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.