

## CHAPTER 4

### DISCUSSION

#### **Life phase of *P. boryana***

The percentage of reproduction was inferred by the percentage of sporophytes throughout the year because sporophytes were dominant in the study sites. Many investigators have indicated that sporophytes were dominant and that the gametophytes were rarely found both in intertidal and subtidal zones (Fagerberg and Dawes, 1973; Liddle, 1975; Lewis *et al.*, 1987). *Dictyota* species, also in the Dictyotales group, follow the same pattern (Hwang *et al.*, 2004)

Considering that *Padina* exhibits an isomorphic diplohaplontic life history (Lee, 1999) with an obligatory alternation between haploid gametophytes and diploid sporophytes, a dominance of sporophytes throughout the year is puzzling. It is possible that sporophytes may be able to produce new sporophytes asexually without going through the gametophyte phase (Allender, 1977) and not exhibit a full life cycle. This capacity of sporophyte self-generation appears to promote survival by increasing the number of individual plants of the population efficiently, thus *P. boryana* would become dominant on the shore.

The theory suggests that isomorphic phases are ecologically equivalent (i.e. have equal per capita mortality and fecundity rates) in contrast to the marine macroalgae that exhibit an alternation of heteromorphic generations in which one

generation is more tolerant to unfavorable environmental conditions (Carney and Edwards, 2006) than the other. For example different herbivores might graze on the different morphologies. The ratio of the two phases in dioecious, haploid-diploid life cycle of many marine algae should be  $\sqrt{2}$  gametophytes: 1 sporophyte (~60% haploids and 40% diploids) is expected at equilibrium (Thornber and Gaines, 2004; reviewed by Thornber, 2006). This prediction arises because of the cost of sex; every diploid individual can produce haploid offspring, whereas only haploid female gametophytes can produce diploid offspring. Although, many seaweeds do not follow that ratio, they do show that the demographic ratios between phases vary widely due to the differences of ecological response between two phases (Luxoro and Santelices, 1989; Scrosati *et al.*, 1994; reviewed by Thornber and Gaines, 2003; Carney and Edwards, 2006).

A low percentage of female gametophytes were found throughout the year but male gametophytes were found only in May, June and July at SNP and April and May and June at TKB. It appears that male gametophytes have high survival rates in the dry season and also a high success of fertilization since only a small number of gametophytes were found during this season. As reviewed by Thornber (2006), it appears that the advantages of diploid living include the ability to mask mutation and adapt more quickly to environmental variation. Further investigation on life phase, sex ratio and developmental timing of sporophytes and gametophytes would allow us to understand better this important aspect of algal life histories as well as the strategy for survival of *P. boryana*.

### **Population structure, reproductive potential and recruitment of *P. boryana***

The structure of populations that determine birth and death processes are sensitive to changes in their environments. Population changes depend both on the variations in the environment and the life span of the organism. The fundamental model of population dynamics is the normal distribution model, the bell-shape curve. In addition, populations are regulated to stabilize below the equilibrium level or carrying capacity level (Neal, 2004). The stabilizing factor involves the numbers of individuals in the population or is density dependent. In addition, when the population is above equilibrium level, it tends to decrease in numbers and when it is below equilibrium level, it tends to increase (Maurer and Taper, 2002; Saller and Bredeweg, 2003).

Two populations of *P. boryana* at SNP and TKB showed a similar population distribution pattern, however they do not fit the normal distribution pattern. They have right tail shaped curve, dominated by the smaller thalli and only a few large ones throughout the year. Similar patterns are found in other brown seaweeds such as *Sargassum muticum* (Yendo) Fensholt (Arenas and Fernández, 2000), *Turbinaria triquetra* (J. Agardh) Kützing (Ateweberhan *et al.*, 2005) and *Sargassum lapazeanum* (Rivera and Scrosati, 2006) all members of the order Fucales. The data has suggested that new individuals developed continuously throughout the year providing new smaller thalli. The *Dictyosphaeridia* stage of *Padina* was frequently observed in all plots in this study except those covered by the sediment. This filamentous stage developed into a visible blade size 0.5-1 cm. in 1 month. Such new thalli could develop throughout the year since *Dictyosphaeridia* was always found in the experiment plots.

