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台灣北部鹽寮灣海域珊瑚群聚之研究

Studies on the Coral Communities in Yenliao Bay, Northern Taiwan

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中文摘要

台灣北部的鹽寮灣海域屬於亞熱帶及邊緣性的環境，珊瑚的生長多以珊瑚群聚的方式呈現，這些群聚的特徵是珊瑚覆蓋率和物種多樣性偏低以及珊瑚礁的發育受到限制。為了更清楚瞭解這些珊瑚群聚的動態變化，從 2003 年到 2009 年，在鹽寮灣海域的三處岩礁，以固定樣框的調查方式進行了以每半年為區間的長期監測研究。本研究的目的是：（1）調查鹽寮灣石珊瑚的群聚結構與特徵，（2）研究珊瑚群聚的動態和長期變化，（3）研究石珊瑚的幼生入添模式和入添率，（4）探討珊瑚群聚的變動與環境因子的關係。

以非計量多維尺度分析法（non-metric multidimensional scaling, nMDS）分析 12 次連續的調查結果發現，在 2005 年 7 月與 11 月的兩次調查之間，珊瑚群聚出現明顯的變化，時間點與 2005 年夏天經過鹽寮灣的三個強烈颱風一致。由於珊瑚的生長形態隨種類而有所不同，其對颱風擾動的忍受度亦有所不同。比較 2005 年 7 月與 11 月的兩次調查發現，在局部死亡率(partial colony mortality)與整個群體死亡率(whole colony mortality)上，不同型態的珊瑚出現明顯差異。其中葉片型和表覆形的珊瑚例如微孔珊瑚屬(*Montipora*)、波紋珊瑚屬(*Pachyseris*)和碓珊瑚屬(*Hydnopora*)等死亡率較高，而團塊形的珊瑚包括菊珊瑚屬(*Favia*)、角菊珊瑚屬(*Favites*)、細菊珊瑚屬(*Cyphastrea*)及圓菊珊瑚屬(*Montastrea*)等在颱風擾動後死亡率較低。

從 2006 年 5 月開始至 2009 年 9 月，利用附著板在本海域進行珊瑚群聚的幼生入添研究，其結果顯示，珊瑚幼生主要出現在夏至秋季，以鹿角珊瑚科(Pocilloporidae，52～90％）和軸孔珊瑚科（Acroporidae，10～41％）幼生最為常見。本研究也發現珊瑚幼生具有附著偏好，幼生在附著板上表面和垂直面的數量和水深呈現負相關，顯示在這些亞熱帶珊瑚群聚，光照強度可能是控制亞熱帶及邊緣性珊瑚群聚珊瑚幼生附著和生存的主要因素。此外，珊瑚幼生的入添率(recruits/m^2)具有顯著年間變動，從 2006 年和 2007 年的結果來看，幼生入添率和

一般熱帶珊瑚礁的入添率相當接近，這顯示珊瑚幼生的入添率很可能不是鹽寮灣珊瑚群聚發展和維持的限制因子。

經由分析珊瑚覆蓋率和環境因子之間的關係發現，鹽寮灣的磷酸鹽，總氮和總磷的濃度與珊瑚覆蓋率在時間序列的變化上呈現正相關。此結果顯示，在光強度較低的亞熱帶環境中營養鹽可能對於珊瑚的生長是有益處的。推測可能是豐富的營養鹽提升了共生藻的光合作用因而促進了珊瑚生長。

綜合而論，本研究的結果顯示，在鹽寮灣的亞熱帶珊瑚群聚容易受到颱風的擾動影響而出現明顯的年間變動。颱風擾動引起的珊瑚死亡率會因珊瑚的生長形態不同而有所差異，從而導致珊瑚群聚的變動。由於鹽寮灣的幼生入添率與熱帶珊瑚礁入添率相當，此海域的珊瑚群聚的恢復和維持可能不是受到幼生入添率的限制。此外因為無機營養鹽和珊瑚的覆蓋率之間有相當一致的正相關，營養鹽可能對珊瑚群聚的恢復是有益的。由於邊緣型的環境可能作為熱帶地區的造礁珊瑚面臨氣候變遷威脅時的避難所，本研究的結果可以增加我們對邊緣型環境中的珊瑚群聚動態的了解，有利於面臨日益嚴重環境壓力的珊瑚群聚的管理和保育。

關鍵詞：珊瑚群聚，群聚動態，珊瑚入添，邊緣型環境，富營養鹽。

Abstract

Coral communities in Yenliao Bay were characterized by low coral cover, low species diversity and limited reef-building activities due to its subtropical and marginal environment for reef corals. To better understand the dynamics of these coral communities, a long-term monitoring study by permanent belt quadrats at semi-annual intervals was conducted on three rocky reefs in Yenliao Bay, northern Taiwan, from 2003-2009. The objectives of this study were (1) to examine the general characteristics of the scleractinian coral communities, (2) to examine the dynamics and long-term changes of coral communities, (3) to study the recruitment pattern and recruitment rate of scleractinian corals, (4) to investigate the possible environmental factors related to the changes of coral communities in Yenliao Bay.

Non-metric multidimensional scaling (nMDS) analysis of coral communities among 12 consecutive surveys showed distinct temporal variations and the major change occurred between July 2005 and November 2005 which was coincident with major typhoon disturbances in summer 2005. Coral species with different growth forms varied greatly in partial and whole colony mortalities due to their susceptibility to typhoon disturbances. Foliaceous and encrusting corals such as *Montipora, Pachyseris*, and *Hydnopora* species suffered higher mortality, while massive corals including *Favia*, *Favites*, *Cyphastrea*, and *Montastrea* species suffered lower mortality after typhoon

disturbances.

Coral recruitment in these subtropical coral communities was studied by settlement plates from May 2006 to September 2009. The results showed that coral recruits occurred in summer and early autumn only and the most common taxa were Pocilloporidae (52~90%) and Acroporidae (10~41%). The number of coral recruits on top and vertical surfaces was negatively correlated with depths suggesting that light intensity is possibly the primary factor controlling settlement and survival of coral recruits in these subtropical coral communities. In addition, there was a large variation of recruitment rates (recruits/m^2) among years. The high recruitment rates in 2006 and 2007 were comparable with those of tropical reefs suggesting that recruitment might not be a limiting factor for the maintenance and development of coral communities in Yenliao Bay.

Studies on the relationships between coral coverage and environment factors showed that the concentrations of phosphate, total nitrogen, and total phosphorus were positively correlated with the changes of coral coverage among years in Yenliao Bay. This suggests that nutrients enrichment might be beneficial for coral growth through the enhancement of photosynthesis of zooxanthellae in subtropical environment where light intensity is relatively low.

In conclusion, this study demonstrated that the subtropical coral communities in

Yenliao Bay were susceptible to typhoon disturbances and large changes might occur among years. Typhoon disturbances induced differential mortality to coral species related to their growth forms, hence resulted in the changes of coral communities. The recovery and maintenance of coral communities was possibly not limited by recruitment since the high recruitment rates were comparable with those of tropical reefs. Besides, nutrients enrichment might be beneficial to the recovery of coral communities since there were consistent positive correlations between dissolved inorganic nutrients and coral coverage among years. Since marginal coral areas might act as refuges for tropical reef corals to face with the threats of climate change, this study can contribute to our knowledge of coral community dynamics in marginal environment and benefit the management and conservation of coral community facing the increasing environmental stresses in the future.

Key words: coral community, community dynamics, coral recruitment, marginal environment, nutrient enrichment.

Table of Contents

Acknowledgements

Abstract in Chinese..I

Abstract in English..III

Table of contents..VI

Content of tables..VIII

Content of figures..X

Chapter 1 General Introduction..1

Chapter 2 Scleractinian coral communities..8

2-1 Introduction..8

2-2 Materials and Methods..11

2-3 Results..14

2-4 Discussion..16

2-5 Tables..21

2-6 Figures..27

Chapter 3 Dynamics of subtropical coral communities..32

3-1 Introduction..32

3-2 Materials and Methods..34

3-3 Results..35

3-4 Discussion..38

3-4 Tables..44

3-5 Figures..47

Chapter 4 Coral recruitment of subtropical coral communities..55

4-1 Introduction..55

4-2 Materials and methods..57

4-3 Results.....59

4-4 Discussion.....62

4-5 Tables.....69

4-6 Figures.....73

Chapter 5 Coral community dynamics and environmental factors.....81

5-1 Introduction.....81

5-2 Materials and Methods.....83

5-3 Results.....86

5-4 Discussion.....89

5-5 Tables.....92

5-6 Figures.....96

Chapter 6 Conclusions.....100

References.....103

Content of tables

Table 2.1 A list of scleractinian species recorded at survey sites in Yenliao Bay in August 2003....21

Table 2.2 The order of scleractinian genera by colony number and cover recorded in the study area in August 2003..22

Table 2.3 A list of scleractinian species recorded at survey sites by two methods...........................23

Table 2.4 Coral community parameters and diversity indices of two survey methods at study sites...25

Table 2.5 Results of SIMPER analysis comparing the coral community structure based on genera percentage cover data from two survey methods...26

Table 3.1 Results of the repeated measures ANOVAs, Trend analysis, and Pairwise comparisons for detecting the changes of coral cover among 12 surveys at the three sites..................................44

Table 3.2 A list of 14 typhoons passed or close to Yen-laio Bay during study years.......................45

Table 3.3 Results of the repeated measures ANOVAs, Trend analysis, and Pairwise comparisons for detecting the changes of coral cover among 12 surveys at the three sites..................................46

Table 4.1 Summary of statistical tests for comparisons of coral recruitment rates..........................69

Table 4.2 Summary of statistical tests for comparisons of coral recruitment rates........................70

Table 4.3 Correlation analyses (*Z* test) between depths and number of coral recruits on different surfaces of plates...71

Table 4.4 Comparison of coral recruitment rates on settlement plates at high-latitude or marginal locations around the world...72

Table 5.1 Environmental variables (mean ± SE) in Yenliao Bay from August 2003 to September 2009..92

Table 5.2 Correlation coefficients (*R*) between environmental parameters and coral cover in 12 surveys (n=12) from August 2003 to September 2009..94

Table 5.3 BIO-ENV results showing the combinations of environmental variables that best match the coral community resemblance matrix..95

Content of figures

Fig. 2.1 Map of the study area showing three rocky reefs (A, B, C) and three study sites (blank squares)....27

Fig. 2.2 Layout and locations of 10 permanent quadrats on three reefs in Yenliao Bay, northern Taiwan....28

Fig. 2.3 Frequency distribution of colony sizes of total coral colonies recorded in August 2003.....29

Fig. 2.4 nMDS ordination plot comparing the coral community structures using percentage cover of coral genera by quadrat along transect method and belt quadrat method....30

Fig. 2.5 Dendrogram showing the clustering of coral communities using percentage cover of coral genera by quadrat along transect method and belt quadrat method....31

Fig. 3.1 Changes of hard coral cover (mean±SE) at 3 sites from 2003 to 2009....47

Fig. 3.2 nMDS plot based on Bray-Curtis similarities showing the relationship of the coral communities among 12 surveys in the study area from August 2003 to September 2009..........48

Fig. 3.3 Stacked histograms of hard coral cover of major genera at three sites from 2003 to 2009..49

Fig. 3.4 Mortality rates of coral genera at three sites after major disturbance in 2005....51

Fig. 3.5 Changes of relative abundance of major coral genera at three sites between August 2003 and September 2009....52

Fig. 3.6 Changes of coral colony number (mean ± SE) of four size classes at three sites from 2003 to 2009....53

Fig. 4.1 Time frame of deployments and retrievals of settlement plates....73

Fig. 4.2 A set of settlement plates used for coral recruitment surveys in this study....74

Fig. 4.3 Coral recruitment rate (mean ± SE) in Yenliao Bay in 2006 to 2009....75

Fig. 4.4 Density of coral recruits (mean ± SE, n = 3) on 12 short-term surveys in 2006-2009.........76

Fig. 4.5 Taxonomic composition of coral recruits....77

Fig. 4.6 Coral recruits (mean ± SE) on top, bottom, and vertical sides of the settlement plates........78

Fig. 4.7 Relationships between depth and density of coral recruits on different sides of settlement plates in 2006-2007 (n = 80 plates) 79
Fig. 4.8 Monthly variations of sea surface temperature (mean ± SD) in the study area 2007-2009..80
Fig. 5.1 Map of the study area indicating the sampling sites of water quality (asterisks) and macroalgae (blank squares) 96
Fig. 5.2 Changes of coral coverage and concentrations of environmental variables (phosphate, TN: total nitrogen, TP: total phosphate) from August 2003 to September 2009................................97
Fig. 5.3 Results of LINKTREE analysis indicating the environmental factors that best explain the 12 surveys of coral cover data at the study sites...98
Fig. 5.4 Relationship among variables, canonical variates, and the first pair of canonical variates (three coral communities and four environmental variables) 99

Chapter 1 General Introduction

Coral reefs communities have been well documented for their tremendous biological diversity and high ecological values (Connell 1978; Knowlton 2001). However, they suffered dramatic declines throughout the world in the last few decades due to the impacts of climate change and anthropogenic disturbances (Wilkinson 1999, 2000, 2004, 2008; Buddemeier 2001; Knowlton 2001). A recent report stated that 19% coral reefs around the world were considered totally degraded, while 15% will be threatened with immediate collapse within 20 years and 20% in the future 20-40 years (Wilkinson 2008). In addition, one-third of reef-building corals were reported to face elevated extinction risk from climate change and local impacts (Carpenter et al. 2008). Therefore, there is an urgent need to increase our knowledge of the responses of coral reef communities to the natural disturbances under climate change and anthropogenic stresses to the environment (Hoegh-Guldberg et al. 2007).

The key knowledge to understand how corals could survive in the future, with changing climate, may be acquired from the study of how corals exist in already stressful environments. Environmental parameters that occur in tropical regions with shallow and clear waters are widely regarded as being ‘‘optimal’’ for coral growth and reef-building. In contrast, marginal settings are environments where coral communities or framework reefs occur either close to well-understood environmental thresholds or in areas with fluctuating environmental conditions for coral survival (Perry and Larcombe 2003). Characteristics of marginal environments are high or low temperatures, salinities, enriched nutrient levels, or low light penetration and low aragonite saturation states (Kleypas et al. 1999; Guinotte et al. 2003; Perry and Larcombe 2003).

Marginal coral communities frequently occur at high latitudes (above 25° S and 25° N), upwelling-influenced settings, and turbid environments (Perry 2003; Perry and Larcombe 2003). Examples of marginal or high latitude coral communities (Kleypas et al. 1999) include New Zealand in low seawater temperature (13.9°C), high temperature in Persian Gulf (33.6-34.4), high salinity in Gulf of Aqaba, Red Sea (41.8 PSU), and high nitrate concentration in Galapagos islands (3.24-5.61 μmol liter^{-1}). Living under these highly variable and extreme conditions, subtropical or higher latitudinal coral communities are commonly characterized by reduced growth rates, low species diversity, high turnover of rare species, few branching corals (*Acropora*), and live coral cover without obvious limestone accretions (Veron and Done 1979; Crossland 1988; Veron 1995; Lough and Barnes 2000). However, these communities have been infrequently studied, compared with tropical coral reefs.

Previous studies suggested that high latitude coral communities might be better adapted for survival in an environment modified by global climate change through their existence in already stressed conditions (Glynn 1996; Riegl and Piller 2003). Subtropical coral communities distributed in higher latitude compare with tropical reefs. In this region, sea water is cooler and light penetration is reduced than tropical reefs (Veron 2000). As sea water temperature increase, coral species and perhaps reefs may move to higher latitude area (Greenstein and Pandolfi 2008; Yamano et al. 2011). In that context, subtropical oral communities might provide refuges for reef corals facing the threats of global warming and climate change (Hughes et al. 2003; Greenstein and Pandolfi 2008). Therefore, evaluate the status of subtropical coral community, their community dynamics and recovery potential after disturbances, recruitment ability, and relationship with environmental factors are important. The findings may elucidate the processes of reef corals subjected to deteriorating conditions and how they persist in marginal environment (Harriott and Banks 2002; Perry and Larcombe 2003) and information will be helpful for management & conservation of these subtropical coral communities.

Most coral reefs are subject to recurrent disturbances and in a cycle of destruction and recovery (Connell 1978; Hughes et al. 1992). Disturbance is thought to be the major source of temporal and spatial heterogeneity in the dynamics of natural communities and has been recognized as a major factor that shapes the community structure of coral reefs (Connell 1978; Sousa 1984; Connell et al. 1997; Bythell et al. 2000). Typhoons are one of the major disturbances to influence coral communities. In general, their effects are acute and not only damage, remove or kill live corals but also affect the physical environment (e.g., substrate) (Connell et al, 1997), and the induced complex interacting events could cause a phase shift from a coral- to an algal-dominated system (Hughes 1989, 1994; Knowlton 1992). Recent studies have suggested that global warming could increase the frequency and intensity of strong hurricanes (Webster et al. 2005; Elsner et al. 2006a, b). If the frequency and intensity of tropical cyclones and typhoons increase as hurricanes in the Atlantic, there may be no enough time for coral assemblages to recovery under such frequent disturbances (Connell 1997; Hughes and Connell 1999). In such a context, to better understand the dynamics and recovery of coral communities under increasing threats of typhoon disturbances is necessary. However, studies on the effects of typhoons on subtropical coral communities are scarce, especially time series or long-term monitoring studies on the coral communities before and after typhoon disturbances. A detailed understanding of how different coral species might respond to typhoon disturbances in marginal environment is also poorly documented. Therefore, identifying how subtropical coral communities respond to typhoon disturbances will be helpful in predicting coral community dynamics under climate change.

Resilience is the ability of coral communities recovering to their original situation after disturbances (Connell 1997; West and Salm 2003). West and Salm (2003) suggested that the ability to produce abundant larvae was one of the most critical intrinsic, biological or ecological characteristics to evaluate the resilience level. Since the recruitment rate in high latitude coral communities were lower than those of most tropical reefs (Harriott and Smith 2000; Nozawa et al. 2008), this low recruitment rate may be responsible for the low species diversity and may constrain the resilience of these coral communities. In coral reef systems, recruitment is not only a key factor in the maintenance of communities, particularly in their recovery and replenishment following disturbances (Gittings et al. 1988; Sammarco et al. 1991; Glassom et al. 2004, 2006), but also important for understanding the population dynamics and community structures (Caley et al. 1996; Quinn and Kojis 2003; Glassom et al. 2004). However, major factors of less recruitment rates in subtropical coral communities have not been fully understood. Thus, more comprehensive studies of coral recruitment in this area are needed.

Harriott and Banks (2002) proposed a qualitative biophysical model to describe the possible environmental factors regulating coral reefs. These factors include temperature, salinity, nutrients, light availability, and aragonite saturation states were termed as marginal for coral communities (Kleypas et al. 1999; Perry and Larcombe 2003). Among them, nutrient enrichment is of increasing global concern and considered a major factor contributing to a global decline of coral reefs (Fabricius 2005). High levels of nutrients have been reported to reduce coral growth, calcification (Tomascik 1991; Stambler et al. 1991; Stimson, 1992), and negatively affect coral reproduction (Harrison and Ward 2001; Koop et al. 2001). High nutrient loads also stimulate macroalgal overgrowth enabling macroalgae to rapidly cover and smother living corals (Lapointe 1997). In recent years many threats to the coral reef ecosystem have been revealed, however, information on the effects of environmental factors on subtropical coral communities is limited.

This study aims to better understand the community structure and the dynamics of scleractinian corals at subtropical or marginal environment in Taiwan. Moreover, this study also investigated the recruitment process and the relationship between environment factors and coral community. The study site was located at Yenliao Bay, northern Taiwan (25° 3' N, 121° 56' E), where subtropical coral communities characterized by low coral coverage and limited reef-building activity with more than 100 coral species occurred (Yang and Dai 1982).

The objectives of this study are to:

(1) Examine the general characteristics and structure of coral communities in Yenliao Bay.

(2) Investigate the dynamics of subtropical coral communities under the impacts of

typhoons. A detailed survey was conducted on all visible-sized scleractinian corals in a total area of 100 m^2 in six years.

(3) Investigate the pattern of coral recruitment at Yenliao Bay and to examine whether the recruitment rate is the major limiting factor for the maintenance of coral communities.

(4) Examine the environmental factors and their relationships with coral communities in Yenliao Bay

Chapter 2 Scleractinian coral communities

2-1 Introduction

Scleractinian corals are framework builders on coral reef ecosystems, they play a key role on ecological functioning of coral reefs and thus of particular importance to study the composition and structure of coral communities. Quantitative studies of coral communities started in 1970s (e.g., Loya 1972; Glynn 1976; Goodwin et al. 1976; Bak and Engel 1979; Bouchon 1981). These studies mainly focused on description of species composition, zonation, diversity pattern and possible factors affecting the observed distributions and structure of communities. According to the distribution of scleractinian species, coral communities exhibit a distinct biogeographic pattern of reduced biodiversity with increasing latitude (Stehli and Wells 1971; Veron 1995, 2000). In a small scale of 400 km around Taiwan, well-developed coral reefs are found in southern Taiwan and non-reefal coral communities exit in northern Taiwan (Chen 1999). Previous studies also suggested the factors controlling the global distribution of coral reefs included salinity, temperature, light, nutrients, wave exposure and hydrodynamic factors, sediment, and aragonite saturation (Harriott and Banks 2002; Sheppard et al. 2009).

In comparison with tropical coral communities, relatively few studies have been conducted on subtropical coral communities. These studies showed that subtropical coral communities usually have lower species diversity and coral cover (Crossland 1988; Veron 1995), although higher species diversity and coral cover might occur in some specific cases (Harriott et al. 1999; Harriott and Banks 2002; Perry 2003). Coral species compositions in subtropical coral communities are also different from those of tropical coral reefs. van Woesik and Done (1997) showed that the abundances of massive *Porites* and branching *Acropora* declined with increasing latitude, while foliaceous or encrusting species such as *Turbinaria* and *Montipora* species increased with latitudes along the eastern coast of Australia. The absence of the dominant coral species of tropical reefs at high latitudes suggests that they are unable to establish and survive at sub-optimal environmental conditions such as cooler temperatures, lower light levels, and higher sedimentation rates (Perry and Larcombe 2003).

A variety of sampling methods have been applied to quantitative studies of coral communities including line-intercept transect, line-point transect, video transect, mapped quadrats, and photo quadrats (Loya 1978; Hill and Wilkinson 2004; Leujak and Ormond 2007). Line intercept transect is one of the earliest quantitative technique, in which a transect line is laid close to the bottom and benthic cover is calculated as the fraction of the total length of line (Loya 1978). Line-point transect is a recommended quicker method modified from line-intercept transect and now mainly used by monitoring programs such as Reef Check and Reef Keeper (Hodgson 1999; Hill and

Wilkinson 2004). Video transect method is a belt transect filmed by video cameras which can provide a permanent record of benthic organisms. This method has become increasingly popular due to the improvement of digital camera and camcorder (Brown et al. 2004; Houk and van Voesik 2006). Quadrat method has been used for monitoring reef communities since 1970s. Different assessment techniques such as detailed mapping of quadrats, point-sampling or outlining benthos of photo quadrat images can be used in determining the cover of different benthos inside the quadrat (Leujak and Ormond 2007). Although the performance of different coral community methods have been compared in many studies, a clear conclusion remains unavailable to date (Weinberg 1981; Ohlhorst et al. 1988; Done 1995; Lam et al. 2006; Nadon and Stirling 2006). However, when information of numbers and sizes of colonies or processes causing change is required, use of photo-quadrats will be preferred to line transect methods (Leujak and Ormond 2007), especially in a low coral coverage area (Fung 2007).

