

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, Airoidi and Cinelli, 1997). Direct effects of sediment on algae in marine habitats include smothering and scouring and not providing a solid substrate for settlement (Airoidi 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; Airoidi 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 is 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 longer-

lived (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 dominance 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?