation level varies little then the emersion time at low tide was not different between each shore level (Thongroy *et al*., 2007). Results showed that all sites did not have a significant difference in three dominant algal percentage covers but there was a difference in numbers of species between each site. All patches both at the sheltered and semi-exposed shores were dominated by *U. paradoxa*. *Padina* in Vaughaniella stage was mainly found at the sheltered shore and formed a slight cover at the semi-exposed shore. At the exposed shore, this Vaughaniella stage was only found for the first two months then disappeared until the end of the study. Meanwhile, *P. sphaerocarpa* had a very low cover at all sites.

In this study, the percentage covers of three dominant algal species in the cleared patches of the exposed shore were lower than in the cleared patches of both the sheltered and semi-exposed shores. It might be because the substrate in this exposed shore comprised of coral rubbles and fragments (personal observation). The absence of a stable and suitable substrate for algal recruitment can contribute to poor recruitment and survival of many algae (Vadas, Johnson, & Norton, 1992). In addition, wave action might be influencing the arrival, settlement, and survival of new recruits and algal propagules (Vadas *et al*., 1992). The algae at the sheltered and semi-exposed shores were less affected by wave action than the algae at the exposed shore. Wichachucherd, Liddle, and Prathep (2010) investigated the recruitment of *Padina* at an exposed shore and a sheltered shore of two different study sites and found that the recruitment was higher at the sheltered shore than the exposed shore. They suggested that more spores could settle under low wave action. On the other hand, strong wave action resulted in the washing away of spores and may prune or tear off any algal thallus, and may remove germlings or mature plants from the substrate. Corkum and Trites (2001) also found that high wave exposure could inhibit growth and increased the mortality rates of the brown alga, *Ascophyllum nodosum*. Granhag *et al*. (2007) reported that the settlement of *Ulva intestinalis* spores, its germling density, and biomass decreased with an increase of flow speed. In this study, however, Vaughaniella stage of *Padina* has often been observed in both semi-exposed and exposed shores. This Vaughaniella stage is known to be an early recruitment stage and the morphological plasticity of *Padina* allows it to form such creeping rhizomes which facilitate persistence during strong wave actions (Wichachucherd *et al*., 2010).

4.1 Conclusions

This study showed the simple pattern of algal succession during the first stages observed in this tropical intertidal shore. Nine algal species with three dominant species: *U. paradoxa*, *Padina* in Vaughaniella stage, and *P. sphaerocarpa* have been found colonizing and recruiting in the cleared patches. *U. paradoxa* was the pioneer species and the dominant species in this study. The species diversity varied between sites. The shore elevation level and the degree of wave exposure did not influence three dominant algal percentage covers significantly. However, the cleared plots of the exposed shore had the lowest percentage covers of algal species because wave action and absence of a stable and suitable substrate might be influencing the arrival, settlement, and survival of new recruits. Although disturbances such as timing of disturbance, herbivory, and nutrient can influence recruitment and succession patterns, studies in the tropical rocky shores and intertidal zones still remain unexplored. Then, the further experimental studies would allow us to assess and investigate the disturbance effects on algal successional patterns in order to get a better understanding about the tropical intertidal systems.

Acknowledgements

Special thanks to the Seaweed and Seagrass Research Unit team, PSU for helping me in the field. Special thanks to Dr. A. Prathep and Prof. Dr. J.H. Kim for providing critical comments and suggestions. Also thanks to Dr. B. Hodgson for assistance with the English. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

References

Anderson, M. J., & 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. doi:10.1007/s00 4420050104

Baamonde López, S., Baspino Fernández, I., Barreiro Lozano, R., & Cremades Ugarte, J. (2007). Is the cryptic alien seaweed *Ulva pertusa* (Ulvales, Chlorophyta) widely distributed along European Atlantic coasts? *Botanica Marina, 50,* 267-274. doi:10.1515/BOT.20 07.030

Belliveau, S. A., & Paul, V. J. (2002). Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. *Marine Ecology Progress Series,232,* 105-114. doi:10.3354/meps232105