Yenliao Bay (25° 2' N, 121° 56' E) is a semi-enclosed bay located on the northeastern coast of Taiwan (Fig.1). Major relevant environmental conditions in this area include a low wintertime sea temperature (< 18 °C), heavy sedimentation from runoffs of adjacent rivers during rainy seasons, and physical and biological erosion. Yang and Dai (1982) provided the first descriptive studies of the coral communities in

Yenliao Bay, and a total of 106 scleractinians species in 43 genera and 14 families were recorded. The most specious families were Faviidae, Agariciidae and Pectiniidae and the growth forms were mostly massive or foliaceous. Although branching *Acropora* and *Pocillopora* species were rare, this area still had well-developed coral communities in northern Taiwan. However, no quantitative study on coral communities has been conducted in this area.

The aims of this study are to examine the community structure of scleractinian corals in northern Taiwan using both quadrats and quadrats along line transect methods, and to evaluate the application of these methods on studying coral communities.

2-2 Materials and methods

Study area

Yenliao Bay (25° 2' N, 121° 56' E) is a semi-enclosed bay located on the northeastern coast of Taiwan (Fig. 2.1). The bay is approximately 3 km long (north to south) and 1 km wide (east to west), and there are three rocky reefs (designated as A, B, and C) sited at depths between 0 and 15 m. These reefs are extensions of shale and sandstone formations from land which provide hard substrate for corals and other benthic organisms. Major environmental conditions include a low sea temperature (< 18°C) in winter, heavy sedimentation from runoffs of adjacent rivers during rainy season, and physical and biological erosion. Consequently, coral reefs in Yenliao Bay are poorly developed and coral communities are characterized by depauperate scleractinian fauna (Yang and Dai, 1982).

Sampling

Belt quadrats

On each of the rocky reefs (A, B, C, Fig. 2.1), three to four permanent quadrats (each 1 x 10 m) were established on a relatively flat area (ca. 200 m^2) in 2003 (Fig. 2.2). These quadrats were photographed twice annually from August 2003 to September 2009 using a 1 × 1 m frame and a digital camera (Nikon D70 with a 12-24 mm lens in a Subal underwater housing) from above. The images of a quadrat were first processed in Adobe Photoshop and combined as a complete image of the quadrat in ArcGis. All visible scleractinian coral colonies on the images were identified to species. All coral colonies were mapped and their projected areas were measured using the ArcGis.

Quadrats along line transect

In order to provide a comparison of the belt quadart method, quadrats sampling along transect was applied (English et al. 1997) in 2009-2010. At each reef, three transect lines (each 30 m long) were laid haphazardly and run parallel to depth contours at three depths (5, 10, 15 m), except Reef A where the survey were conducted at 10 and 15 m in depth since its shallowest part was about 10 m. Along each transect, 10 quadarts (each 100 cm × 70 cm) were randomly placed and all benthic organisms underneath the quadrats were photographed by the same equipment. In total, 240 quadarts with 168 m^2 in area were sampled from three reefs.

The images were first processed in Abobe Photoshop to reduce distortion. Then were analyzed with CPCe (Coral Point Count with Excel extensions, Kohler and Gill 2006) to quantify the proportion of benthic organisms and substrate types. Thirty random selected points were automatically spread on each image and codes corresponding to the recognized objects in the image were denoted. All corals were identified to species and the coverage of each coral species was calculated.

Data analysis

Both coral cover and colony number in August 2003 were used to reveal the structure of coral community. Community indices including the Shannon diversity index, Simpson index, and Species evenness index were also calculated. Cluster analysis and non-metric multidimentional scaling (nMDS) analysis of Bray-Curtis similarity measures (PRIMER, version 6, Clarke and Warwick 2001) using the coverage of each genera were employed to reveal the relationship of survey sites by the two methods (belt quadrats in 2009, quadrats along line transect in 2009-2010). Analysis of similarity (ANOSIM) was applied to determine if there was any significant difference in species compositions using the two methods. Similarity Percentage (SIMPER, Primer, v. 6) analysis was performed to identify the coral genera that contributed to the similarities and difference between the two methods.

2-3 Results

In total, 1404 coral colonies of 69 scleractinian species in 26 genera and 8 families were recorded at the study sites in August 2003 (Table 2.1, 2.2). These corals cover 16.2% of the reef surface. The most specious family was Faviidae (31 species) and they accounted for 44.9% of the total number of species, followed by Acroporidae (17 species, 24.6%) and Agariciidae (7 species, 10.1%). Moreover, Lobophyllidae (5 species, 7.2%), Fungiide (4 species, 5.8%), Poritide (2 species, 2.9%), Pocilloporidae (2 species, 2.9%), and Plesiastreidae (1 species, 1.4%) were also recorded.

In terms of both colony number and coverage (Table 2.2), Faviidae was the most abundant family, composing more than half of the communities (63.9% and 60.2%, respectively) followed by Acroporidae (16.7%, 24.5%). Other major families were Pocilloporidae (11.8%, 4.3%), and Agariciidae (3.6%, 6.1%). At genus level, the top 5 genera in colony number were *Favites* (31.1%), *Montipora* (12.9%), *Favia* (11.5%), *Stylophora* (11.2%), and *Cyphastrea* (7.1%). In terms of coral cover, the top 5 genera were *Favites* (23.1%), *Montipora* (22.9%), *Favia* (11.4%), *Cyphastrea* (6.1%), and *Platygyra* (6.1%).

Size-frequency distribution of all coral colonies in August 2003 are shown in Fig. 2.3. The log-transformed data of colony number showed major classes of colonies were intermediate size ($32cm^2$~$128cm^2$). Colonies of the largest size (> $2048cm^2$) and smallest size (< $4cm^2$) classes were relatively rare.

Comparisons of quantitative methods

The species compositions of coral community were similar using the two methods (Table 2.3). The most abundant families revealed by both methods were Faviidae (Belt quadrats: 49.2%, Quadrats along transect: 54.1%). However, coral cover, species number, and diversity indices were higher in quadrats along line transect method than in permanent belt quadrats (Table 2.4).

Although the result of nMDS showed a grouping pattern between Sites (Fig. 2.4), the result of ANOSIM suggested that the two survey methods were not separated with significant differences (R = 0.259, P = 0.3). In addition, the results of cluster analysis and nMDS grouping showed that the surveyed sites of the same methods tended to form a cluster while those at Site C were independent groups (Fig. 2.4, 2.5).

The results of SIMPER analysis showed that average similarities were 62.11% within belt quadrats method and 67.27% within quadrats along line transect method (Table 2.5a). In belt quadrats method, *Favites*, *Favia*, *Cyphastrea*, *Porites*, *Montastrea*, and *Platygyra* were the most contributive genera. In quadrats along line transect method, *Favites*, *Favia*, *Goniastrea*, *Cyphastrea*, *Porites*, and *Platygyra* were the most contributive genera. The average dissimilarity was 39.26% between belt quadrats and quadrats along line transect method (Table 2.5b).

2-4 Discussion

Community structure

This study showed that the abundance and cover (1404 colonies/100m^2, 16.8% cover) of scleractinian corals at Yenliao Bay were comparable with those of other high-latitude or subtropical reefs. For example, in the Solitary Islands Marine Reserve, eastern Australia, coral cover ranged from 8.5 to 50.9% (Harriott et al. 1994). In Amakusa, southern Japan, coral colonies and cover were 2471 colonies/100 m^2 and 28.3% (Nozawa et al. 2008). In Hong Kong, coral cover ranged from 12.6 to 36.2% (Tam and Ang 2008). However, the coral cover recorded in 2003 were much lower comparing with that reported in Yang and Dai (1982).

The coral community of Yenliao Bay was dominated by species of families Faviidae, Acroporidae, Agariciidae, and Lobophylliidae. Faviid species of massive or encrusting forms was the most abundant ones (31 spp. from 69 in total). The species composition in Yenliao Bay was similar to other high latitude coral communities (Veron and Done 1979; Harriott et al. 1994; Nozawa et al. 2008; Wicks et al. 2010). For example, Faviidae was the most specious family (22 spp. from 54) in Amakusa, southwestern Japan. In Kermadec Islands, New Zealand, The most common species were two Faviidae species i.e., *Montastraea curta*, *Hydnophora pilosa* and an encrusting *Montipora* sp. In contrast to the scleractinian assemblages in southern Taiwan (Dai 1993), the abundance of main reef builders such as branching *Acropora* or *Pocillopora* species was unusually low. This may be the main reason for poor reef formation in study area. About 30 species of *Acropora* and 9 species of *Pocillopora* were recorded in southern Taiwan, while only *A. solitaryensis*, *A. valida*, *P. damicornis*, and *Stylophora pistillata* were frequently found in Yenliao Bay. Moreover, low seawater temperature in winter (< 18℃) is suggested to be the main factor that limit the growth rates and reef-building activities of hermatypic corals in this area (Yang and Dai 1982).

Previous studies indicated that environments with high wave energy favor compact growth forms of corals (Veron 1993; Hughes and Connell 1999). In this study, Faviidae was the most abundant family in Yenliao Bay. This is probably related to the morphological differences of coral species due to selective effect of strong waves generated by occasional typhoons and seasonal monsoon that caused greater mortality to foliaceous or branching corals (Hughes and Connell 1999). Such a selective effect on coral species with different growth forms generally agrees with the observations in high latitude areas worldwide. In Amakusa, Japan, massive or encrusting forms (e.g., Faviidae) were the dominant morphologies of scleractinian species (Nozawa et al. 2008). In the Kermadec, Julian Rocks and Cook Island, the low abundance of branching species (e.g., acroporids, pocilloporids) was suggested to be caused by high degrees of wave exposure (Wicks et al. 2010). At Lord Howe Island, Australia, reef-building species were able to establish assemblages, but only in lagoonal areas; they were uncommon on the seaward slopes where reef accretion capacity was very limited (Harriott et al. 1995). In addition, low water temperature in winter, strong monsoon, and high water turbidity may inhibit the recovery of laminar or branching species after typhoon disturbances. As a consequence, massive and encrusting species may become the dominant morphologies of coral communities in the study area.

Comparisons of quantitative methods

Many comparative studies have been conducted to assess the performances of different sampling methods. However, the performance of monitoring method is likely to vary under different circumstances and only very limited number of studies has tried to assess the accuracy of the monitoring methods (Weinberg 1981; Ohlhorst et al. 1988; Lam et. al. 2006). The use of quadrat method is recommended for general monitoring program as it provides the most reliable estimation of the coral cover under most circumstances (Weinberg 1981; Fung 2007; Leujak and Ormond 2007). In this study, the differences between percentage of coral cover, number of species, and diversity indices by the two methods were similar. However, these parameters were all higher in quadrat along line transect method than those in permanent belt quadrat method (Table. 2.4). This may be due to the total area surveyed in quadrat along line transect method (126 m^2) was larger than that in permanent belt quadrat method (100 m^2).

According to the results of multivariate comparisons on coral community structure, there were no significant differences in species composition between permanent belt quadrat method and quadrat along line transect method (P = 0.3, ANOSIM). The result of ANOSIM also showed that the two methods were not separated (R = 0.259). High similarity of dominant genera was found within methods as well as low dissimilarity between methods (SIMPER, Table 2.5). The within group similarity (62.22 and 67.27%) was only higher than the between group similarity (60.74%). This gave additional evidence that samples generated from the 2 methods were not clearly separated from each other.

Based on the results of nMDS ordination plot and cluster analysis (Figs. 2.4, 2.5), the community structure revealed by these methods showed higher similarity at Sites A and B. The separation of samples at Site C was probably related to the spatial heterogeneity of coral distribution. The results indicate the permanent belt quadrat method is appropriate for monitoring the dynamics of coral communities in Yenliao Bay.

Table 2.1 A list of scleractinian species recorded at survey sites in Yenliao Bay in August 2003.

Family	Species	Family	Species	Family	Species
Acroporidae	*Montipora aequituberculata*		*L. yabei*		*F. flexuosa*
	M. efflorescens		*Pachyseris speciosa*		*F. halicora*
	M. foveolata	Pocilloporidae	*Pocillopora damicornis*		*F. pentagona*
	M. grisea		*Stylophora pistillata*		*F. russelli*
	M. informis	Fungiidae	*Lithophyllon undulatum*		*F. complanata*
	M. millepora		*Leptastrea pruinosa*		*Goniastrea aspera*
	M. mollis		*L. purpurea*		*G. australensis*
	M. monasteriata		*Psammocora profundacella*		*G. pectinata*
	M. spongodes	Lobophylliidae	*Echinophyllia aspera*		*G. retiformis*
	M. tuberculosa		*E. echinoporoides*		*Cyphastrea chalcidicum*
	M. turgescens		*Lobophyllia hemprichii*		*C. microphthalma*
	M. venosa		*Oxypora lacera*		*C. serailia*
	Acropora solitaryensis		*Symphyllia agaricia*		*Echinopora lamellosa*
	A. valida	Faviidae	*Favia favus*		*Montastera valenciennesi*
	A. verweyi		*F. laxa*		*Platygyra daedalea*
	Astreopora expansa		*F. lizardensis*		*P. lamellina*
	A. gracilis		*F. maritima*		*P. pini*
Poritidae	*Porites lichen*		*F. maxima*		*P. sinensis*
	P. lobata		*F. pallida*		*Hydnophora exesa*
Agariciidae	*Pavona explanulata*		*F. rotundata*		*Mycedium elephantotus*
	P. varians		*F. speciosa*	Plesiastreidae	*Plesiastrea versipora*
	P. venosa		*F. veroni*		
	Leptoseris explanata		*Favites abdita*	Total: 8 families, 26 genera, 69 species	
	L. mycetoseroides		*F. chinensis*		

Table 2.2 The order of scleractinian genera by colony number and cover recorded in the study area in August 2003. Data in parentheses are percentages.

Genus	No. of colonies	Rank	Genus	Total cover (cm^2)	Rank
Favites	436 (31.1)	1	*Favites*	37518 (23.1)	1
Montipora	181 (12.9)	2	*Montipora*	37094 (22.9)	2
Favia	161 (11.5)	3	*Favia*	18512 (11.4)	3
Stylophora	157 (11.2)	4	*Cyphastrea*	9958 (6.1)	4
Cyphastrea	99 (7.1)	5	*Platygyra*	9958 (6.1)	4
Platygyra	75 (5.3)	6	*Montastrea*	9590 (5.9)	6
Goniastrea	63 (4.5)	7	*Stylophora*	6692 (4.1)	7
Acropora	51 (3.6)	8	*Goniastrea*	5135 (3.2)	8
Montastrea	35 (2.5)	9	*Hydnophora*	4193 (2.6)	9
Porites	24 (1.7)	10	*Pachyseris*	3671 (2.3)	10
Leptoseris	21 (1.5)	11	*Leptoseris*	3457 (2.1)	11
Pavona	20 (1.4)	12	*Pavona*	2786 (1.7)	12
Echinopora	15 (1.1)	13	*Porites*	2202 (1.4)	13
Psammocora	12 (0.9)	14	*Acropora*	2166 (1.3)	14
Pachyseris	9 (0.6)	15	*Echinophyllia*	1805 (1.1)	15
Pocillopora	9 (0.6)	15	*Echinopora*	1644 (1.0)	16
Hydnophora	7 (0.5)	17	*Oxypora*	1227 (0.8)	17
Echinophyllia	6 (0.4)	18	*Mycedium*	1108 (0.7)	18
Mycedium	6 (0.4)	18	*Psammocora*	884 (0.5)	19
Oxypora	5 (0.4)	20	*Symphyllia*	676 (0.4)	20
Astreopora	3 (0.2)	21	*Lithophyllon*	609 (0.4)	21
Leptastrea	3 (0.2)	21	*Astreopora*	512 (0.3)	22
Lithophyllon	2 (0.1)	23	*Pocillopora*	241 (0.1)	23
Plesiastrea	2 (0.1)	23	*Plesiastrea*	185 (0.1)	24
Lobophyllia	1 (0.1)	25	*Lobophyllia*	183 (0.1)	25
Symphyllia	1 (0.1)	25	*Leptastrea*	182 (0.1)	26
Total colonies	1404		Total	162187	

Table 2.3 A list of scleractinian species recorded at survey sites by two methods.

Family	Species	Belt quadrats	Quadrats along line transect
Acroporidae	*Montipora aequituberculata*	X	X
	M. foveolata	X	X
	M. informis	X	X
	M. millepora	X	X
	M. spongodes	X	X
	M. tuberculosa	X	X
	M. venosa	X	
	Acropora solitaryensis	X	X
	A. valida	X	X
	A. verweyi	X	X
Poritidae	*Porites lichen*	X	X
	P. lobata	X	X
	P. lutea		X
	Goniopora columna	X	X
Agariciidae	*Pavona explanulata*	X	
	P. varians		X
	P. venosa	X	
	Leptoseris explanata	X	X
	L. mycetoseroides	X	X
	Pachyseris speciosa		X
Euphyllidae	*Euphyllia ancora*		X
Pocilloporidae	*Pocillopora damicornis*	X	X
	Stylophora pistillata	X	X
Fungiidae	*Lithophyllon undulatum*	X	
	Leptastrea pruinosa	X	X
	L. purpurea	X	X
	Psammocora profundacella	X	X
	P. superficialis		X
	Coscinaraea columma		X
Lobophylliidae	*Lobophyllia hemprichii*	X	
	Symphyllia agaricia	X	
	S. radians		X
	Echinophyllia aspera	X	X
	E. echinata	X	
	E. echinoporoides	X	
	Oxypora lacera	X	
Faviidae	*Favia favus*	X	X

	F. laxa	X	X
	F. lizardensis	X	X
	F. maritima	X	X
	F. pallida	X	X
	F. rotundata	X	
	F. speciosa	X	X
	F. veroni	X	X
	Barabattoia amicorum	X	X
	Favites abdita	X	X
	F. chinensis	X	X
	F. complanata	X	X
	F. flexuosa	X	X
	F. halicora	X	
	F. pentagona	X	X
	F. russelli	X	X
	Goniastrea aspera	X	X
	G. australensis	X	X
	G. edwardsi		X
	G. pectinata		X
	G. favulus		X
	G. retiformis	X	X
	Platygyra daedalea		X
	P. lamellina		X
	P. pini	X	X
	P. sinensis	X	X
	Oulophyllia crispa		X
	Cyphastrea chalcidicum	X	X
	C. microphthalma	X	X
	C. serailia	X	X
	M. valenciennesi	X	X
	Echinopora gemmacea	X	
	E. lamellosa	X	X
	Merulina ampliata		X
	Hydnophora exesa	X	X
	Mycedium elephantotus	X	X
Plesiastreidae	*Plesiastrea versipora*	X	X
	Genera no.	27	27
	Species no.	59	61

Table 2.4 Coral community parameters and diversity indices of two survey methods at study sites. Surveys of permanent belt quadrats (PBQ) was conducted in September 2009, and those of quadrats along line transect (QLT) was in August 2009-April 2010.

Parameters/Diversity Indices	PBQ	QLT
Coral cover	9.34%	9.93%
Species no.	59	61
Shannon Index	3.19	3.66
Species Evenness	0.78	0.89
Simpson Index	0.93	0.97

Table 2.5 Results of SIMPER analysis comparing the coral community structure based on genera percentage cover data from two survey methods. (a) Similarity within group, (b) dissimilarity between groups. %: percentage of contribution.

(a)

Belt quadrat		Quadrat along transect	
Coral genus	%	Coral genus	%
Favites	15.01	*Favites*	13.57
Favia	12.64	*Favia*	13.25
Cyphastrea	10.21	*Goniastrea*	12.13
Porites	9.85	*Cyphastrea*	11.19
Montastrea	7.74	*Porites*	7.63
Platygyra	6.91	*Platygyra*	7.15
Similarity within group	62.11	Similarity within group	67.27

(b)

	Quadrat along transects	
Belt quadrats	Coral genus	%
	Montastrea	8.11
	Montipora	7.46
	Leptoseris	6.4
	Goniastrea	5.9
	Stylophora	5.64
	Favites	5.28
	Dissimilarity between groups	39.26

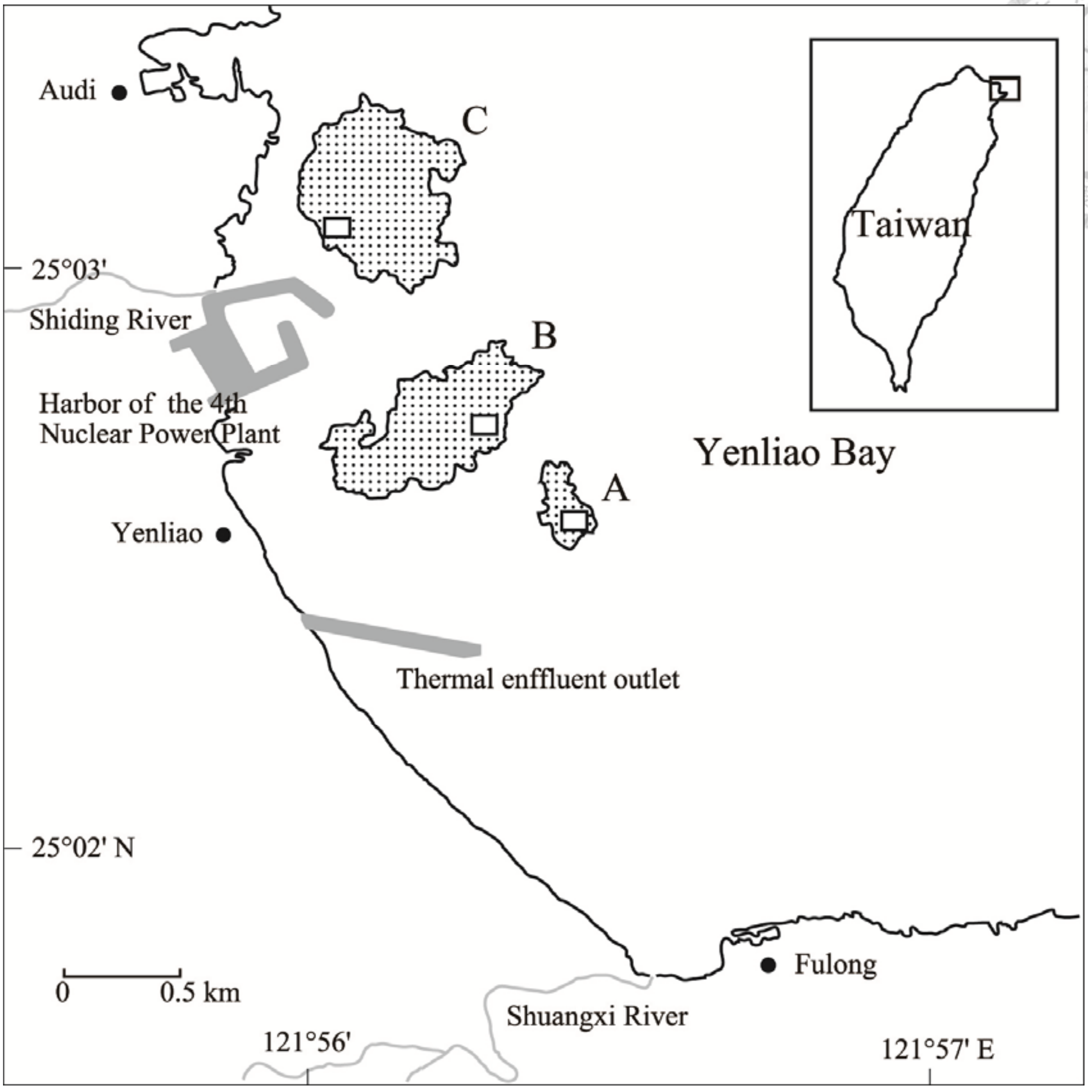


Fig. 2.1 Map of the study area showing three rocky reefs (A, B, C) and three study sites (blank squares).