New recruits of *P. boryana* were found throughout the year at both sites in the experiment plots. However, recruitment was higher at TKB, a sheltered shore, where the average percentage cover was more than 40%. Lower wave action could allow a higher concentration of spores to settle whereas higher wave action diluted and washed away the new recruits of spores at SNP, a more exposed habitat (Gordon and Brawley, 2004). Another primary effect of wave action is the physical destruction of thalli and tearing the organisms from the substrates (Zacharias and Roff, 2001). This may explain that at the lower shore *P. boryana* recruited less than those on the upper shore, where there is less exposure to wave action.

Wave motion would be stressful for growth of *P. boryana* due to the size of thallus which was smaller at SNP than at TKB. *Padina* is one of few genera that can tolerate exposure during the low tide. The wave action, therefore, could cause it to have a reduced thallus size at SNP. The smaller size survives higher water action and has a decreased risk of being broken or torn (De Ruyter Van Steveninck and Breeman, 1987). Generally, many species of algae have to adapt themselves in response to water flow or wave exposure for survival. Reduced size (Kitzes and Denny, 2005), stronger holdfast and more flexible thalli (Denny and Roberson, 2002) are examples of such adaptations.

At both sites, *P. boryana* could not recruit on the permanent plots covered by sediment. Mayakun (2006) studied sediment accumulation between shore levels and showed that there were significant differences in grain size and amount of sediment between shallower and deeper zones at SNP. The high accumulation of sediment might happen in the rainy season because the rainfall passes sediment downward the substrate. In addition, I also observed greater sedimentation at SNP than at TKB. Sediment can

therefore be considered a limiting factor for recruitment at both sites. Sediment has been shown by other researchers to inhibit or prevent the attachment and survival of macroalgal spores (Eriksson and Johansson, 2003; Isæus *et al.*, 2004; Schiel *et al.*, 2006). The scouring of sediment from moving water can affect early post-settlement stages (Eriksson and Johansson, 2003, Vadas *et al.*, 1992). Sediment can also affect growth indirectly by shading and inhibiting photosynthesis (Grant, 2000; Zacharias and Roff, 2001; Chapman and Fletcher, 2002). Likewise sediment itself is not a suitable substrate for propagule settlement. *P. boryana* might attach on the sediment temporarily but it could not attach on the hard substrata beneath the sediment.

The recruitment study provides an understanding of algal succession, a process that includes *P. boryana*, at two contrasting sites on the same island. As on many shores, filamentous algae, known as *r*-species, were the first colonizers, (Lubchenco, 1983; Gårdmark *et al.*, 2003, Mayakun, 2006). They were established quickly on the cleared plots and became dominant in the area. They are small fast-growing thalli. Also in less than 1 month, *Dictyosphaerula*, the creeping filamentous stage of *P. boryana*, occupied the same space along with the filamentous green and red algae. New juvenile fan-shaped thalli were evident in only 2 months. At around the same time the filamentous algal populations decreased and the new *P. boryana* thalli soon dominated the experimental plots. The rapid succession of *P. boryana* shows that it competes well with the other algae.

The ability of *P. boryana* to recruit rapidly is also reflected in the success of spore recruitment. The results showed that they produce spores throughout the year, providing a high reproductive potential. Even on the small thalli of *P. boryana*  $1.06 \pm 0.25$

cm<sup>2</sup>, the spores were already observed. The numbers of released spores, with a maximum of fewer than 10,000 spores/ thallus is much less than the furoid algal zygotes (Maggs and Callow, 2002). Furoid algae produced approximately 10<sup>9</sup> zygotes/thallus. Therefore, *P. boryana* has a very high success of spore recruitment since they produce relatively few in number. Liddle (personal communication) reports that, in culture, germination of spores is 100%. This fecundity helps explain the success of *P. boryana* in the stressful intertidal environment.

The factors that affect spore release also help us understand the distribution of *P. boryana*. Greater numbers of spores were released during the shift of seasons, from rainy to dry and also from dry to rainy season. The acute changes in the environmental conditions can trigger a greater number of spores released as reported in many studies (De Ruyter Van Steveninck and Breeman, 1987; Flores-Moya *et al.*, 1996; Yoshida *et al.*, 2001; Ateweberhan *et al.*, 2005). Such factors also influence the 2 populations of *P. boryana* in this study. Even if the plants were senescent the last crop of new spores would be the recruits that maintain the population. The new recruitment and die off cycle was less than 6 months long. Therefore *P. boryana* is highly dynamic and coordinated with broad annual changes. The successful recruitment and adaptation of the basic life history to the critical environmental factors helps explain the distribution patterns of *Padina boryana* throughout the year at two locations on Phuket Island.