Benedetti-Cecchi, L., & Cinelli, F. (1993). Early patterns of algal succession in a midlittoral community of the Mediterranean sea: a multifactorial experiment. *Journal of Experimental Marine Biology and Ecology, 169,* 15-31. doi:10.1016/0022-0981(93)90040-U

Benedetti-Cecchi, L., & Cinelli, F. (1994). Recovery of patches in an assemblage of geniculate coralline algae: variability at different successional stages. *Marine Ecology Progress Series, 110,* 9-18. Retrieved from www.int-res.com/articles/ meps/110/m 110p009.pdf

Benedetti-Cecchi, L., & Cinelli, F. (1996). Patterns of disturbance and recovery in littoral rock pools: nonhierarchical competition and spatial variability in secondary succession. *Marine Ecology Progress Series, 135,* 145-161. doi:10.3354/meps135145

Callow, M. E., Callow, J. A., Pickett-Heaps, J. D., & Wetherbee, R. (1997). Primary adhesion of *Enteromorpha* (Chlorophyta, Ulvales) propagules: quantitative settlement studies and video microscopy. *Journal of Phycology, 33,* 938-947. doi:10.1111/j.0022-3646. 1997.00938.x

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science, 199,* 1302-1310. doi:10.1126/ science.199.4335.1302

Connell, J. H. (1985). The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology, 93,* 11-45. doi:10.10 16/0022-0981(85)90146-7

Connell, S. D., & Anderson, M. J. (1999). Predation by fish on assemblages of intertidal epibiota: effects of predator size and patch size. *Journal of Experimental Marine Biology and Ecology, 241,* 15-29. doi:10.1016/S0022-0981(99)00067-2

Corkum, M., & Trites, M. (2001). Demography and growth dynamics of the intertidal population of *Ascophyllum nodosum*: A study of exposed and sheltered areasin the Quoddy Region. Retrieved from http:// www.mta.ca/~iehrman/jalgaeholics/volume1 number 1.htm

Foster, M. S. (1975). Algal succession in a *Macrocystis pyrifera* Forest. *Marine Biology, 32,*313-329. doi:10.1007/BF00388989

Foster, M. S., Nigg, E. W., Kiguchi, L. M., Hardin, D. D., & Pearse, J. S. (2003). Temporal variation and succession in an algal-dominated high intertidal assemblage. *Journal of Experimental Marine Biology and Ecology, 289*, 15-39. doi:10.1016/S0022-0981(03)0 0035-2

Granhag, L. M., Larsson, A. I., & Jonsson, P. R. (2007). Algal spore settlement and germling removal as a function of flow speed. *Marine Ecology Progress Series, 344,* 63-69. doi:10.3354/meps06950

Haring, R. N., Dethier, M. N., & Williams, S. L. (2002). Desiccation facilitates wave-induced mortality of the intertidal alga *Fucus gardneri*. *Marine Ecology Progress Series, 232,* 75-82. doi:10.3354/meps232 075

Hoffmann, A. J., & Ugarte, R. (1985). The arrival of propagules of marine macroalgae in the intertidal zone. *Journal of Experimental Marine Biology and Ecology, 92,* 83–95. doi:10.1016/0022-0981(85)90023-1

Hutchinson, N., & Williams, G. A. (2001). Spatio-temporal variation in recruitment on a seasonal, tropical rocky shore: the importance of local versus non-local processes. *Marine Ecology Progress Series, 215,* 57-68. doi:10.3354/meps215057

Kim, J. H. (1997). The role of herbivory, and direct and indirect interactions, in algal succession. *Journal of Experimental Marine Biology and Ecology, 217,* 119-135. doi:10.1016/S0022-0981(97)00054-3

Kim, J. H., & DeWreede, R. E. (1996). Effects of size and season of disturbance on algal patch recovery in a rocky intertidal community. *Marine Ecology*

Progress Series, 133, 217-228. doi:10.3354/meps133217

Lewmanomont, K., & Ogawa, H. (1995). *Common seaweeds and seagrasses of Thailand*. Bangkok, Thailand: Integrated Promotion Technology Co. Ltd.