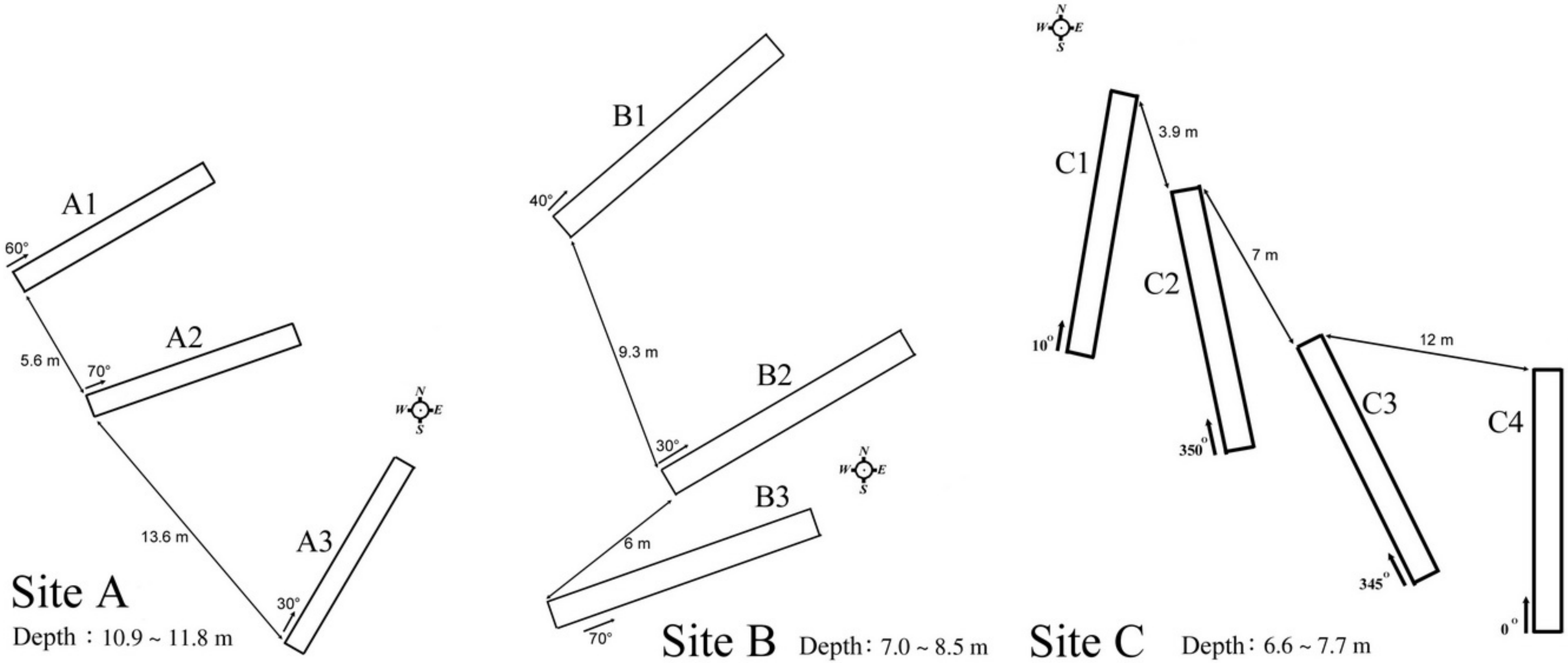


Fig. 2.2 Layout and locations of 10 permanent quadrats on three reefs in Yenliao Bay, northern Taiwan.

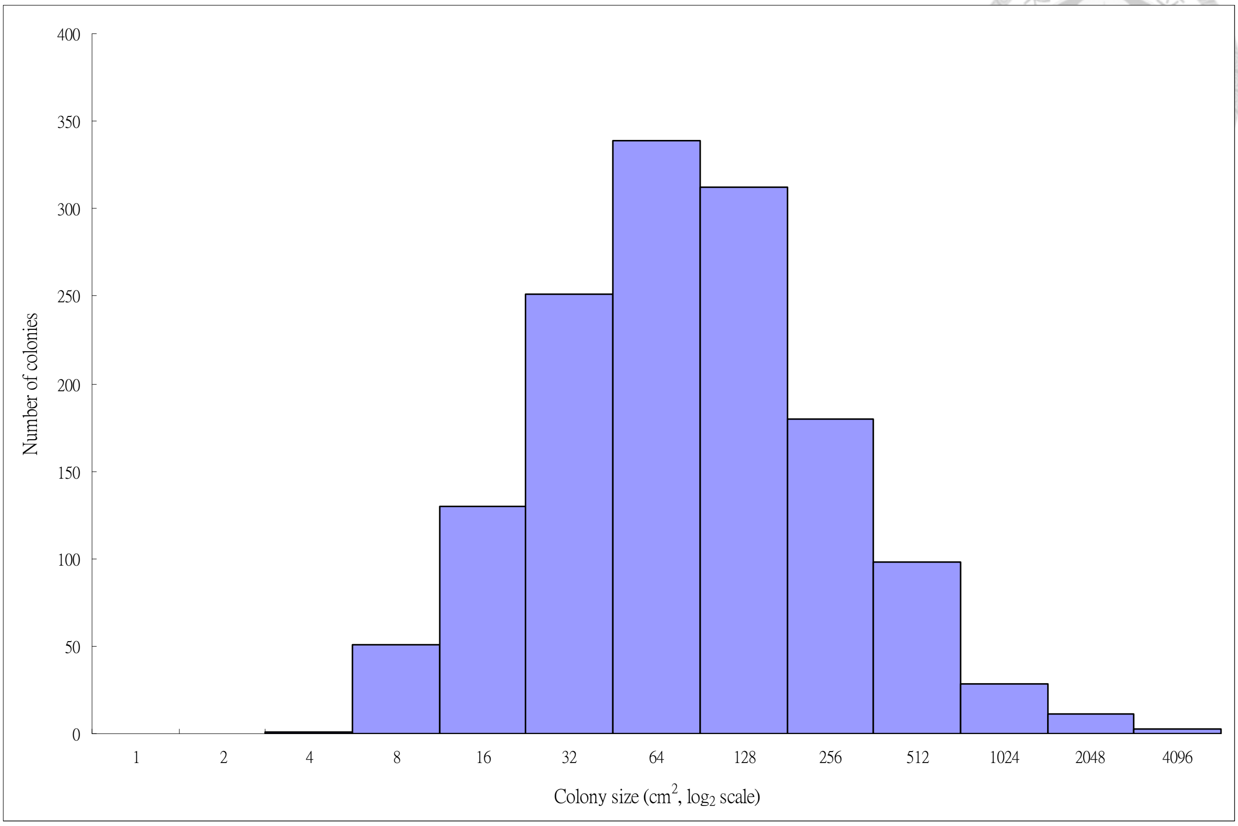


Fig. 2.3 Frequency distribution of colony sizes of total coral colonies recorded in August 2003.

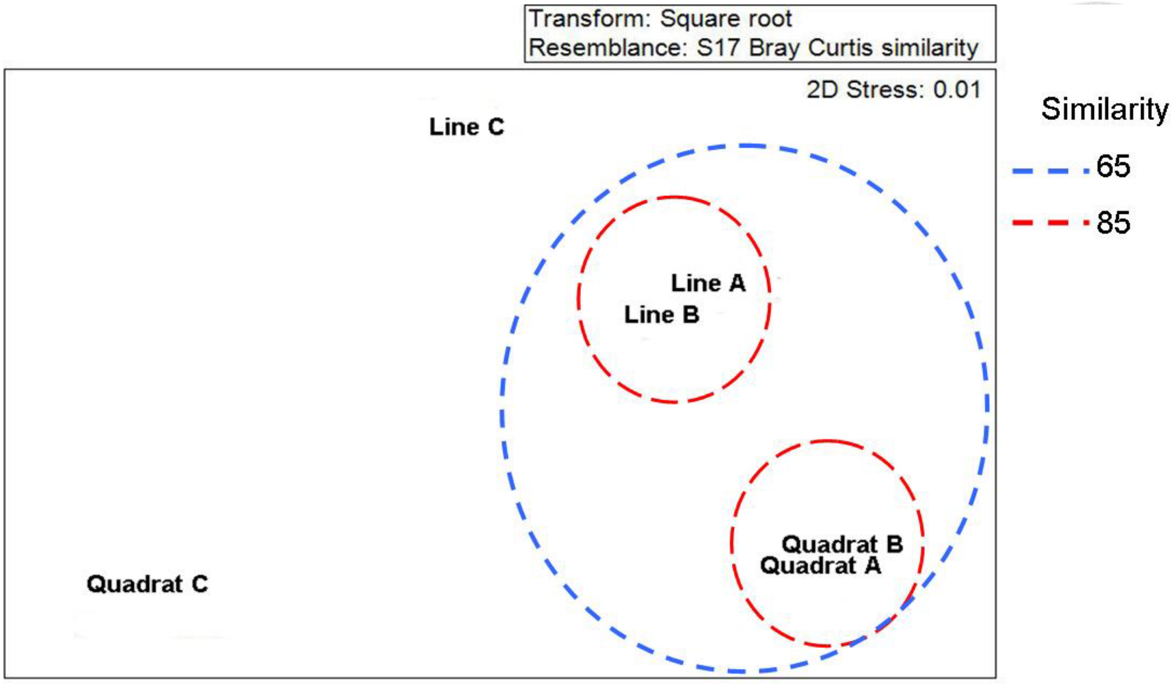


Fig. 2.4 nMDS ordination plot comparing the coral community structures using percentage cover of coral genera by quadrat along transect method (Line) and belt quadrat method (Quadrat), A, B and C denote sampling Sites A, B, C.

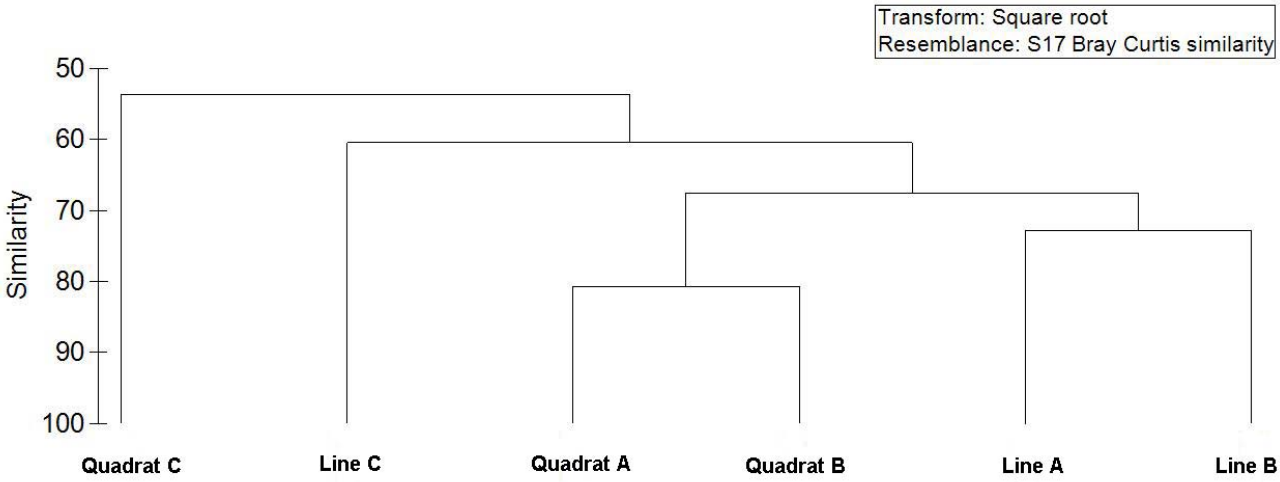


Fig. 2.5 Dendrogram showing the clustering of coral communities using percentage cover of coral genera by quadrat along transect method (Line) and belt quadrat method (Quadrat), A, B and C denote sampling Sites A, B, C.

Chapter 3 Dynamics of subtropical coral communities

3-1 Introduction

Coral reefs are often recognized as one of the most diverse marine ecosystems with high ecological and economic values (Connell 1978; Knowlton 2001). In recent decades, coral reef systems worldwide are declined rapidly and dramatically by natural and anthropogenic disturbances (Knowlton 2001; Hughes et al. 2003; Wilkinson 2004), such as strong tropical cyclones or hurricanes (Hughes 1994, 1996; Connell et al. 1997; Hughes and Connell 1999; Guillemot et al. 2010), mass bleaching and the population outbreak of the crown-of-thorns starfish. Recent studies have suggested that global warming could increase the frequency and intensity of strong hurricanes (Webster et al. 2005; Elsner et al. 2006a, b). If the frequency and intensity of tropical cyclones and typhoons increase as the hurricanes in Atlantic, there may be no enough time for coral assemblages to recovery under such frequent disturbances (Connell 1997; Hughes and Connell 1999). In such a context, it is an important issue to better understand the dynamics of coral reef ecosystems under increasing threats of climate change and to assess the response of coral reef communities to natural disturbances.

The impacts of tropical storms on coral reefs have been well documented for decades (e.g., Connell et al. 1997; Hughes and Connell 1999). The immense and intensive wave forces, severe flood, and heavy terrestrial runoff associated with tropical storms have been shown to cause severe damage and mortality to coral colonies (Connell 1997; Connell et al. 1997). Tropical storms may also have negative effects on coral recruitment and may result in rapid changes of coral communities (Hughes and Connell 1999; Crabbe et al. 2002; Mallela and Crabbe 2009). The recurrence of tropical storms has been shown to be responsible for the change of coral communities and result in the dominance of morphologically resistant species such as massive corals (Connell et al. 1997; Hughes and Connell 1999; Loya et al. 2001; Guillemot et al. 2010). For example, coral reefs of Rio Bueno, northern Jamaica have been struck by Hurricane Allen in 1980, the covers of two branching species, *Acropora palmata* and *A. cervicorinis* which accounted for half or more of the total cover, dropped from 30% to nearly zero, while massive species, *Colpophyllia natans* and *Montastrea annularis* remained virtually unchanged. By 1993, branching *Acropora* remained rare while *C. natans* and *M. annularis* accounted for 40% of the total cover (Hughes and Connell 1999).

A number of long-term studies have been conducted to assess the impacts of tropical storms on coral reefs and the following trajectory of recovery (e.g., Connell et al. 1997; Hughes and Connell 1999; Guillemot et al. 2010). However, long-term studies on the effects of typhoons on marginal coral communities are scarce. Similarly, selective effect of physical disturbances on coral species with different growth forms in subtropical areas have been reported (Nozawa et al. 2008; Tam and Ang 2008), but its long-term effects have rarely been studies. Such a study is useful to better assess the fate of subtropical coral communities under increasing threat of climate change.

In this study, the data of a long-term monitoring program in 6 years including pre- and post-typhoons was presented. The objectives are (1) to examine the impacts of typhoons on marginal coral communities; (2) to assess the responses of different coral species under the impact of typhoons; and (3) to evaluate the recovery of coral communities in northern Taiwan.

3-2 Materials and methods

The study area and sampling methods have been described in Chapter 2.

Data analysis

In order to determine the temporal changes of coral cover at each site, the differences of coral cover among surveys and the trend of changes were evaluated by repeated measures ANOVA because the data were collected from repeated samplings of the same quadrats. Non-metric multidimentional scaling (nMDS) analysis of Bray-Curtis similarity measures were employed (PRIMER, version 6, Clarke and Warwick 2001) using the cover of each genera to reveal the relationship of coral communities in 12 surveys. In addition, all coral colonies in each quadrat were classified into four size classes: < 50 cm^2, 50-100 cm^2, 100-250 cm^2, > 250 cm^2. Differences between size classes and temporal trend of each size class at each site among censuses were also analyzed using repeated measures ANOVA and post-hoc pair comparisons to assess the temporal patterns of each size class.

3-3 Results

Changes of coral cover at three reefs

The changes of coral covers at three reefs showed a similar trend from August 2003 to September 2009 (Fig. 3.1). The coral cover at Sites A, B, and C declined from 23.9 ± 6.7 (mean ± SE), 16.8 ± 1.5, 10.0 ± 1.1% in August 2003 to 9.1 ± 0.9, 8.3 ± 1.0, 2.2 ± 0.3% in July 2007, then increased gradually to 14.1 ± 0.5, 13.2 ± 1.2, and 2.9 ± 0.5% in September 2009, respectively (Fig. 3.1). Changes of coral cover among 12 surveys were highly significant at Sites B and C, but not significant at Site A, mainly due to the large variations among quadrats (Table 3.1). The decline of coral cover was the greatest during the period from July to November 2005, and there were three major typhoons (namely Haitan, Talim, and Longwang, that hit the study area on July 18, August 31, and October 1, successively, data from the Central Weather Bureau, Taiwan. http://rdc28.cwb.gov.tw/data.php) in summer 2005 (Table 3.2). The trends of decline in coral cover were similar at three sites, although that at Site A was not significant (Table 3.1). In addition, the recoveries of coral cover between July 2007 and September 2009were significant at Sites A and B (Table 3.1), but not significant at Site C.

Changes of species composition of coral communities

Non-metric multidimensional scaling (nMDS) analysis of coral communities among 12 consecutive surveys showed distinct grouping (Fig. 3.2). Three periods could be identified in the course of this study, i.e., August 2003-July 2005, November 2005-September 2006, and July 2007-September 2009. During these periods, the changes of coral cover varied among genera and resulted in conspicuous changes in taxonomic composition of coral communities (Fig. 3.3). Coral genera with major changes included encrusting *Montipora* which decreased by 95.8-96.6% at three sites and foliaceous *Pachyseris* which was totally disappeared at Sites A and C during the study period. Besides, the branching *Stylophora* at Sites A and B decreased by 71.0-71.2% after the typhoon disturbances in 2005, however, it recovered to 41.1% and 94.1%, respectively, in September 2009. In contrast, only moderate changes (< 24%) in cover were detected between 2003 and 2009 for massive corals including *Favia*, *Favites*, *Cyphastrea*, and *Montastrea* at Sites A and B. Nevertheless, the covers of massive corals decreased greatly by 35.6%-87.3% at Site C during the same period.

Partial and whole colony mortality varied greatly among coral genera after the remarkable typhoon disturbances in 2005 (Fig. 3.4). Branching, foliaceous and encrusting species (*Stylophora*, *Pachyseris*, and *Montipora*) suffered higher whole mortality rates (37-67%). In contrast, massive faviids (*Favia*, *Favites*, *Montastrea*, *Platygyra*, and *Cyphastrea*) suffered much lower whole mortalities (0-42%), but higher partial mortalities (0-69%) following typhoon disturbances. There was a significant difference of living coral cover among growth forms throughout the survey period, especially those coral with susceptible forms. The covers of most corals in foliaceous and encrusting forms decreased to less than 1% after the disturbances (Fig. 3.5). In contrast, massive corals remained abundant at most study sites except at Site C. Hence, a notable change of community structure after typhoon disturbances was detected.

Temporal variation of colony size class

During the study period, differences among four size classes of hard coral colonies were significant at three sites (Fig. 3.6, Table 3.3). Moreover, all size classes of coral colonies showed similar trends at three reefs except for the smallest size (< 50 cm^2). Between 2003 and 2009, the colony number of smallest colony size (< 50 cm^2) at Sites A and B (Trend Analysis, $p < 0.05$) increased gradually, meanwhile, the smallest colonies decreased in the beginning, then increased at Site C (Trend Analysis, $p < 0.01$).

The proportion of coral colonies of smallest colony size ranged from 40.7%~51.1% in August 2003 to 57.1%~68.1% in September 2009. Meanwhile, the proportion of largest coral colonies (> 250 cm^2) decreased from 13.3%~8.5% in August 2003 to 4.6%~2.4% in September 2009 (Table 3.3, trend Analysis, p = 0.187, $p < 0.05$, $p < 0.05$). The proportion of median colony sizes (50~100, 100~250 cm^2) increased gradually at Sites A and B, but decreased in the beginning then increased slightly at Site C. Although most of the largest size colonies suffered whole or partial mortalities at all sites after typhoon disturbances in 2005, the number of coral colonies at Sites A and B increased mainly due to fragmentation of colonies. Nevertheless, at Site C, total colonies of all size classes decreased 41.4% even though the percentage of small colonies was increasing. This indicated that most coral colonies at Site C suffered partial mortality during this period.

3-4 Discussion

Effects of typhoon disturbances on coral communities

Significant declines of coral communities were detected between 2003 and 2009 in Yenliao Bay. The major decline occurred in July-November 2005 corresponding to the occurrences of three exceptionally strong typhoons that hit northern Taiwan successively. This temporal coincidence suggested that the significant decline of scleractinian corals were likely due to the damage of strong waves and heavy sedimentation associated with typhoon disturbances. Tropical storms (cyclone, hurricane, and typhoon) have been considered one of the large scale disturbances that may cause extensive and severe impacts on coral reefs (Moran et al. 1988; Birkeland and Lucas 1990; Connell 1997; Connell et al. 1997; Hoegh-Guldberg 1999; Wilkinson 1999; Hughes et al. 2003; Osborne et al. 2011). In addition, the damage induced by strong waves of storms seems to be the most common cause of coral mortality in high latitude reefs (Harriott and Smith 2000; Nozawa et al. 2008). Since there was no other major disturbance during the same period, the typhoon disturbances were considered as the major factor responsible for changes of coral communities (Harriott and Banks 2002; Harriott and Smith 2000; Nozawa et al. 2008).

Changes of species composition of coral communities

The results of nMDS analysis showed distinct temporal variations of coral communities among 12 consecutive surveys (Fig. 3.2) and the results highlighted the variability of typhoon disturbances among coral species in Yenliao Bay. The composition of coral communities shifted from a combination of branching, foliaceous, encrusting and massive corals in 2003 to those dominated by massive corals in 2009 (Fig. 3.5). This change was consistent with the observations worldwide (Hughes and

Connell 1999) and could be attributed to the selective effects of typhoons on different growth forms. The growth forms of coral colonies are thought to be an important character for their resistance and survival under the impacts of severe disturbances such as recurrent typhoons or high seawater temperatures (Connell et al. 1997; Hughes and Connell 1999; Loya et al. 2001; Guillemot et al. 2010). For example, at Solitary Islands, Australia, a cyclone in 1976 caused a decrease of > 40% in delicate tabular corals, while massive and encrusting corals showed little change (Connell et al. 1997). At Sesoko Island, Japan, branching corals (mostly *Acropora* and *Pocillopora*) were more susceptible to bleaching induced by higher seawater temperatures, while massive and encrusting corals (mainly faviids and poritids) survived (Loya et al. 2001). These evidences showed that physical disturbances caused significantly damage to more vulnerable forms and favored resistant massive corals (Harriott and Smith 2000; Nozawa et al. 2008).

In Yenliao Bay, differential susceptibility of corals to typhoon disturbances was clearly linked to colony morphology. During the major typhoon disturbances in 2005, different coral species varied greatly in partial and whole colony mortality (Fig. 3.4). Branching, foliaceous and encrusting species (*Stylophora*, *Montipora*, *Pachyseris*, and *Hydnopora*) suffered higher mortality, while those massive faviids (*Favia*, *Favites*, *Cyphastrea*, *Montastrea*, and *Platygyra*) suffered much lower mortalities and showed stable trajectories following typhoon disturbances. Unlike other high latitude areas, most of the reduction of coral cover in Yenliao Bay was attributable to the decrease of encrusting species (e.g., *Montipora*), rather than branching species *Acropora* and *Pocillopora* in southwest Japan (Nozawa et al. 2008) and Southern Australia (Harriott and Smith 2000). The low abundance of branching corals at Yenliao Bay may be due to frequent impacts of strong wave actions generated by typhoons and monsoon that constraint the growth of branching corals and favor the growth of corals with compact forms (Veron 1993; Harriott 1999a). This morphological selection is a feature of disturbances, a large number of studies have provided evidences of selective mortality among corals induced by tropical storms (e.g., Woodley et al. 1981; Hughes and Connell 1999; Guillemot et al. 2010). If the frequency and intensity of storm disturbances increase as projected (Webster et al. 2005; Elsner et al. 2006a, b), a shift of community structure to the dominance of more resistant massive corals may occur on subtropical or marginal coral communities.

Recovery of the coral communities

From 2007 to 2009, the cover of scleractinian corals increased gradually and varied among sites in Yenliao Bay. At Sites A and B, coral cover showed significant increase (Table 3.1, Repeated measures ANOVA, pairwise comparison: $p < 0.05$, $p < 0.01$

respectively), while Site C remained almost no change throughout this period. Since Site C was close to the coastline and facing the input terrestrial sediment from Shiding Stream, the lack of recovery at Site C might be attributable to heavy sedimentation that impeded coral growth (Nugues and Roberts 2003; Wilkinson 2000). In addition, the competition with macroalgae might also constrain or limit the growth and recruitment of corals (Nozawa et al. 2008; Nugues and Roberts 2003; van Woesik et al. 1995). The nutrients enriched water from Shiding River seems to cause the bloom of macroalgae at Site C and resulted in extensive overgrowth of coral colonies.

The recovery of coral communities could be verified by comparing the trajectory of different colony sizes. In the study period, all large coral colonies (> 250 cm^2) at Sites A and B decreased (Fig. 3.6) and showed no significant change (Fig 3.6, Table 3.3), while small colonies (< 50 cm^2) increased remarkably after the typhoon disturbances in 2005 ($p > 0.05$). The mortality of large colonies by strong wave actions is likely a limiting factor for the development of coral communities and reef accretion (Grigg 1998; Harriott and Smith 2000; Nozawa et al. 2008). In the meantime, the number of median size colonies (50-100, 100-250 cm^2) remained stable or increased. This indicated that small colonies might include the fragments of larger colonies that suffered partial mortality as well as newly settled juveniles. The increase of total colony number suggested that coral communities at Sites A and B showed the sign of recovery. In contrast, even though small colonies (< 50 cm^2) were increasing after 2005 at Site C, most of the largest size colonies suffered whole or partial colony mortality and median size colonies decreased significantly. Besides, the total number of colonies of all size classes decreased as well. Therefore, the coral community at Site C did not show any sign of recovery.

In conclusion, significant declines of coral cover and changes of species composition of coral communities were detected at three reefs in Yenliao Bay from 2003 to 2009. These changes were resulted from differential mortality and contrasting trajectories of different coral genera during and after the typhoon disturbances. It is also noted that the recovery of coral communities might be impeded by localized stresses such as those at Site C and this is likely responsible for the spatial heterogeneity of coral communities in this subtropical environment.

Table 3.1 Results of the repeated measures ANOVAs, Trend analysis, and Pairwise comparisons for detecting the changes of coral cover among 12 surveys at the three sites.

Site	A	B	C
Coral coverage change among surveys	n.s. (p = 0.087)	$p < 0.001$ ***	$p < 0.001$ ***
Trend analysis of coral coverage	n.s. (p = 0.076, quadratic)	$p < 0.05$ * (quadratic)	$p < 0.01$ ** (quadratic)
Pairwise comparisons			
August 2003, July 2007	n.s. (p = 0.128)	$p < 0.01$ **	$p < 0.01$ **
July 2007, September 2009	$p < 0.05$ *	$p < 0.01$ **	n.s. (p = 0.135)

Levels of significance (p values) for the repeated measures ANOVAs and trend analysis: n.s.: not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 3.2 A list of 14 typhoons passed or close to Yen-laio Bay during study years. Sources: The Central Weather Bureau, Taiwan.

Date	Name	Maximum gust speed near the center (m/s)	Minimum Sea level pressure near the center (hpa)	Closest distance (from the center to Yenliao Bay)
Aug. 8, 2009	Morakot	40	955	50 - 100 km
Sep. 28, 2008	Jangmi	53	925	50 - 100 km
Sep. 13, 2008	Sinlaku	51	925	< 25 km
Jul. 17, 2008	Kalmaegi	33	970	50 - 100 km
Oct. 6, 2007	Krosa	51	925	< 25 km
sep. 18, 2007	Wipha	48	935	50 - 100 km
Jul. 13, 2006	Bilis	25	978	< 50 km
Oct. 1, 2005	Longwang	51	925	100 - 150 km
Aug. 31, 2005	Talim	53	920	100 - 125 km
Jul. 18, 2005	Haitang	55	912	50 - 100 km
Oct. 25, 2004	Nock-Ten	43	945	< 50 km
Sep. 12, 2004	Haima	18	998	< 50 km
Aug. 24, 2004	Aere	38	960	< 50 km
Jul. 2, 2004	Mindulle	45	942	< 50 km

Table 3.3 Results of the repeated measures ANOVAs, Trend analysis, and Pairwise comparisons for detecting the changes of coral cover among 12 surveys at the three sites.

Site	A	B	C
Differences between colony size	$p < 0.001$ ***	$p < 0.001$ ***	$p < 0.001$ ***
Trend analysis of < $50cm^2$	$p < 0.05$ *	$p < 0.05$ *	$p < 0.01$ **
Trend analysis of $50cm^2$-$100cm^2$	$p < 0.05$ *	$p < 0.05$ *	$p < 0.01$ **
Trend analysis of $100cm^2$-$250cm^2$	$p < 0.05$ *	n.s. ($p = 0.055$)	$p < 0.01$ **
Trend analysis of > $250cm^2$	n.s. ($p = 0.178$)	$p < 0.05$ *	$p < 0.05$ *
Tukey test	$P < 0.001$*** (< $50cm^2$ vs. 50-$100cm^2$, 100-$250cm^2$, > $250cm^2$)	$P < 0.001$*** (< $50cm^2$ vs. 50-$100cm^2$, 100-$250cm^2$, > $250cm^2$)	$P < 0.001$*** (< $50cm^2$ vs. 50-$100cm^2$, > $250cm^2$), p < 0.01 ** (< $50cm^2$ vs. 100-$250cm^2$)

Levels of significance (p values) for the repeated measures ANOVAs and trend analysis: n.s.: not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

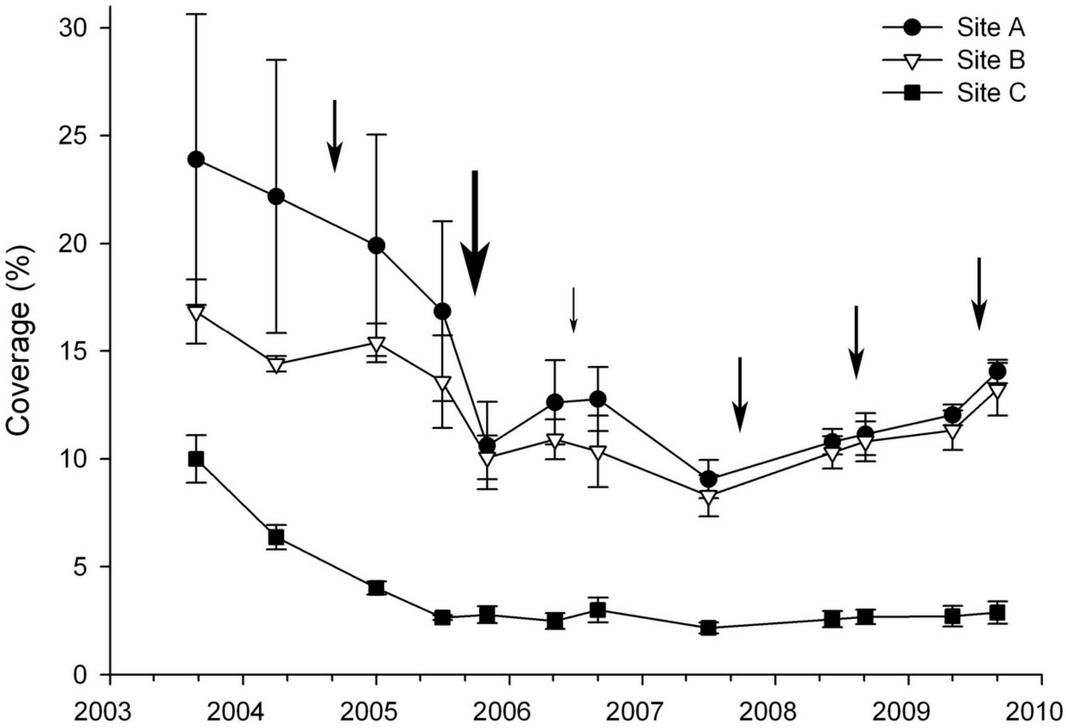


Fig. 3.1 Changes of hard coral cover (mean±SE) at three sites from 2003 to 2009. Arrows indicate the major typhoon events and the arrow size represents the relative intensity of typhoon disturbances.

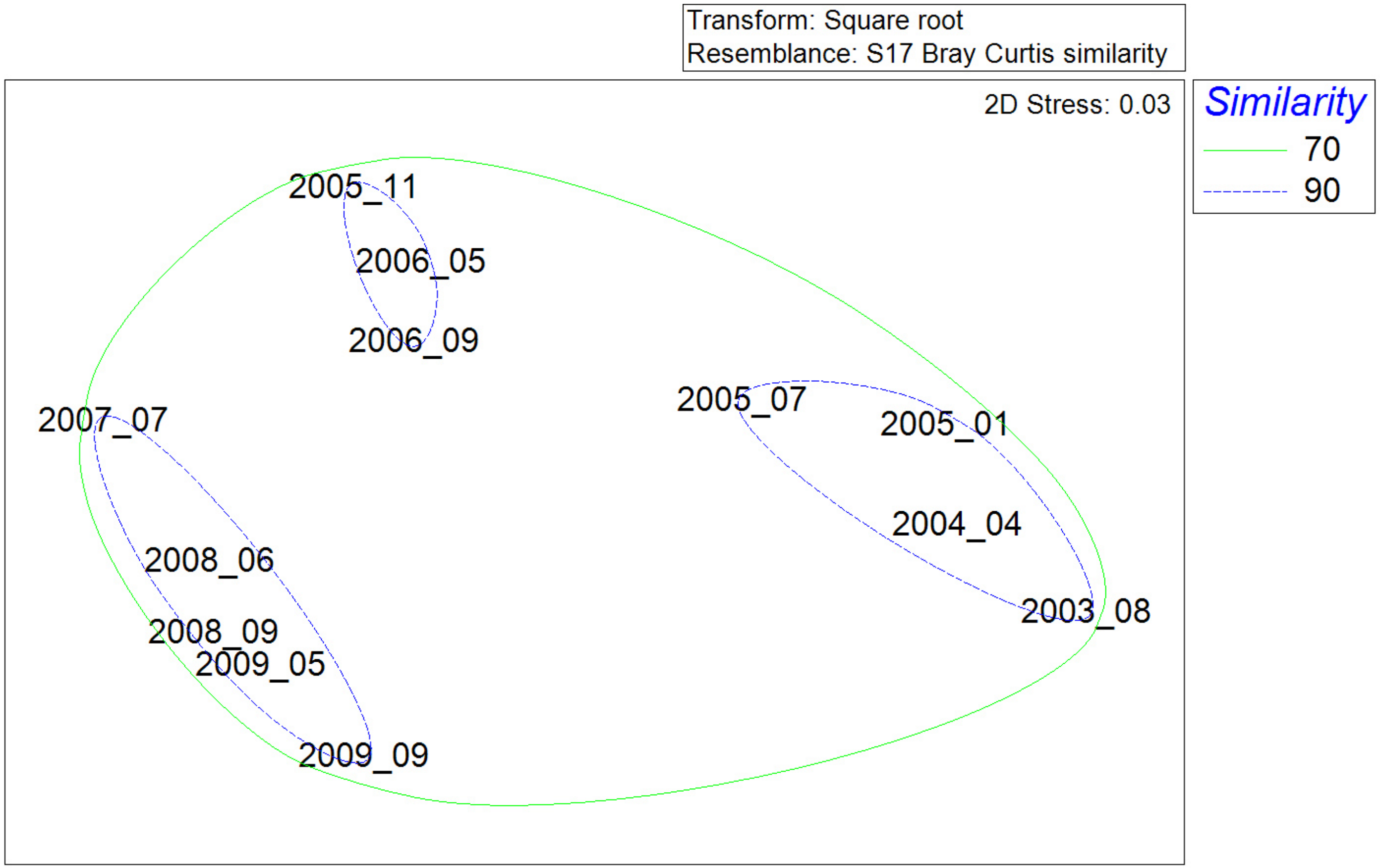
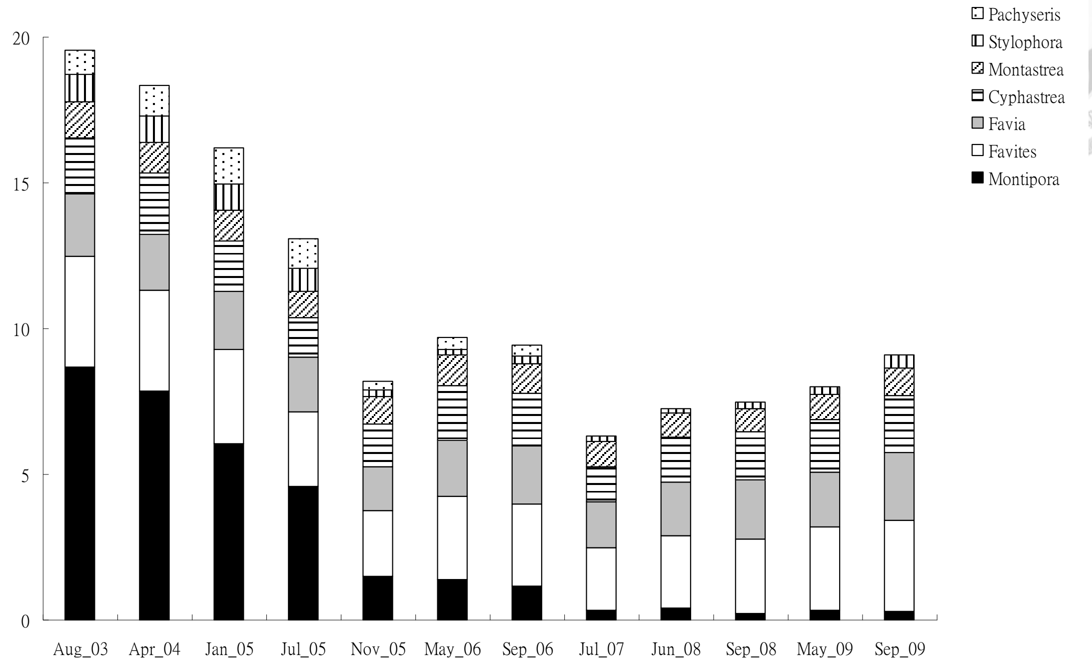
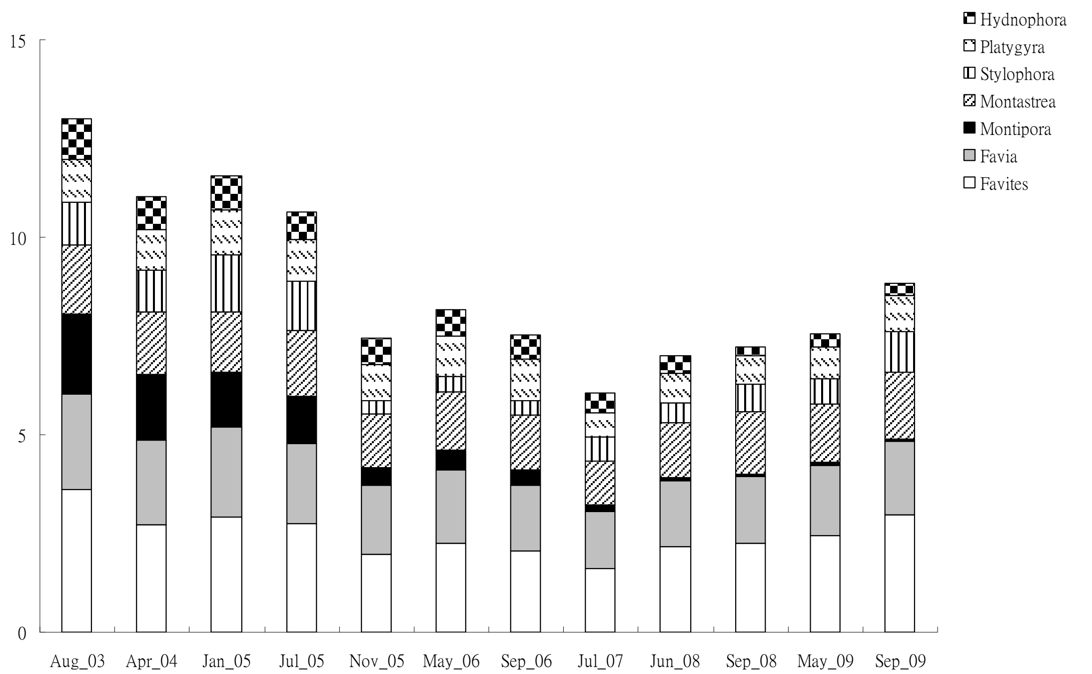


Fig. 3.2 nMDS plot based on Bray-Curtis similarities showing the relationship of the coral communities among 12 surveys in the study area from August 2003 to September 2009. Each symbol represents the coral composition of one survey.

Site A


Pachyseris
Stylophora
Montastrea
Cyphastrea
Favia
Favites
Montipora
20
15
10
5
0
Aug_03
Apr_04
Jan_05
Jul_05
Nov_05
May_06
Sep_06
Jul_07
Jun_08
Sep_08
May_09
Sep_09

Site B


Hydnophora
Platygyra
Stylophora
Montastrea
Montipora
Favia
Favites
15
10
5
0
Aug_03
Apr_04
Jan_05
Jul_05
Nov_05
May_06
Sep_06
Jul_07
Jun_08
Sep_08
May_09
Sep_09

Site C

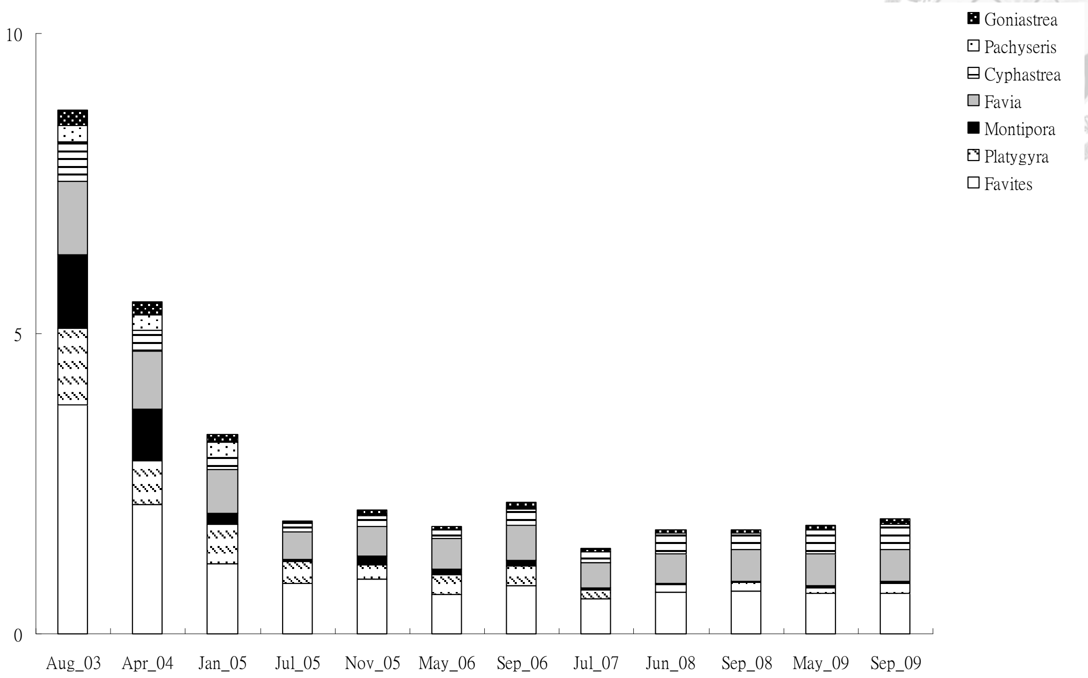


Fig. 3.3 Stacked histograms of hard coral cover of major genera at three sites from 2003 to 2009.