Littler, D. S., & Littler, M. M. (2000). *Caribbean Reef Plants : An Identification Guide to the Reef Plants of Caribbean, Bahamas, Florida and Gulf of Mexico*. Washington, DC: Offshore Graphics, Inc.

Littler, M. M., & Littler, D. S. (1985). *Handbook of Phycological Methods: Ecological Field Methods: Macroalgae.* New York: Cambridge University Press.

Lotze, H. K., Worm, B., & Sommer, U. (2000). Progagule banks, herbivory and nutrient supply control population development and dominance patterns in macroalgal blooms. *Oikos, 89,* 46-58. doi:10.1034/j.1600-0706.2000.890106.x

Lubchenco, J. (1978). Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *The American Naturalist, 112,* 23-39. doi:10.1086/283250

Mayakun, J., Kim, J. H., & Prathep, A. (2010). Effects of herbivory and the season of disturbance on algal succession in a tropical intertidal shore, Phuket, Thailand. *Phycological Research, 58,* 88-96. doi:10.1111/j.1440-1835.2010.00566.x

McClanahan, T. R. (1997). Primary succession of coral-reef algae: Differing patterns on fished versus unfished reefs. *Journal of Experimental Marine Biology and Ecology, 218,* 77-102. doi:10.1016/S0022-0981(97)00069-5

Prathep, A. (2003). Spatial and temporal variations in percentage cover of two common seagrasses at Sirinart Marine National Park, Phuket; and a first step for marine base. *Songklanakarin Journal of Science and Technology, 25,* 651–658. Retrieved from rdo.psu.ac.th/sjstweb/journal/25-5/12seagrasses.pdf

Prathep, A. (2005). Spatial and temporal variations in diversity and percentage cover of macroalgae at Sirinart Marine National Park, Phuket Province, Thailand. *ScienceAsia, 31,* 225–233. doi:10.2306/scienceasia1513-1874.2005.31.225

Prathep, A., Wichachucherd, B., & Thongroy, P. (2007). Spatial and temporal variation in density and thallus morphology of *Turbinaria ornata* in Thailand. *Aquatic Botany,86,* 132-138. doi:10.1016/j.aquabot.2006.09.011

Sousa, W. P. (1979a). Experimental investigations of disturbance and ecological succession : in a rocky intertiedal algal community. *Ecological Monographs, 49,* 227-254. doi:10.2307/1942484

Sousa, W. P. (1979b). Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity. *Ecology, 60,* 1225-1239. doi:10.2307/1936969

Sousa, W. P. (1980). The responses of a community to disturbance: the importance of successional age and species' life histories. *Oecologia, 45,* 72-81. doi:10.1007/BF00346709

Sousa, W. P. (1984). The role of disturbance in natural communities. *Annual Review Ecology and Systematics, 15,* 353-391. doi:10.1146/annurev.es.15.110184.002033

Thongroy, P., Liao, L. M., & Prathep, A. (2007). Diversity, abundance and distribution of marcroalgae at Sirinart Marine National Park, Phuket Province, Thailand. *Botanica Marina, 50,* 88-96. doi:10.1515/BOT.2007.010

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. *Journal of Experimental Marine Biology and Ecology, 231,* 291-306. doi:10.1016/S0022-0981(98)00091-4

Underwood, A. J. (1999). Physical disturbances and their direct effect on an indirect effect: responses of an intertidal assemblage to a severe storm. *Journal of Experimental Marine Biology and Ecology, 232,* 125-140. doi:10.1016/S0022-0981(98)00105-1

Vadas Sr., R. L., Johnson, S., & Norton, T. A. (1992). Recruitment and mortality of early post-settlement stages of benthic algae. *British Phycological Journal, 27,* 331-351. doi:10.1080/00071619200650291

Wichachucherd, B., Liddle, L. B., & Prathep, A. (2010). Population structure, recruitment, and succession of the brown alga, *Padina boryana* Thivy (Dictyotales, Heterokontophyta), at an exposed shore of Sirinart National Park and a sheltered area of Tang Khen Bay, Phuket Province, Thailand. *Aquatic Botany, 92,* 93-98. doi:10.1016/j.aquabot.2009.10.008