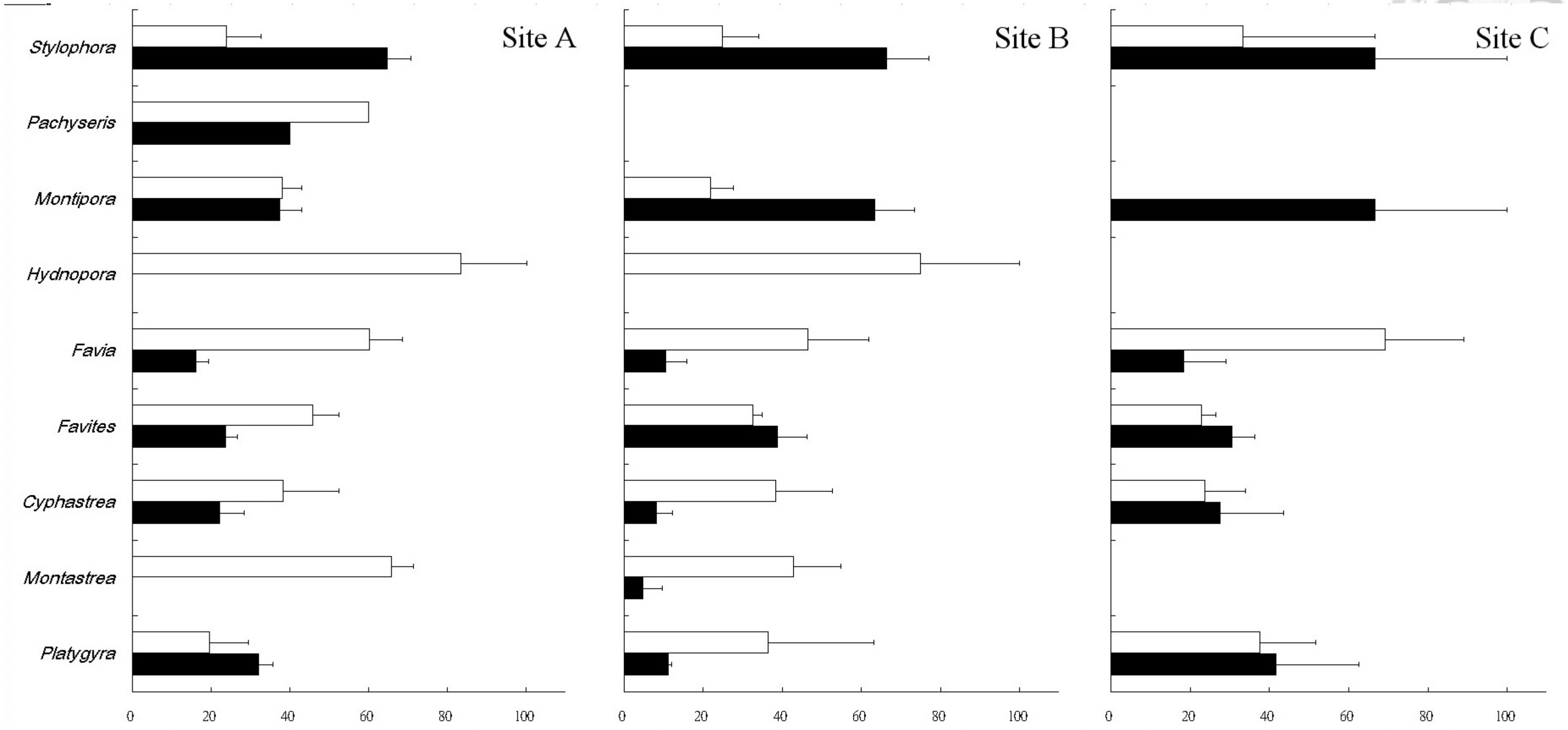


Fig. 3.4 Mortality rates of coral genera at three sites after major disturbance in 2005. Black bar: whole mortality; white bar: partial mortality.

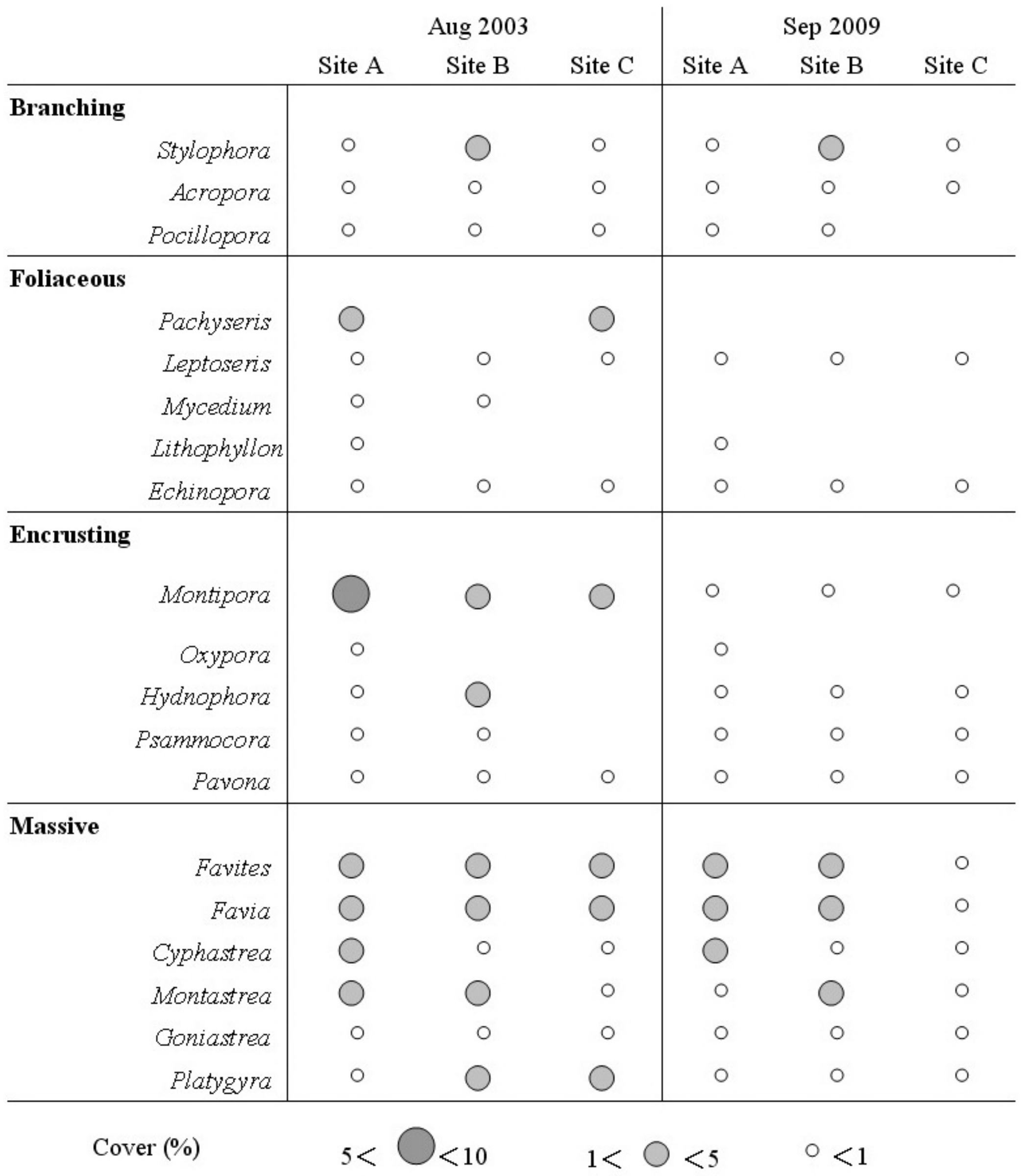
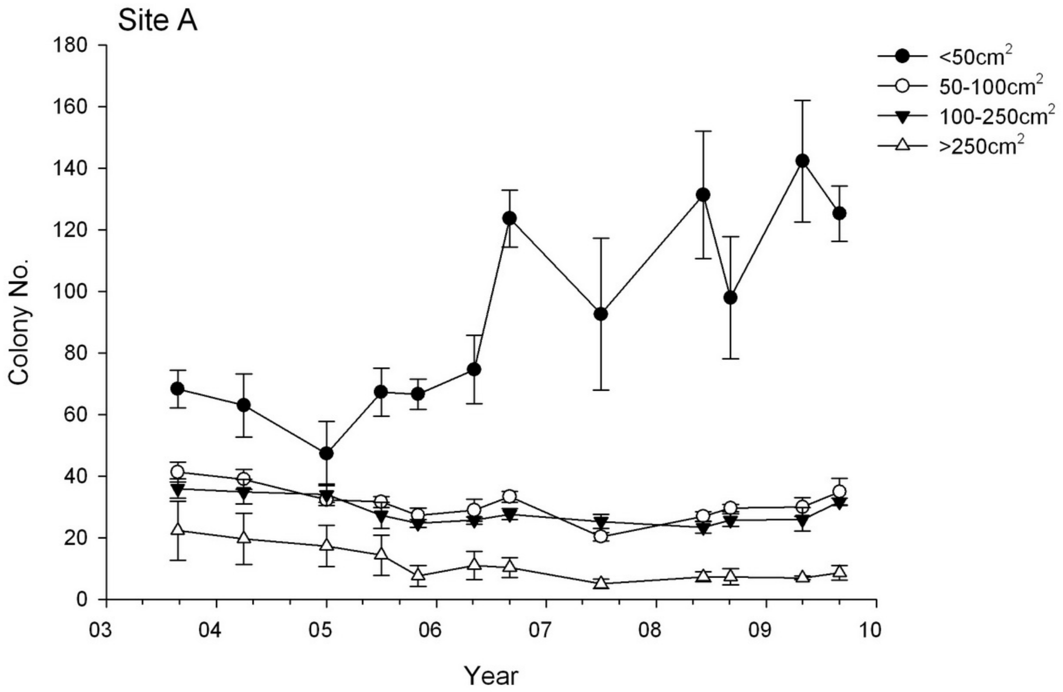
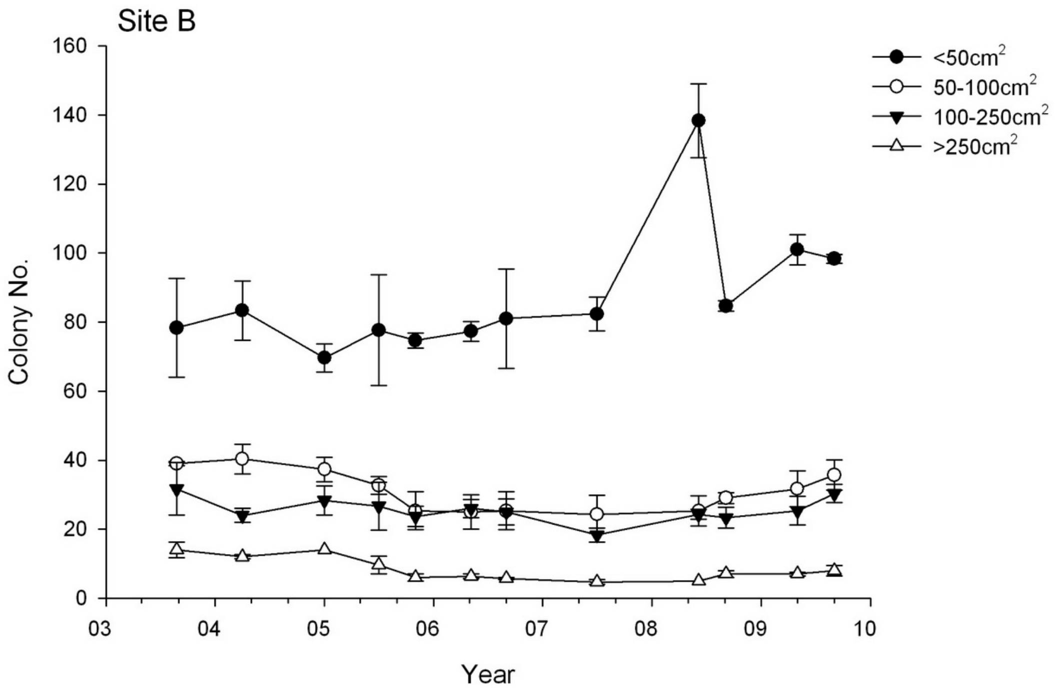


Fig. 3.5 Changes of relative abundance of major coral genera at three sites between August 2003 and September 2009.


Site A
Colony No.
Year
<50cm2
50-100cm2
100-250cm2
>250cm2
0
20
40
60
80
100
120
140
160
180
03
04
05
06
07
08
09
10


Site B
Colony No.
Year
<50cm2
50-100cm2
100-250cm2
>250cm2
0
20
40
60
80
100
120
140
160
03
04
05
06
07
08
09
10

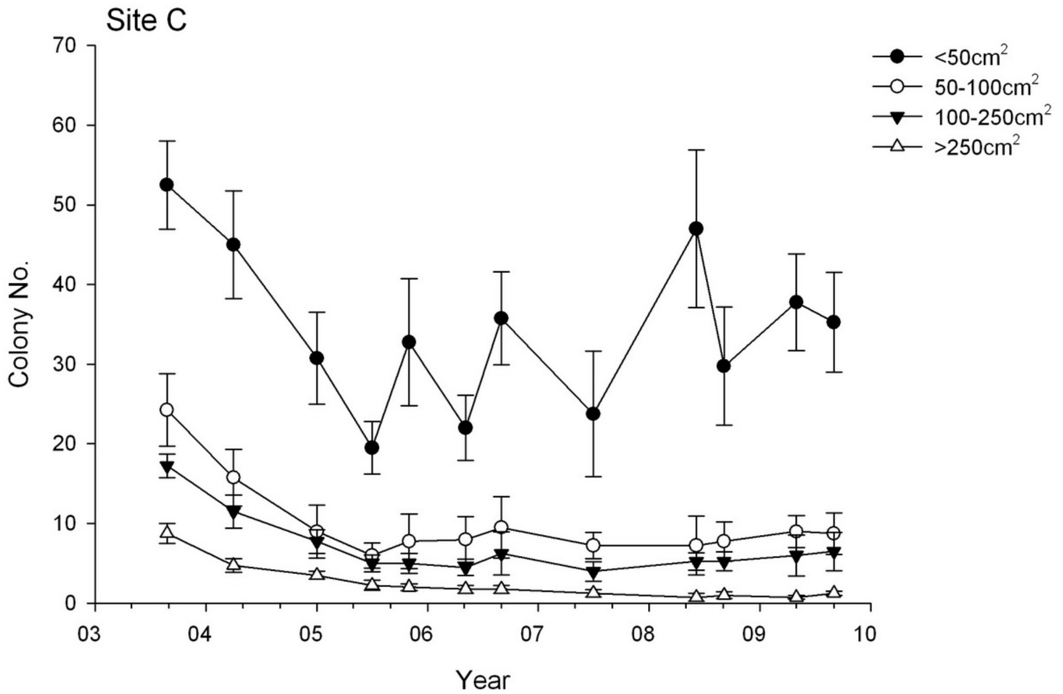


Fig. 3.6 Changes of coral colony number (mean ± SE) of four size classes at three sites from 2003 to 2009.

Chapter 4 Coral recruitment of subtropical coral communities

4-1 Introduction

Coral recruitment has been recognized as the critical process in determining the robustness and resilience of coral reef systems, especially when such systems are subjected to threats or damages (Gittings et al. 1988; Hughes and Tanner 2000; Kojis and Quinn 2001). Recruitment is also a key factor for understanding the population dynamics and community structures in these ecosystems (Caley et al. 1996; Quinn and Kojis 2003; Glassom et al. 2004). Hence, it is widely recognized that investigating the patterns of coral recruitment is essential for reef conservation and management practices. However, insufficient attention has been paid to understand the recruitment processes in marginal coral communities (Harriott and Banks 2002; Hoey et al. 2011).

Coral recruitments have been intensively studied in different geographic regions during the past three decades (e.g., Birkeland 1977; Harriott 1992; Hughes et al. 1999; Soong et al. 2003; Glassom et al. 2004; Nozawa et al. 2006; Adjeroud et al. 2007; Salinas-de-León et al. 2013). These studies have pointed out that recruitment rates are highly variable on spatial and temporal scales. Recruitment rates vary with geographical positions, depth, light availability, substrate topography, biotic interactions, and other biophysical factors (Birkeland 1977; Maida et al. 1995; Babcock and Mundy 1996; Hughes et al. 1999; Glassom et al. 2004). Hughes et al. (2002) reported that recruitment rates of corals decreased with increasing latitudes in the Great Barrier Reef. Other studies, however, showed that there was no consistent pattern in recruitment rates between subtropical and tropical reefs (Harriott 1992; Harriott and Simpson 1997; Glassom et al. 2006). Several studies have showed that recruitment rates on subtropical reefs are highly variable in both spatial and temporal scales (Harriott and Banks 1995; Tioho et al. 2001; Glassom et al. 2004). The recruitment of broadcast-spawning corals were reported to decline toward higher latitudes (Harriott 1999b; Hughes et al. 2002), while the opposite trend was found among brooding corals, resulting in the dominance of brooders at higher latitudes (Glassom et al. 2004, 2006; Tioho et al. 2001; Nozawa et al. 2006).

Coral communities in Yenliao Bay are typical marginal coral communities characterized by low coral coverage and limited reef-building activity (Yang and Dai 1982). The main environmental conditions restricting reef development are possibly low sea temperature, strong northeast monsoon, and high turbidity in winter. Soong et al. (2003) showed that coral recruitment rate was very low in northern Taiwan based on the surveys conducted in March to May. This low recruitment rate may be responsible for the low species diversity and may constrain the resilience of this marginal coral community. However, Soong et al. (2003) did not examine coral recruitment in other months, especially during the spawning season of corals in northern Taiwan which was reported to occur in June and July (Dai et al. 1992). Thus, more comprehensive studies of coral recruitment in this area are needed. Furthermore, this subtropical coral community may become the refuge of tropical coral species under the impacts of climate change (Tsai et al. 2005). However, this will be mainly determined by the availability of coral recruitments in subtropical coral communities. In this study, we investigated the patterns of coral recruitment at Yenliao Bay in northern Taiwan with an aim to reveal the recruitment pattern and to examine whether the recruitment rate is the major limiting factor for the maintenance and development of coral communities.

4-2 Materials and Methods

The study sites have been described in Chapter 2.

Recruitment study

Two groups of settlement plates for short-term and long-term surveys, respectively, were repeatedly deployed at sites A, B, and C from 2006 to 2009 (Fig 4.1). For short-term surveys, the settlement plates were deployed and retrieved in approximately 3-month intervals, and the aim was to investigate the seasonal pattern of coral recruitment including recruitment rate, temporal variations, and taxonomic composition. For long-term surveys, the plates were deployed and retrieved in approximately 1-year intervals, and the aim was to study the survival rate of coral recruits. Coral recruits settled on plates deployed for 1-year intervals was assumed to be comparable to those settled on plates deployed for 3-month intervals in the same time. Therefore, the survival rate could be assessed as recruitment rate of the long-term survey divided by that of the short-term survey in the spawning season. For each group of survey, a total of 10 sets of settlement plates were installed at sites A (three sets), B (three sets), and C (four sets), at depths 12 to 13, 8 to 10, and 6 to 8 m, respectively. Each set of settlement plates comprised four ceramic tiles attached horizontally to a stainless steel frame with approximately 10 cm between them and was anchored to the substrata with approximately 20 cm above the sea floor (Fig. 4.2). The unglazed ceramic tiles (12 × 12 × 1 cm) used in Harriott and Fisk (1987) were applied as the settlement plates for coral recruitment studies. These ceramic tiles have been showed to be effective in attracting coral recruits and have been widely applied in coral recruitment studies (Harriott 1999b).

All retrieved plates were preserved in 95% alcohol for further lab examination. Each plate was checked under a dissecting microscope for coral recruits, and all coral recruits were counted and identified to family level if possible (Baird and Babcock 2000; Babcock et al. 2003). Positions of coral recruits on the plate surfaces (top, lower, or vertical) were also recorded.

Data analysis

Statistical analyses were conducted using SPSS 16 (SPSS Inc., Chicago IL, USA) and StatView 5.0.1 (SAS Institute Inc., Cary, NC, USA). The recruitment data were first tested for homogeneity and normality. In case of non-normality and heterogeneity of the data, a non-parametric Kruskal-Wallis rank test was applied to examine variations in number of coral recruits among years, sites, and plate surfaces. Mann-Whitney U test with Bonferroni correction as post hoc test was then used for the multiple comparisons since it is an efficient and robust method for heterogeneous data. In addition, the relationship between total number of coral recruits on different surfaces of settlement plates and depths was examined using correlation and linear regression analyses.

4-3 Results

Coral recruitment and timing

A total of 298 coral recruits were found on settlement plates in 12 short-term surveys in 2006 to 2009. The total numbers of coral recruits in each year (sites combined) varied significantly among the four consecutive years (Fig. 4.3, Table 4.1 part a, Kruskal-Wallis test, $p < 0.0001$). Recruitment rate was the highest in June to October 2006 (116.4 ± 42.4 recruits m^{-2}, mean ± SE), followed by that in May to

August 2007 (86.9 ± 36.0 recruits m^{-2}) (Fig. 4.4). Recruitment rates were lower than 12.1 ± 4.1 recruits m^{-2} in the other five short-term surveys, and no coral recruit was observed in the rest of the surveys (Fig. 4.4). Recruitment rate also showed a significant difference among years at each study site, except site A (Table 4.1 part b). No difference was found in recruitment rates among study sites in each year, except that in 2007 (Table 4.1 part c).

For long-term surveys, the recruitment rate on plates deployed from May 2006 to August 2007 was 13.7 ± 3.8 recruits m^{-2}. This rate was only ca. 12% in comparison with that of the short-term survey in May to August 2006. The recruits recorded in the following two long-term surveys (August 2007 to September 2008 and September 2008 to August 2009) were regarded as newly settled recruits because the time of deployment was in early autumn and all the recruits were comparable or smaller than those recorded in short-term surveys. Therefore, these two surveys were excluded for further analysis.

Taxonomic composition

Of the 298 coral recruits identified over the 3.6-year study period, the most dominant corals were species of family Pocilloporidae which constituted 52% to 90% of total recruits in each year (Fig. 4.5), followed by species of family Acroporidae (10% to 41%). Other recruits of families Poritidae and Faviidae were rare. However, on the settlement plates of long-term deployment from May 2006 to August 2007, coral recruits of family Acroporidae were the dominant one (77%), followed by Pocilloporidae (18%) and Poritidae (6%) (Fig. 4.5).

Coral recruits on different surfaces

Regarding the number of coral recruits on different surfaces of the settlement plates, the majority (53%, n = 158) were found on the top surface, followed by 42% (n = 125) on the vertical surface, and 5% (n = 15) on the bottom surface (Figure 4.6). On the plates of long-term surveys, coral recruits were found on top and vertical surfaces, and no recruit was found on the bottom surface. The recruitment rates on different surfaces of the plates were significantly different (Table 4.2 part a, Kruskal-Wallis test, $p < 0.0001$). Among years, the recruitment rates differed significantly only in 2006 and 2007 (Table 4.2 part b, Kruskal-Wallis test, $p < 0.01$). Furthermore, the recruitment rates on top and vertical surfaces were significantly higher than those on bottom surfaces in 2006 and 2007 (Table 4.2 part c, Mann-Whitney U test with Bonferroni correction, $p < 0.01$, $p < 0.001$).

Recruitment rates and depths

Since most of the coral recruits occurred in two short-term surveys (May to October

2006 and May to August 2007), these data were applied to show the relationship between depths and recruitment rates on different surfaces. The total number of recruits per plate was negatively correlated with depth (Fig. 4.7, Table 4.3, p = 0.0001). In addition, among the three surfaces of plates, the recruitment rates on top and vertical surfaces were negatively correlated with depths (Table 4.3, $p < 0.05$, $p < 0.0001$).

4-4 Discussion

Coral recruitment rates

During the 4-year study period, coral recruitments peaked in summer and early autumn (June to October) in each year (Fig. 4.4). This timing of coral recruits is consistent with the reproductive season of corals in northern Taiwan which has been showed to occur in early June and July (Dai et al. 1992; Fan and Dai 1995). Coral recruitment rates in this study were about five times higher than those reported by Soong et al. (2003) in northeastern Taiwan. This difference was mainly due to the timing of plate deployment since the survey of Soong et al. (2003) was conducted in April to May, about 2 months before the reproductive season of corals in northeastern Taiwan (Dai et al. 1992).

Coral recruitment rates varied greatly among the four consecutive reproductive seasons with significantly higher values found in 2006 and 2007 (Fig. 4.3). Many studies have showed great variations of coral recruitment at different spatial and temporal scales (Table 4.4), especially in high-latitude coral communities (Harriott and Banks 1995; Tioho et al. 2001; Glassom et al. 2004). The variation of coral recruitments may be related to the greater variations of environmental factors such as sea temperature and light intensity. Previous studies indicated that wintertime sea temperature in Yenliao Bay occasionally fell below 18°C, and corals in northern Taiwan spawned in the summer during the periods of maximum sea temperatures (Yang and Dai 1982; Dai et al. 1992). Wintertime sea temperature in the study area was below 18°C in 2008 (minimum 13.3°C in February), and the rise of maximum sea temperatures delayed for almost 2 months in 2008 and 2009 (Fig. 4.8). The delay of seawater temperature rising may have significant influences on coral reproduction. Nozawa (2012) reported that the exact timing of spawning in a subtropical coral community varied among years and was correlated with the cumulative seawater temperature during the late period of gametogenesis (0 to 3 months before spawning). The lower seawater temperature and delayed rising of seawater temperature in 2008 and 2009 might have significant impacts on coral reproduction by delaying the spawning time in Yenliao Bay.

The recruitment rates of coral communities at Yenliao Bay in 2006 and 2007 were comparable with those reported from other high-latitude or marginal areas of the world (Table 4). The lower recruitment rates in 2008 and 2009 were similar to those recorded in high-latitude coral communities in southern Japan (Tioho et al. 2001; Nozawa et al. 2006). Furthermore, the survival rate of coral recruits in Yenliao Bay from 2006 to 2007 was also comparable with that reported in southern Japan (Nozawa et al. 2006). Based on similar recruitment and survival rates, Harriott (1999b) suggested that the low recruitment rates should be sufficient to maintain the high-latitude coral communities. Moreover, the recruitment rates of corals at Yenliao Bay in 2006 and 2007 were higher than that reported in a tropical reef in Nanwan Bay (32.5 spats m^{-2}), southern Taiwan (Kuo and Soong 2010). Therefore, it seems that the recruitment rate is not a limiting factor for the maintenance and development of coral communities in Yenliao Bay.

Taxonomic composition

Pocilloporid corals were the most abundant recruits during the study period (Figure 6), and most of the recruits were possibly *Stylophora pistilllata*, the common pocilloporid coral in Yenliao Bay (Yang and Dai 1982). This is consistent with the pattern of high-latitude coral communities where brooding corals (mainly pocilloporids) are the most abundant recruits (Tioho et al. 2001; Hughes et al. 2002; Glassom et al. 2004, 2006; Nozawa et al. 2006). It seems that brooding pocilloporids release planulae only in summer and early autumn in northern Taiwan, while they have extended reproductive season throughout the year in southern Taiwan (Dai et al. 1992). The short pre-competent period of brooding larvae may result in high contribution to local recruitment of high-latitude coral communities (Harriott 1992; Tioho et al. 2001). The recruits of acroporid corals were less than those of pocilloporids in short-term surveys, while they became the most abundant in long-term surveys. This is possibly due to the higher survivorship of acroporid corals since they tend to form larger spats, and the survivorship of larger spats is often higher than that of smaller spats (Nozawa et al. 2006). However, the branching *Acropora* colonies were susceptible to storm disturbances; thus, their abundance was relatively low compared with the encrusting and foliaceous colonies of *Montipora* species in the coral communities at Yenliao Bay (Yang and Dai 1982).

Orientation of recruits

Coral recruitment patterns may represent the results of habitat selection of pre-settlement larvae (Babcock and Mundy 1996; Kuffner 2001; Baird et al. 2003) and post-settlement factors (Sato 1985; Smith 1997). Most studies on shallow tropical reefs demonstrated that coral recruits had a greater preference for the vertical and bottom surfaces (Harriott and Fisk 1987; Fisk and Harriott 1990; Harrison and Wallace 1990). It is suggested that grazing and sedimentation are the main factors inhibiting the settlement and survival of coral larvae on the top surface (Birkeland 1977; Carleton and

Sammarco 1987; Fisk and Harriott 1990). However, studies on the settlement pattern of subtropical reefs showed that more coral recruits were found on top and vertical surfaces of the settlement plates (Harriott and Banks 1995; Banks and Harriott 1996). Harriott and Banks (1995) suggested that the preference of top surface might be due to low light intensity and competition of other benthos.

Light intensity and solar radiation has been suggested to be one of the important factors responsible for the pattern of coral recruitment (Maida et al. 1994; Harriott and Banks 1995). Coral recruits preferred to settle in the position that offered optimal light condition for spat development, and the survivorship and average size of coral recruits were both higher for those settled in the position of the plates with optimal light condition (Maida et al. 1994). The light intensity in subtropical reefs is often lower than that of tropical reefs mainly due to higher water turbidity and lower solar radiation (Harriott and Banks 1995; Harriott and Simpson 1997; Glassom et al. 2006). Under such an environment, light on the lower surface is likely too low to support the photosynthesis of coral larvae which is critical for their survival and growth. Therefore, coral larvae tend to colonize the top surface, and coral recruits that colonize the top surface have a higher survival rate (Maida et al. 1994).

Competition with other benthos for settlement space and post-settlement mortality due to overgrowth of other organisms may also limit coral recruitment on the bottom surface in subtropical reefs (Birkeland 1977; Harriott and Banks 1995). In this study, the bottom surface of settlement plates was frequently occupied by macrobenthos such as bryozoans, ascidians, polychaetes, and barnacles. These cryptic organisms often have higher growth rates and may quickly occupy the bottom surface, thus prohibiting or excluding the settlement of coral recruits (Birkeland 1977).

The number of coral recruits in Yenliao Bay showed a negative correlation with depths (Table 4.3). Moreover, the number of coral recruits on top and vertical surfaces decreased with increasing depths (Fig. 4.7). Since water turbidity in Yenliao Bay is frequently high due to constant input of runoffs from adjacent rivers and resuspension of sediment, light intensity in the water column reduces rapidly with increasing depths. Light availability at different depths is likely the primary factor controlling the settlement pattern of coral recruits in Yenliao Bay.

In conclusion, we investigated the recruitment pattern of scleractinian corals of a subtropical coral community in northern Taiwan. The recruitment season occurred from summer to early autumn, and this was consistent with the reproductive season of corals in Yenliao Bay. The recruitment rates were highly variable among years and might be influenced by the annual variation of seawater temperatures. The high recruitment rates recorded in 2006 and 2007 were comparable with those of tropical reefs and other subtropical reefs, suggesting that coral recruitment might have the potential to support the maintenance and development of this marginal coral community. Pocilloporid corals were the most abundant recruits, while acroporids had a higher survival rate. Coral recruits settled mainly on the top and vertical surfaces of settlement plates, and the number of coral recruits was negatively correlated with depths, suggesting that light intensity might be the primary factor affecting the settlement and survival of coral recruits.

Table 4.1 Summary of statistical tests for comparisons of coral recruitment rates.

	Part a			Part b									Part c											
	Among years			Site A			Site B			Site C			2006			2007			2008			2009		
	df	*H*	*p*	*df*	*H*	*p*	*df*	*H*	*p*	*df*	*H*	*p*	*df*	*H*	*p*	*df*	*H*	*p*	*df*	*H*	*p*	*df*	*H*	*p*
Years	3	22.95	<0.00001*	3	6.51	0.09	3	9.46	0.02*	3	8.12	0.04*												
Site													2	4.41	0.11	2	6.56	0.04*	2	4.00	0.14	2	1.01	0.60

Part a, among years (three sites combined); part b, among years at each site; part c, among sites in each year. Kruskal-Wallis rank test, *$p < 0.05$ is significant.

Table 4.2 Summary of statistical tests for comparisons of coral recruitment rates.

	Part a			Part b												Part c					
				2006			2007			2008			2009			2006			2007		
	df	*F*	*p*	*df*	*H*	*p*	*df*	*H*	*p*	*df*	*H*	*p*	*df*	*H*	*p*	*df*	*Z*	*p*	*df*	*Z*	*p*
Surfaces	2	21.55	<0.0001*	2	13.17	<0.01*	2	21.49	<0.0001*	2	2.11	0.35	2	1.35	0.51						
T vs. B																9	−3.00	<0.01*	9	−3.66	<0.001*
B vs. V																9	−3.27	<0.01*	9	−3.87	<0.001*
T vs. V																9	−0.34	0.73	9	−2.42	0.015*

Part a, among surfaces (top, bottom, and vertical) in 2006 to 2009, Kruskal-Wallis rank test; *$p < 0.05$ is significant. Part b among surfaces, Kruskal-Wallis rank test; *$p < 0.05$ is significant. Part c among surfaces (T, top; B, bottom; V, vertical), Mann-Whitney U test with Bonferroni correction; *$p < 0.0167$ is significant.

Table 4.3 Correlation analyses (*Z* test) between depths and number of coral recruits on different surfaces of plates.

Groups	***Z* value**	***p* value**
Depth vs. top surface	−2.21	0.027*
Depth vs. bottom surface	0.53	0.599
Depth vs. vertical surface	−4.27	<0.0001*
Depth vs. total recruits	−3.81	0.0001*

Data of 2006 and 2007 combined. n = 80 plates; $*p < 0.05$ is significant.

Table 4.4 Comparison of coral recruitment rates on settlement plates at high-latitude or marginal locations around the world.

Region	**Latitude**	**Material**	**Recruitment rate (number m^{-2} $year^{-1}$)**	**Location**	**Source**
North Pacific	32° N	Slate	2	Amakusa, Japan	Nozawa et al. (2006)
	25° N	Ceramic	106	Yenliao Bay, northern Taiwan	This study
South Pacific	29-30° S	Ceramic	132	Solitary Islands, Eastern Australia	Harriott and Banks (1995)
	26° S	Ceramic	173	Gneering Shoals, Australia	Banks and Harriott (1996)
Caribbean	10° N		3.8	Cubagua Island, Venezuela	Rodrĭguez et al. (2009)
Red Sea	29° N	Ceramic	18	Eilat, Israel	Abelson et al. (2005)
	29° N	Ceramic	190	Eilat, Israel	Glassom et al. (2004)
Indian Ocean	30° S	Ceramic	1,007	Sodwana Bay, South Africa	Glassom et al. (2006)

Coral recruits were calculated following Glassom et al. (2004).

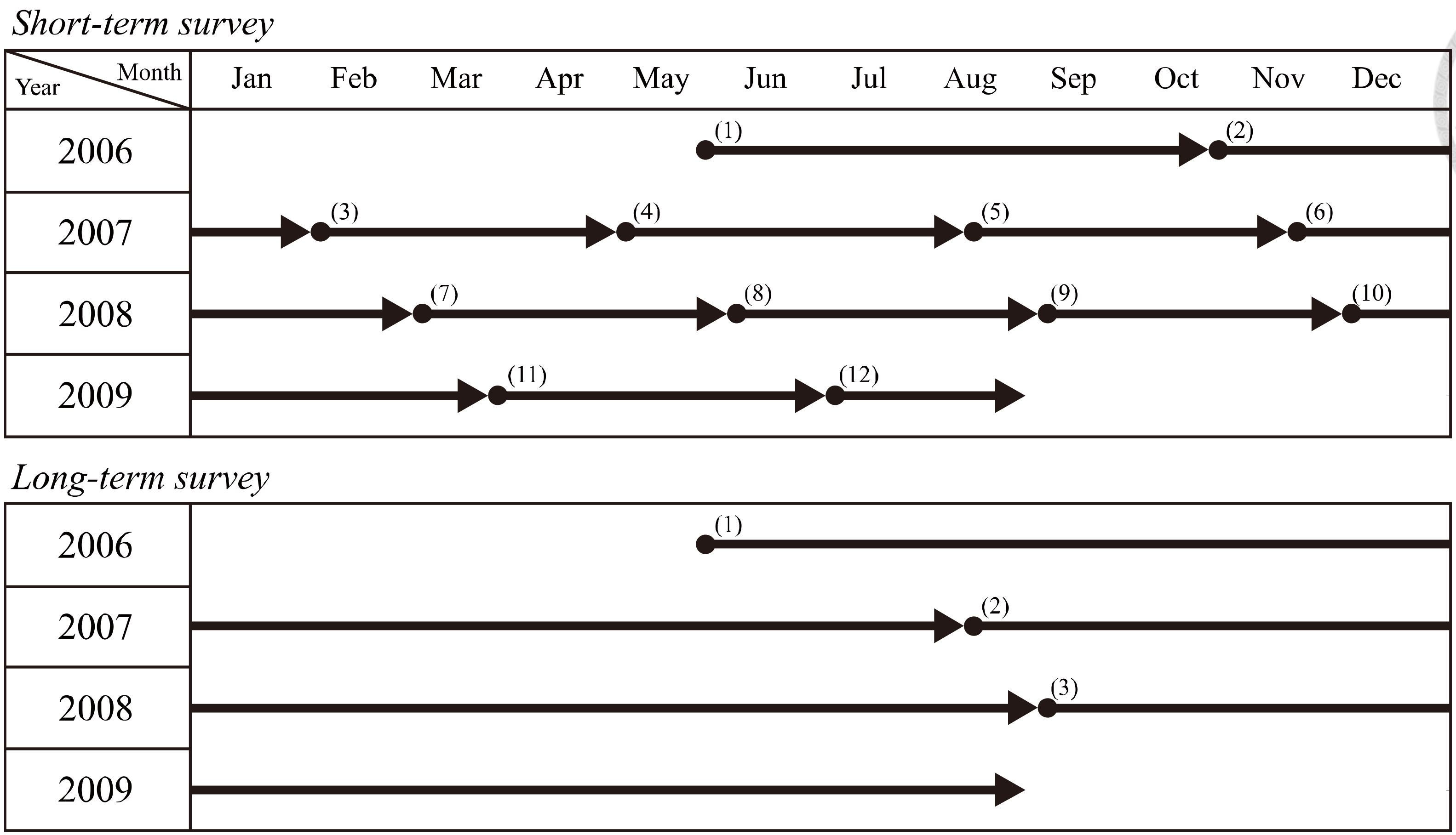


Fig. 4.1 Time frame of deployments and retrievals of settlement plates. They are for 12 short-term (2 to 5 months) and three long-term (11 to 15 months) settling plates in 2006 to 2009.

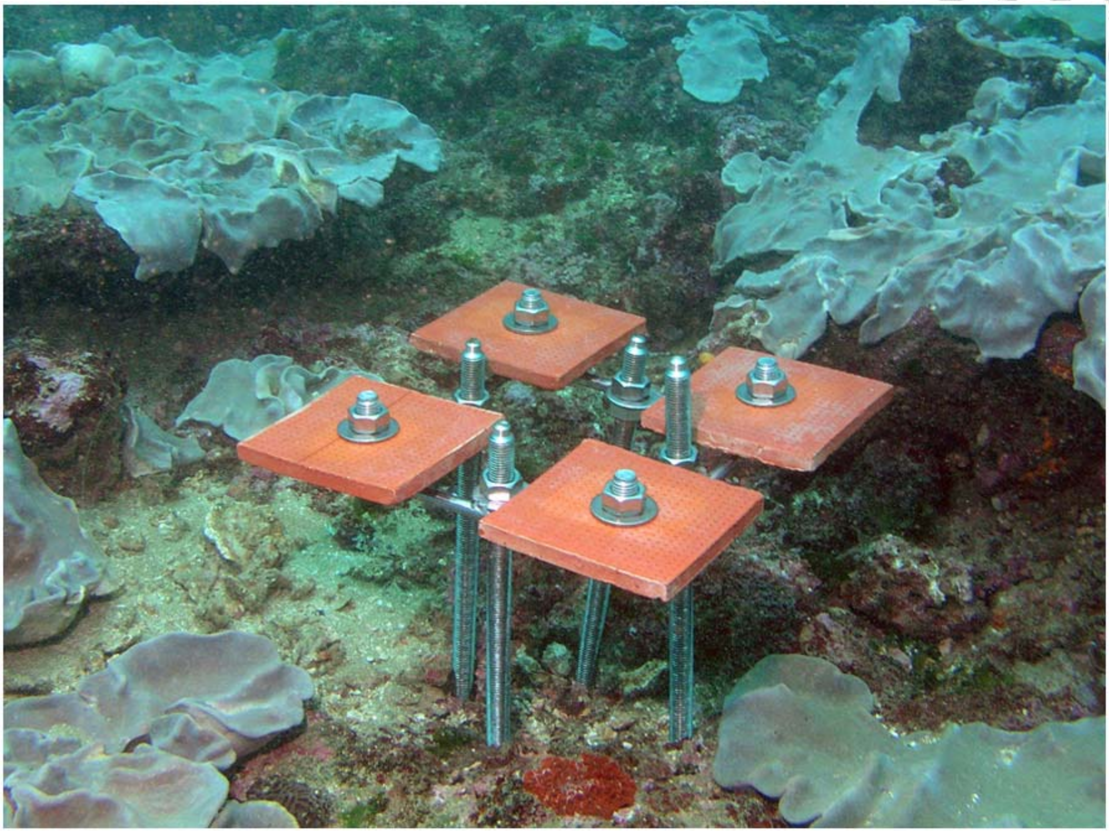


Fig. 4.2 A set of settlement plates used for coral recruitment surveys in this study.

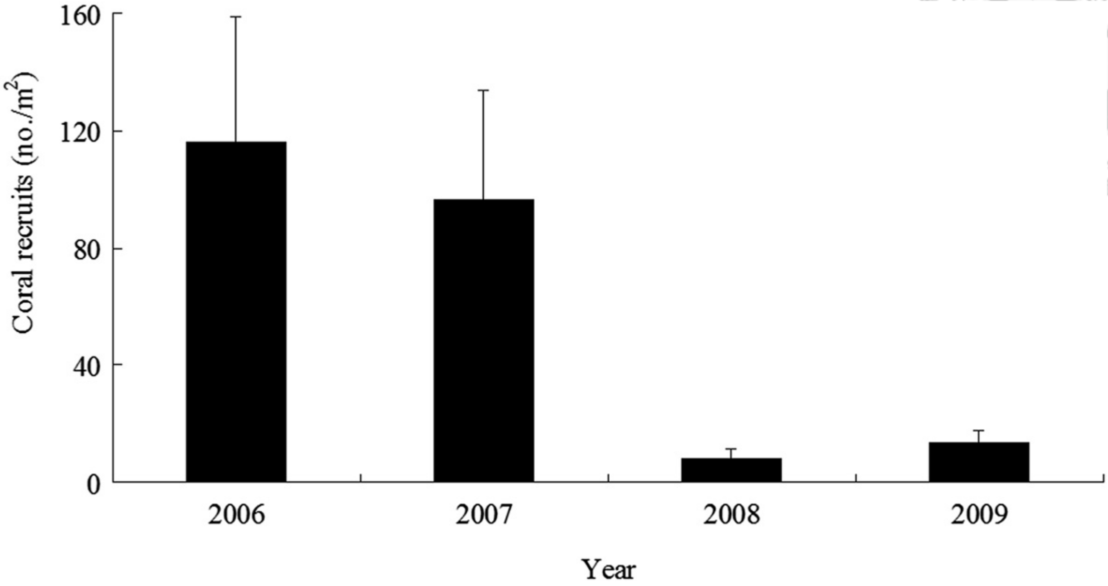


Fig. 4.3 Coral recruitment rate (mean ± SE) in Yenliao Bay in 2006 to 2009. Data of short-term surveys from three study sites (A, B, C) were pooled for comparison.

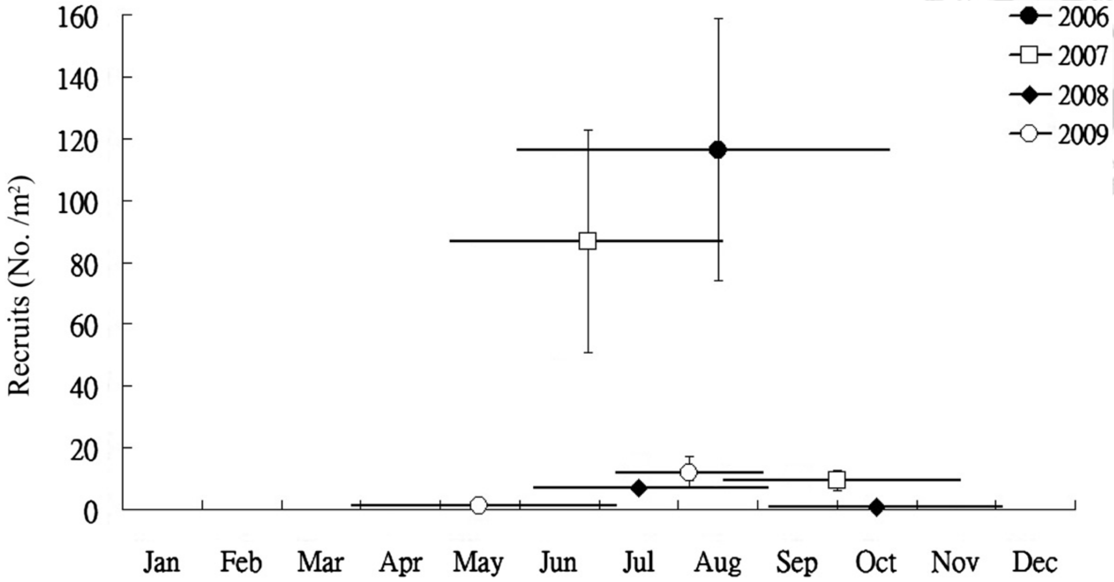


Fig. 4.4 Density of coral recruits (mean ± SE, n = 3) on 12 short-term surveys in 2006-2009. Horizontal bars denote the deployment duration of settlement plates. Five sets with no recruits were omitted.

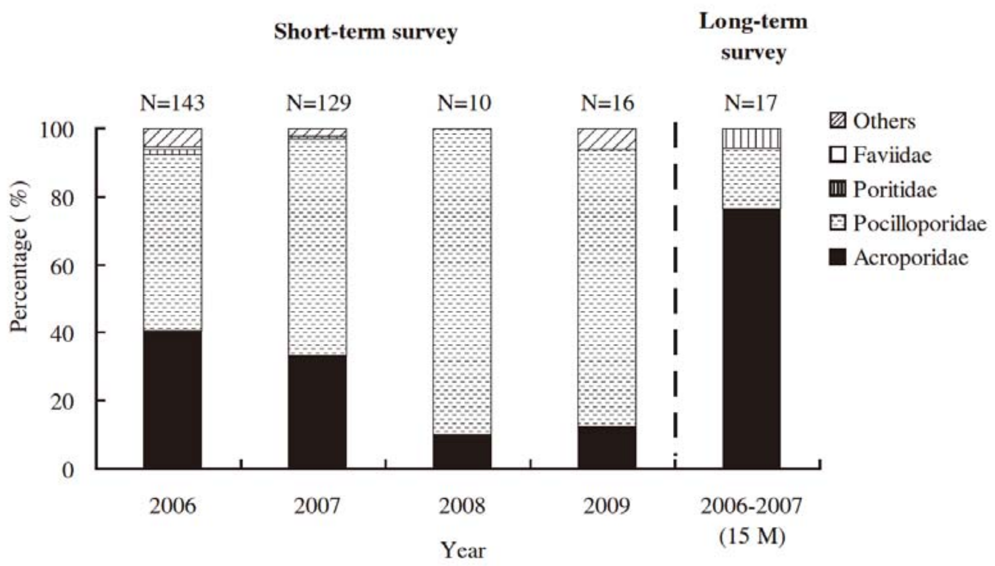


Fig. 4.5 Taxonomic composition of coral recruits. They are based on 12 groups of short-term surveys and 1 group of long-term survey (15 months; May 2006 to August 2007). Data from the three study sites were pooled. Numbers of coral recruits were shown above each bar.

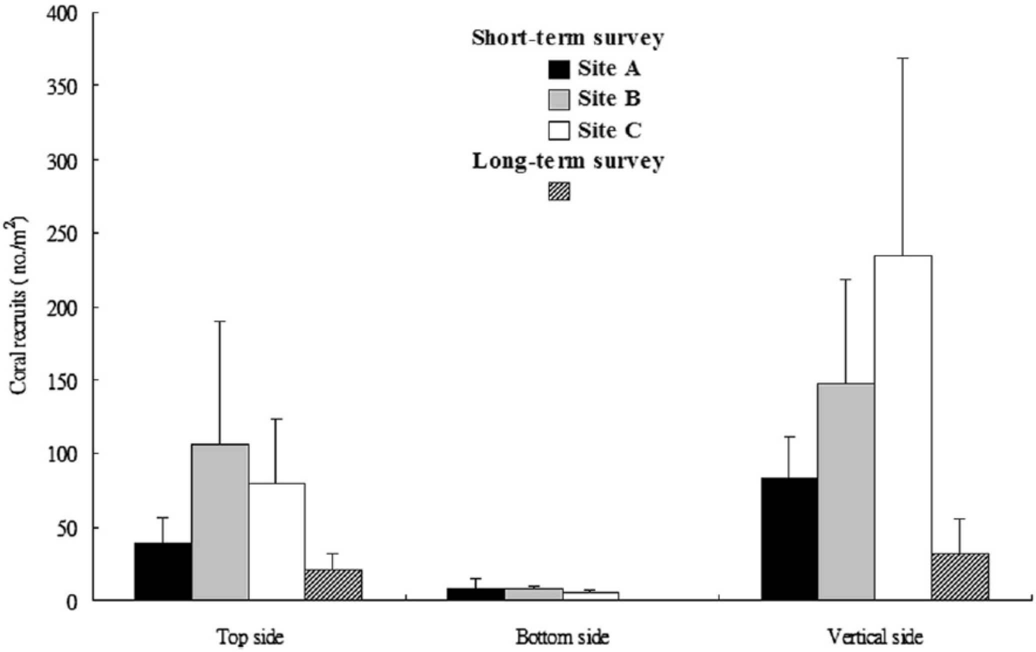


Fig. 4.6 Coral recruits (mean ± SE) on top, bottom, and vertical sides of the settlement plates. They are from 12 groups of short-term surveys and 1 long-term survey. Data of the short-term surveys at each study site were pooled among years (n = 4, 2006 to 2009). Data from the long-term survey were pooled among the three study sites (A, B, C).

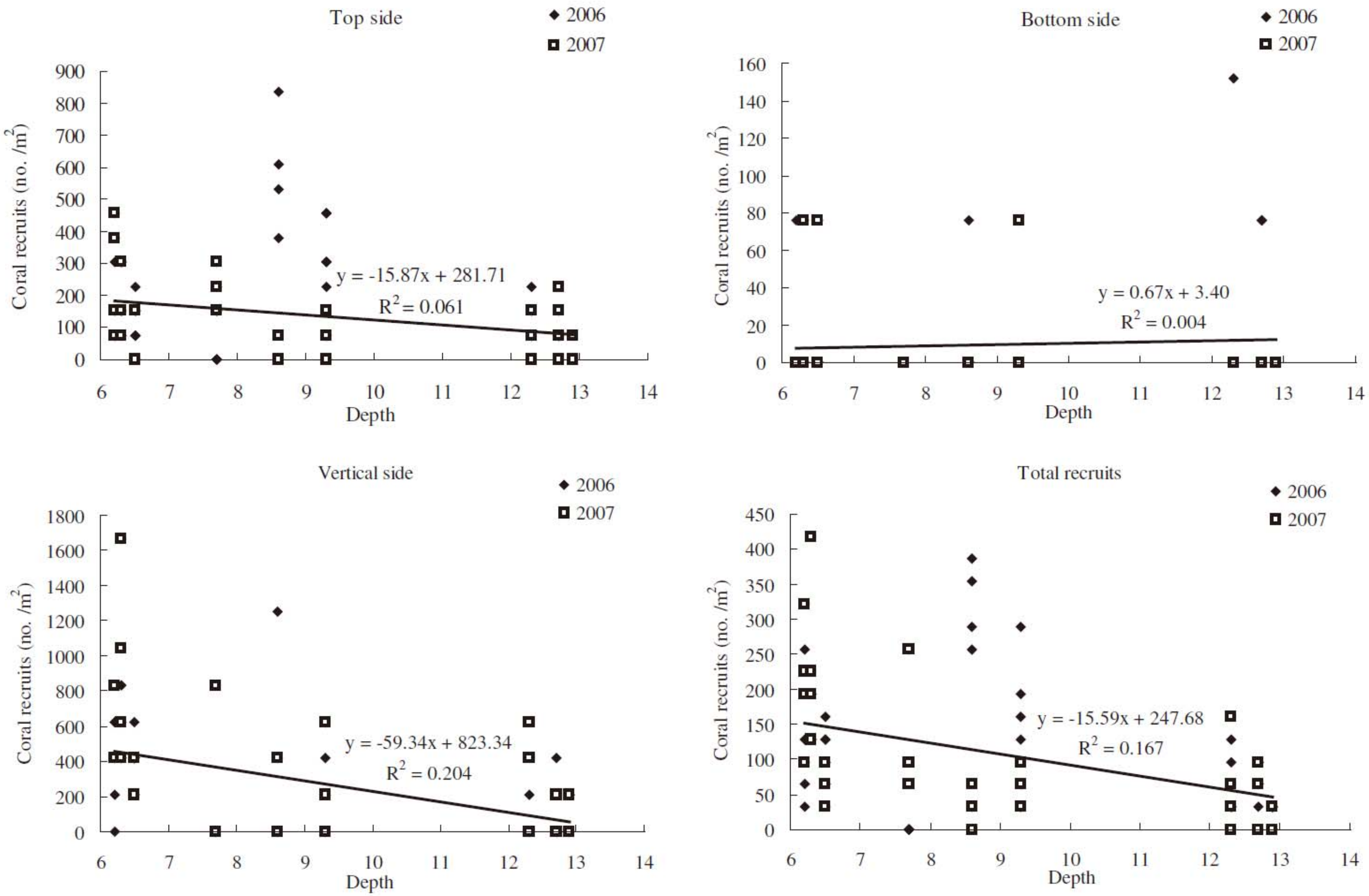


Fig. 4.7 Relationships between depth and density of coral recruits on different sides of settlement plates in 2006-2007 (n = 80 plates). *P* values of depth vs. top, bottom, vertical side, and total recruits: 0.028, 0.598, < 0.0001, < 0.001.

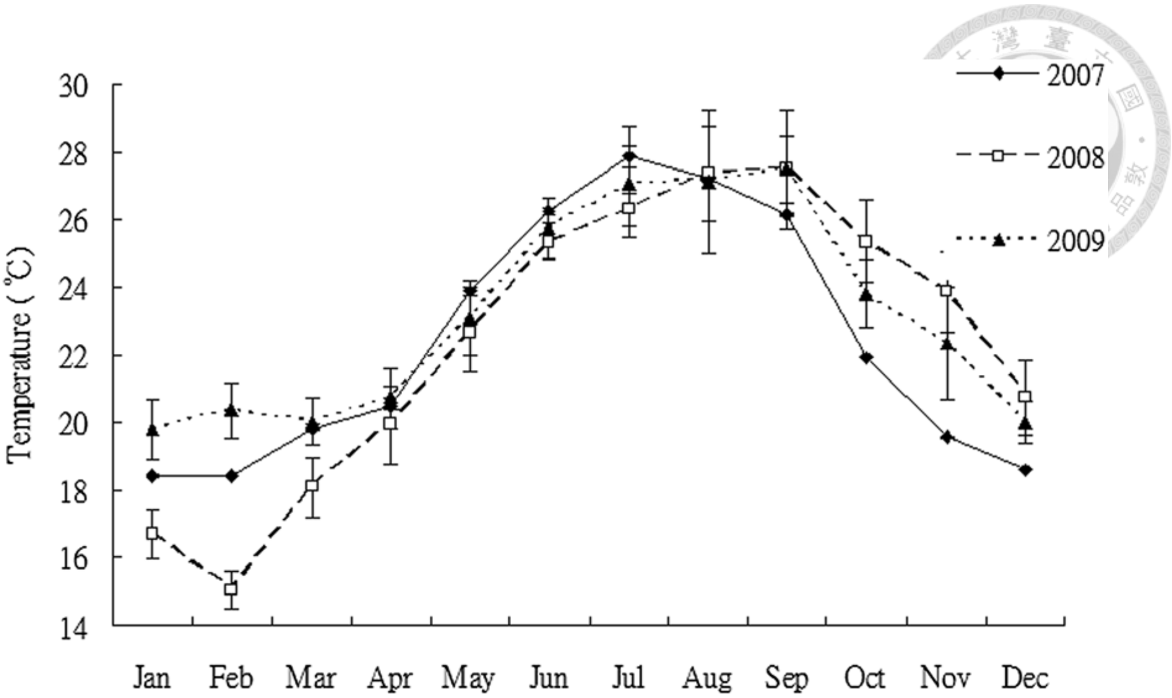


Fig. 4.8 Monthly variations of sea surface temperature (mean ± SD) in the study area 2007-2009. Courtesy of The Central Weather Bureau, Taiwan.

Chapter 5 Coral community dynamics and environmental factors

5-1 Introduction

Nutrient enrichment is of increasing global concern and has been considered a major factor contributing to a global decline of coral reefs (Fabricius 2005). High levels of nutrients have been reported to reduce coral growth and calcification (Tomascik 1991; Stambler et al. 1991; Stimson, 1992) and negatively affect coral reproduction (Harrison and Ward 2001; Koop et al. 2001). High nutrient loads also stimulate macroalgal overgrowth enabling macroalgae to rapidly cover and smother living coral (Lapointe 1997). In addition, nutrient enrichment may modify the physicochemical characteristics of sediment, increase the severity of marine diseases, affect coral–larval settlement and recruitment, and cause shifts in benthic assemblages (Bruno et al. 2003; reviewed in Loya 2007; Holmer et al. 2008).

Although the effects of nutrients on corals have been demonstrated by many literatures (reviewed in Fabricius 2005), parts of the studies indicated that elevated level of nutrients may not necessarily lead to the demise of coral reefs. In Hawaii aquarium, corals flourish in relatively high-nutrient waters (Atkinson et al. 1995). Scoffin et al. (1992) suggested that individual corals might enhance their tissue and skeletal growth in response to moderate nutrient addition. Bongiorni et al. (2003a) reported that the growth rate of both *Acropora eurytoma* branches and *Stylophora pistillata* nubbins in eutrophic water at fish farm site was faster than throse at the oligotrophic reference site. Additionally, massive amounts of POM did not cause detrimental effect on the survival rate of *S. pistillata* nubbins and might supply additional food source to facilitate its growth (Bongiorni et al. 2003b). The controversial results of various studies (Bongiorni et al. 2003a, b; Shafir et al. 2006; Amar and Rinkevich 2007; Shaish et al. 2008) has led to severe debates on the effects of fish farms on adjacent coral reefs in the Gulf of Eilat, Red Sea (Loya and Kramarsky-Winter 2003; Rinkevich et al. 2003; Loya et al. 2004; Abelson et al. 2005; Rinkevich 2005a, b; Loya 2007). These debates indicate that an expanded understanding of the influence of water quality deterioration on corals, and the effects of elevated nutrients on coral community is necessary (Koop et al. 2001; Fabricius 2005).

Coral reefs usually flourish in tropical seas with low levels of inorganic nutrients. Eutrophication is typically caused by the elevated supply and availability of the macronutrients nitrogen (N) and/or phosphorus (P) (Fabricious 2011). Increasing nutrient inputs and associated sediment loads have been suggested to seriously impact coral reefs (Cortes and Risk 1985). However, the complex nature of the nutrient input has made it difficult to identify the components that are responsible for the reported changes, and the actual ways in which corals respond to these nutrients (Grigg and

Dollar 1990; McCook et al. 1997). This has hindered progress towards identifying the factors that are most damaging to coral reefs and hence the development of management strategies that target the sources of important components (Koop et al. 2001).

On local scales, the structure and development of coral reef communities are subject to diverse and often interacting environmental variables such as temperature, light, salinity, solar radiation, sedimentation, and hydrodynamic factors (Brown 1997; Kleypas et al. 1999; Done 2011). Marginal or high-latitude coral communities are distinguished from tropical reef systems by narrow species diversity, low living coral coverage and markedly reduced levels of reef-building activities (Buddemeier and Smith 1999; Perry and Larcombe 2003). In addition, marginal coral communities are often subjected to nutrient enrichment, especially for those in inshore areas facing terrestrial runoffs.

In this study, the environment factors and their relationships with coral communities in Yenliao Bay, northern Taiwan will be investigated based on the data of coral cover and environmental variables collected from 2003 to 2009. In addition, multivariate analyses will be performed to reveal the variables that best explain the change of the coral communities in Yenliao Bay during this period.

5-2 Materials and methods

The study area has been described in Chapter 2.

Water sampling

The sampling and analysis of seawater were following the Guideline for Water Quality Examination and the QA/QC system set up by the Environmental Protection Administration of Taiwan (Hung 1987; Yang 1987). Three sites in Yenliao Bay were selected for monthly seawater sample collection from 2003 to 2009 (Fig. 5.1). At each site, water samples were collected with metal-free Niskin bottles at three depths (surface, three meters, and bottom) onboard a fishing boat. Immediately after collection, water samples were analyzed for temperature, salinity, and pH. The remaining water samples were preserved at 4 ℃ and returned to the laboratory for analysis of the following chemical and biomass parameters: nitrite, nitrate, phosphate, silicate, total nitrogen (TN), total phosphorus (TP), chlorophyll-a (Chl-a), turbidity, and suspended solids (SS).

Macroalgae survey

The cover of macroalgae was surveyed using chain transect method (a 10 m chain) at 2 depths (5 and 10 m) on two reef sites (B, C, Fig. 5.1) every 3 months from August 2003 to September 2009. Four transects were randomly placed at each depth. The length of each macroalga under the chain was measured and the percentage of cover of macroalgae at each site was calculated.

Scleractinian corals coverage

The cover of scleractinian corals at three sites (A, B, C) from 2003 to 2009 were adopted from Chapter 3 for analyses.

Data analysis

All of the hydrographical, chemical, and ecological parameters recorded in Yenliao Bay from August 2003 to September 2009 were analyzed with the values of average and standard error. Pearson correlation coefficient was calculated between coral cover of 12 surveys and each parameter. In order to identify the water quality parameters that showed a similar temporal pattern as the change of coral cover, the biota-environment analysis (BIO-ENV), linkage tree analysis (LINKTREE), and canonical correlation analysis (CCA) were applied.

In BIO-ENV analysis (Clarke and Gorley 2006; Clarke et al. 2008), a combination of water quality parameters whose standardized Euclidean distance showed the highest ρs with the biotic Bray-Curtis similarity matrix was identified (Clarke and Ainsworth 1993; Clarke and Warwick 2001). To estimate the threshold of environmental variables for separation of site groups, LINKTREE analysis, a nonparametric modification of

De'ath's multivariate regression trees (De'ath 2002), was performed using the subset of environmental variables identified by BIO-ENV analysis. An absolute measure of group difference (y-axis for the tree) was given by B%, which was the percentage of the average of the between-group rank similarity to the largest rank similarity in the original Bray-Curtis matrix for the coral community data. Split of the tree was accepted if the SIMPROF test showed a significant difference between the divided site groups. The BIO-ENV analysis and LINKTREE analysis was performed by PRIMER v. 6.1.16 for Windows.

The relationships between coral cover of three study sites and environmental parameters were investigated by canonical correlation analysis. CCA is a standard tool of multivariate statistical analysis to reveal the relationship between two multivariate data. The CCA was computed using square root transformed values in order to minimize differences in variance produced by differences in absolute size and to adjust non-homogeneity of variance among variables. The CCA was performed by STATISTICA v. 6.1 for Windows.

5-3 Results

Environmental factors

Data of the environmental parameters are summarized in Table 5.1. Twelve parameters (temperature, pH, nitrite-N, nitrate-N, phosphate-P, silicate-Si, total nitrogen, total phosphorus, chlorophyll-a, turbidity, suspended solids, macroalgae coverage) were measured and recorded in Yenliao Bay from August 2003 to September 2009 (Table 5.1). Most environmental parameters fluctuated during the survey period. Among them, higher concentrations of phosphate-P, total nitrogen, and total phosphorus were found in early surveys and showed significant correlation with coral cover (Fig. 5.2, Table 5.2). However, temperature, nitrite-N, turbidity, suspended solids, and macroalgae were not significantly correlated with coral cover.

Correlation between environmental factors and change of coral cover

Since phosphate-P, total nitrogen, and total phosphorus showed significant correlation with coral cover, the relationship between nutrients and coral cover was further investigated.

BIO-ENV analysis

The results of BIO-ENV analysis shows that the best combination of environmental variables with the highest correlation with coral cover (*ρw*: 0.597, $p < 0.05$) was a combination of phosphate and total nitrogen (Table 5.3). Both phosphate and total nitrogen were the variables to show consistent correlation with coral cover for almost all combinations. Since nutrients were the major parameters in the results of BIO-ENV analysis, the most four common variables (i.e., nitrate, phosphate, total nitrogen, and total phosphorous) were used for further analyses including LINKTREE and Canonical correlation Analysis).

LINKTREE analysis

The LINKTREE analysis of coral cover based on concentrations of nitrate, phosphate, total nitrogen, and total phosphorous showed that 12 surveys could be classified into six groups (SIMPROF test, $P < 0.05$; Fig. 5.3). The first split separated surveys 1–3 from surveys 4–12 at B% = 94.1, with the threshold of phosphate and TN concentration less than 6.03 $\mu\ l^{-1}$ and 0.108 mg l^{-1} for the latter survey group (Table 5.1, Fig. 5.3). The second division separated surveys 5–7 from site 4 at B% = 48.4, with a higher TP concentration in the former sites. The third division separated surveys 8 from surveys 9–12 at B% = 36.8, with a lower phosphate and TP concentration in the former survey. The rest of the surveys (surveys 9–12) was separated from survey 12 at B% = 18.2 and surveys 9–11, with the former sites showing higher concentrations of TN, TP and phosphate than those of the latter. Overall, the results of LINKTREE showed that the differences of 12 surveys were most closely related to the concentrations of nutrients.

Canonical correlation analysis

The Canonical correlation analysis of coral coverage and environmental factors revealed that one set of canonical variate ($p < 0.001$), with a canonical correlation coefficients 0.99, could explain 88.58% of the total variations. The coefficients of correlation between the original variable and the canonical variate were shown in Fig. 5.4. The canonical variate of environmental parameters was mainly represented by the concentrations of phosphate, TN, and TP. The canonical redundancy analysis showed 84.88% of coral cover variations can be explained by environment variables.

5-4 Discussion

The concentrations of total nitrogen, total phosphorus, and suspended solids in Yenliao Bay were higher than those of the Great Barrier Reefs (De'ath and Fabricius 2008) suggesting that its water quality could be considered as an eutrophic state (Fabricius 2011). During the study period from 2003 to 2009, the changes of mean concentrations of phosphate, total nitrogen, and total phosphorus were consistent and positively correlated with the changes of coral cover (Table 5.2, Fig. 5.2). This suggests that the decline of coral cover is not caused by the increase of dissolved nutrients (TN, TP).

Although nutrient enrichment may cause negative effect on the health of corals (reviewed in Fabricius 2005), elevated level of nutrients may not necessarily lead to the decline of coral cover. In turbid waters, corals demonstrate the capacity to exploit nutrient sources by shifting from autotrophy to heterotrophy (Anthony 1999a, b, 2000; Anthony and Fabricius 2000) by using particulate organic matter (POM) and sediments as additional food sources (Rosenfeld et al. 1999; Anthony and Fabricius 2000; Bongiorni et al. 2003a). Under this circumstance, the tissue thickness, photosynthetic pigment concentrations, and calcification of corals may increase in response to feeding on POM (reviewed in Fabricius 2011). At moderate levels of eutrophication, some hard coral species could compensate for the decrease of photosynthetic carbon gains by increasing particle feeding, while other species were saturated at low particle concentrations and were unable to compensate for the reduction of photosynthesis (Anthony and Fabricius 2000). The results of BIO-ENV also indicated that nutrients (nitrite, TN and TP) were the main parameters that best explained the changes of coral cover in this marginal environment (Table 5.3). Canonical correlation analysis further revealed the consistent trend and positive correlations of these nutrients on all three rocky reefs (Fig. 5.4).

The influences of nutrients on coral communities could be greatly modified by the hydrographic conditions of a reef (Fabricius 2011). Reef areas that are flushed by fast currents are relatively resistant to exposure of higher concentrations of nutrients

(Fabricius 2011). The rocky reefs in Yenliao Bay are exposed to potentially damaging runoff of sediment and nutrient-rich hyposaline waters from Shiding River and Shuang-xi River in the rainy season. However, the water movement induced by tidal currents in this semi-enclosed bay tends to transport the nutrients away from the reef area in a short period of time. This might be the reason that the nutrient concentrations were kept in moderately enriched levels in this area.

Although coral reefs generally flourish in nutrient-poor tropical waters, they actually subsist in seas containing a wide range of nutrients and do flourish in relatively high-nutrient waters (Atkinson et al. 1995; Kelypas et al. 1999). Many studies showed that nutrient enrichment might promote zooxanthellae growth and increase the chlorophyll a content of corals (Hoegh-Guldberg and Smith 1989; Muscatine et al. 1989; Dubinsky et al. 1990; Dubinsky and Stambler 1996) and in some cases, might increase the growth rates of corals (Koop et al. 2001; Bogiorni et al. 2003b; Dunn et al. 2012). This suggests that moderate level of nutrient enrichment might be beneficial for coral growth through the enhancement of photosynthesis of zooxanthellae in subtropical environment where light intensity is relatively low.

Table 5.1 Environmental variables (mean ± SE) in Yenliao Bay from August 2003 to September 2009.

Survey date	2003/08	2004/04	2005/01	2005/07	2005/11	2006/05	2006/09
Temperature (℃)	28.417 ± 0.065	21.467 ± 0.109	18.250 ± 0.128	28.967 ± 0.080	21.583 ± 0.070	26.450 ± 0.085	27.017 ± 0.117
pH	8.280 ± 0.007	7.850 ± 0.050	8.133 ± 0.021	8.200 ± 0.000	7.967 ± 0.021	8.017 ± 0.017	8.167 ± 0.033
Nitrite-N (μg/L)	1.115 ± 0.214	3.041 ± 0.117	1.912 ± 0.148	3.080 ± 0.235	4.117 ± 0.198	3.316 ± 0.511	1.000 ± 0.000
Nitrate-N (μg/L)	12.995 ± 0.899	48.282 ± 3.301	68.408 ± 8.506	26.137 ± 4.902	65.122 ± 5.457	42.900 ± 3.868	24.714 ± 9.263
Phosphate-P (μg/L)	7.508 ± 2.503	6.987 ± 1.397	6.920 ± 1.257	3.630 ± 0.681	6.031 ± 0.613	5.495 ± 0.590	3.571 ± 1.287
Silicate-Si (μg/L)	167.598 ± 19.355	90.057 ± 9.660	175.000 ± 26.579	71.485 ± 9.521	95.359 ± 12.892	109.732 ± 8.457	81.078 ± 16.331
Total nitrogen (mg/L)	0.155 ± 0.016	0.114 ± 0.008	0.184 ± 0.016	0.068 ± 0.017	0.091 ± 0.006	0.059 ± 0.006	0.054 ± 0.011
Total phosphorus (mg/L)	0.082 ± 0.027	0.021 ± 0.005	0.034 ± 0.009	0.025 ± 0.004	0.014 ± 0.001	0.017 ± 0.001	0.018 ± 0.003
Chlorophyll-a (μg/L)	0.397 ± 0.018	0.438 ± 0.035	0.287 ± 0.090	0.397 ± 0.026	0.055 ± 0.007	0.404 ± 0.034	0.756 ± 0.041
Turbidity (NTU)	2.683 ± 0.637	1.342 ± 0.251	5.467 ± 1.668	1.592 ± 0.369	1.092 ± 0.107	2.867 ± 0.545	5.017 ± 0.814
Suspended solids (mg/L)	2.000 ± 0.000	5.025 ± 1.267	8.017 ± 3.697	3.333 ± 1.236	5.750 ± 0.914	3.633 ± 1.304	6.633 ± 0.671
Macroalgae cover (%)	15.891 ± 3.284	18.506 ± 1.743	8.442 ± 1.024	20.184 ± 0.325	11.531 ± 1.943	24.136 ± 1.516	12.183 ± 0.954

Table 5.1 (continued).

Survey date	2007/07	2008/06	2008/09	2009/05	2009/09
Temperature (℃)	28.350 ± 0.076	24.417 ± 0.040	27.167 ± 0.042	22.860 ± 0.043	29.240 ± 0.043
pH	8.083 ± 0.017	8.117 ± 0.017	7.983 ± 0.083	8.300 ± 0.000	8.000 ± 0.000
Nitrite-N (μg/L)	2.687 ± 0.237	4.307 ± 0.164	2.305 ± 1.139	1.525 ± 0.217	3.742 ± 0.278
Nitrate-N (μg/L)	13.483 ± 1.541	12.571 ± 1.282	8.517 ± 1.659	22.557 ± 5.824	14.503 ± 2.276
Phosphate-P (μg/L)	1.093 ± 0.084	3.694 ± 0.245	3.325 ± 0.000	3.918 ± 0.435	3.314 ± 0.000
Silicate-Si (μg/L)	97.068 ± 12.576	140.018 ± 4.346	129.436 ± 21.981	118.907 ± 4.008	90.894 ± 3.757
Total nitrogen (mg/L)	0.077 ± 0.011	0.040 ± 0.002	0.041 ± 0.008	0.062 ± 0.023	0.108 ± 0.006
Total phosphorus (mg/L)	0.008 ± 0.001	0.030 ± 0.002	0.018 ± 0.004	0.046 ± 0.007	0.048 ± 0.013
Chlorophyll-a (μg/L)	0.173 ± 0.023	0.334 ± 0.040	0.735 ± 0.076	0.507 ± 0.061	0.095 ± 0.011
Turbidity (NTU)	6.050 ± 1.573	0.992 ± 0.099	1.558 ± 0.210	0.675 ± 0.038	1.517 ± 0.095
Suspended solids (mg/L)	11.683 ± 2.272	3.000 ± 0.365	7.700 ± 1.253	2.483 ± 0.263	4.350 ± 0.317
Macroalgae cover (%)	16.416 ± 1.807	20.487 ± 2.403	12.769 ± 2.019	17.353 ± 2.016	9.384 ± 2.262

Table 5.2 Correlation coefficients (*R*) between environmental parameters and coral cover in 12 surveys (n=12) from August 2003 to September 2009 (TN: total nitrogen, TP: total phosphorous, Chl.a: Chlorophyll-a, SS: suspended solids).

	Coral coverage	Temperature	pH	Nitrite	Nitrate	Phosphate	Silicate	TN	TP	Chl. a	Turbidity	SS	Macro algae cover
Coral coverage	1.000												
Temperature	-0.135	1.000											
pH	0.144	0.191	1.000										
Nitrite-N	-0.377	-0.045	**-0.585***	1.000									
Nitrate-N	0.169	**-0.786****	-0.328	0.159	1.000								
Phosphate-P	**0.767****	-0.548	-0.081	-0.130	**0.625***	1.000							
Silicate-Si	0.419	-0.357	0.325	-0.303	0.057	0.462	1.000						
TN	**0.761****	-0.384	0.052	-0.255	0.471	**0.671***	0.513	1.000					
TP	**0.687***	0.137	0.557	-0.385	-0.272	0.419	0.543	0.515	1.000				
Chl.a	0.041	0.125	0.212	**-0.616***	-0.314	-0.060	0.021	-0.389	-0.046	1.000			
Turbidity	-0.023	0.023	0.144	-0.444	0.118	-0.152	0.143	0.306	-0.209	0.023	1.000		
SS	-0.375	-0.070	-0.336	-0.081	0.106	-0.407	-0.086	0.043	**-0.603***	-0.072	**0.708***	1.000	
Macroalgae cover	-0.068	0.212	0.080	0.229	-0.191	-0.047	-0.176	-0.465	-0.125	0.151	-0.272	-0.419	1.000

**: $p < 0.01$

*: $p < 0.05$

Table 5.3 BIO-ENV results showing the combinations of environmental variables that best match the coral community resemblance matrix. (ρ=0.597, Significance level: 2.7%). (1: Temperature, 2: pH, 3: Nitrite, 4: Nitrate, 5: Phosphate, 6: Silicate, 7: Total nitrogen, 8: Total phosphorus, 9: Chlorophyll-a, 10: Turbidity, 11: Suspended solids, 12: Macroalgae).

Number of Variables	Correlation coefficient (ρ)	Selections
2	0.597	5,7
3	0.588	5,7,8
4	0.580	4,5,7,8
5	0.571	4,5,6,7,8
4	0.567	5,6,7,8
3	0.564	4,5,7
3	0.561	5,6,7
4	0.558	4,5,6,7
4	0.545	1,5,7,8
5	0.543	2,4,5,7,8
6	0.540	2,4,5,6,7,8
4	0.540	4,5,6,8

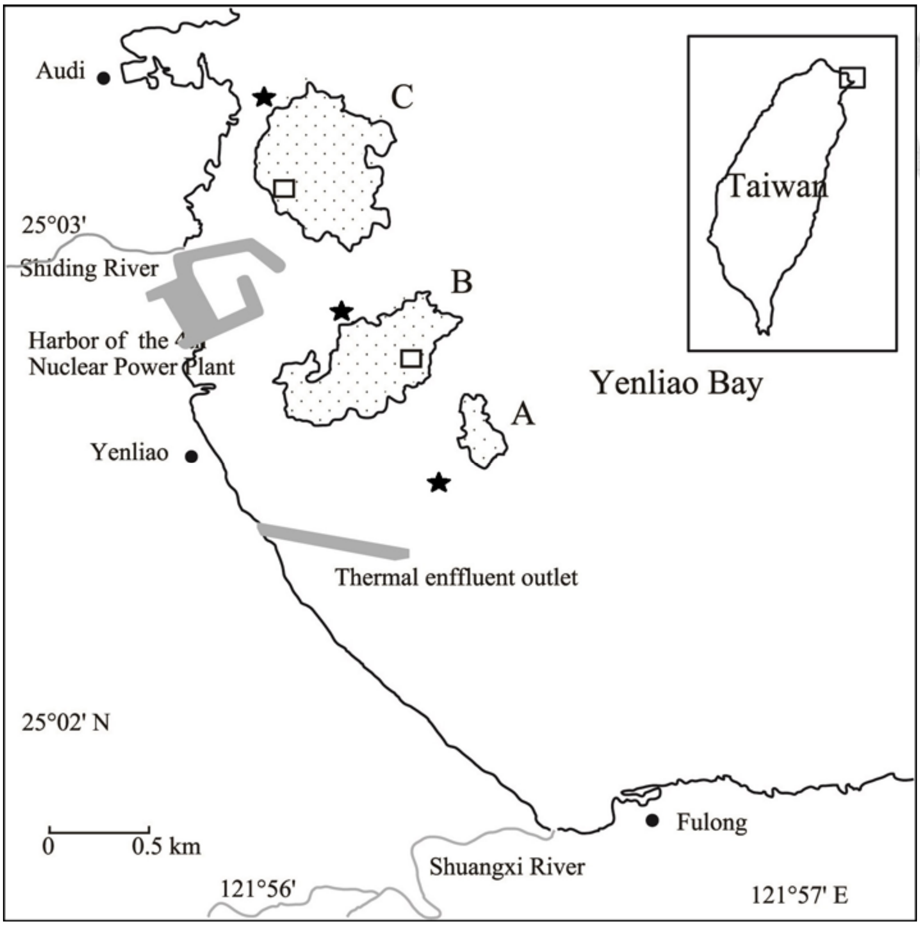


Fig. 5.1 Map of the study area indicating the sampling sites of water quality (asterisks) and macroalgae (blank squares).

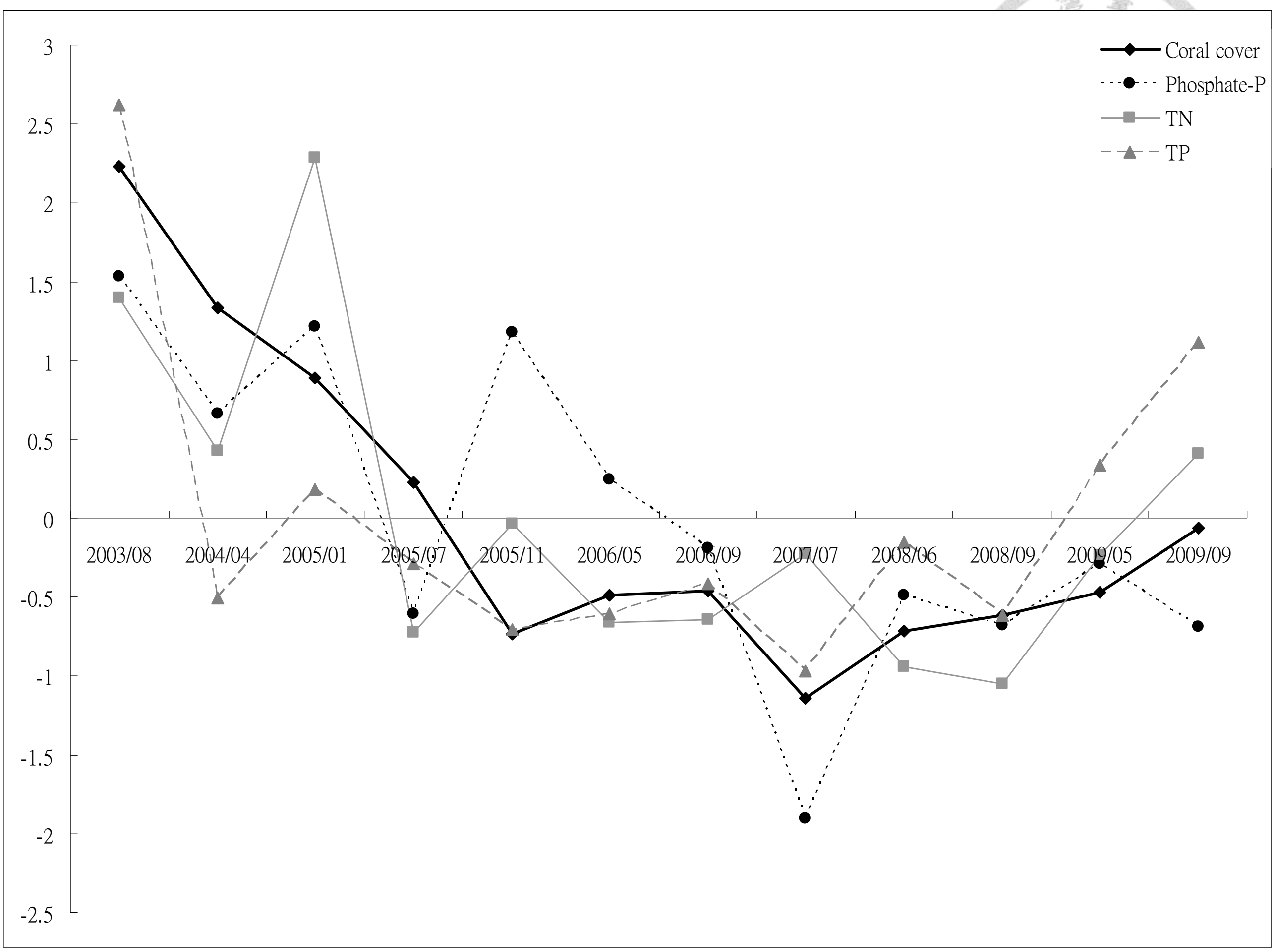


Fig. 5.2 Changes of coral coverage and concentrations of environmental variables (phosphate, TN: total nitrogen, TP: total phosphate) from August 2003 to September 2009 (coral cover and nutrient parameters were all standardized).

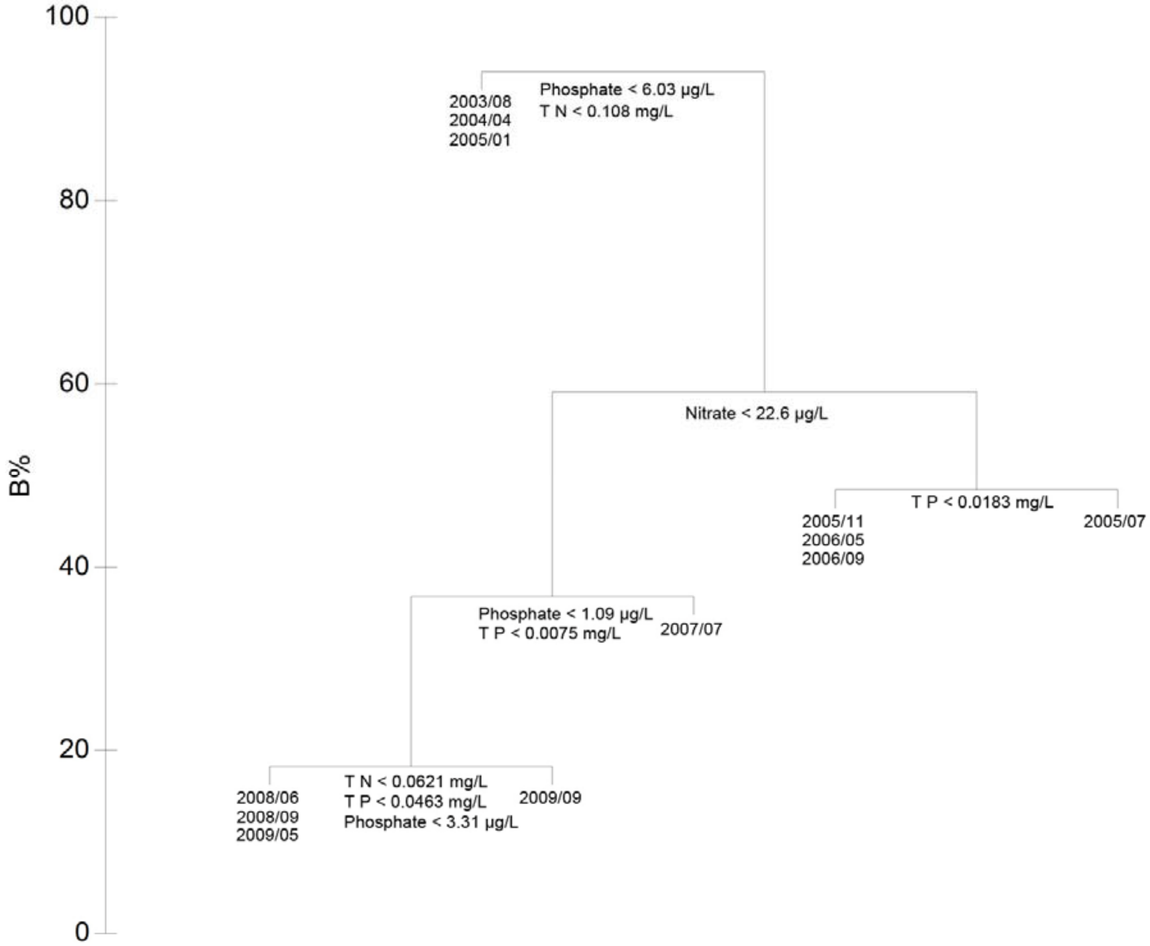


Fig. 5.3 Results of LINKTREE analysis indicating the environmental factors that best explain the 12 surveys of coral cover data at the study sites.

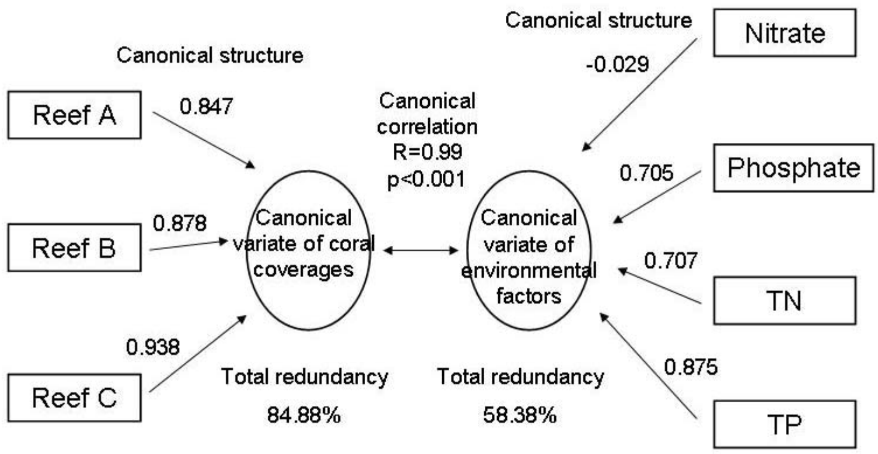


Fig. 5.4 Relationship among variables, canonical variates, and the first pair of canonical variates (three coral communities and four environmental variables).

Chapter 6. Conclusions

This dissertation provided the first quantitative study of coral communities in Yenliao Bay, northern Taiwan and examined the dynamics and recruitment of corals in subtropical or marginal environment. The relationship between coral communities and environmental factors in Yenliao Bay was also investigated. Major findings of this study include: (1) under severe typhoon impacts, different coral species varied greatly in partial and whole colony mortalities in line with growth forms and resulted in a shift of community structure, (2) the high recruitment rates in 2006 and 2007 were comparable with those of tropical reefs suggesting that recruitment might not be a limiting factor for the maintenance and development of coral communities at this subtropical area, (3) there was a negative correlation between the number of recruits and depths suggesting that light intensity is possibly the primary factor controlling settlement and survival of coral recruits in subtropical coral communities, (4) the concentrations of phosphate, total nitrogen, and total phosphorus were positively correlated with the changes of coral cover among years suggesting that nutrients enrichment might be beneficial for coral growth through the enhancement of photosynthesis of zooxanthellae in subtropical or marginal environment where light intensity is relatively low.

In summary, this study demonstrated the dynamics of a marginal coral community located in subtropical region, the recovery potential (coral recruitment) of this coral community, and its relationship with environmental factors. Significant declines of hard coral cover were detected at three reefs from 2003 to 2009, mainly caused by strong typhoon disturbances in July-September, 2005. Differential mortality and contrasting trajectories of different coral genera were demonstrated following the typhoon disturbances. This study indicated the coral community in Yenliao Bay was susceptible to severe disturbances. However, the gradual increase of coral cover and the high recruitment rates suggested the potential of recovery and maintenance of coral community in this subtropical environment. Additionally, the results of this study indicated the possible positive effects of nutrients on coral communities in marginal environment. However, further investigations on the physiological and biochemical processes of coral/nutrient interactions in this marginal environment are needed.

Since marginal or subtropical coral communities might act as refuges for tropical reef corals facing the threats of global warming and climate change, the dynamics of coral communities in Yenliao Bay provides some insights to assess the potential role of marginal environment for the conservation of tropical reef-building corals. Further studies are required to better understand the mechanisms of maintenance and sustainability of marginal coral communities under the impacts of climate change. Meanwhile, there is an urgent need to maintain the healthy condition and the resilience

of coral communities in Yenliao Bay, northern Taiwan.

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