Biogeography of Intertidal Barnacles in Different Marine Ecosystems of Taiwan – Potential Indicators of Climate Change?

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1. Introduction

The Indo-Pacific region contains the highest global marine biodiversity including fishes, molluscs, benthic crustaceans and corals (Tittensor et al., 2010). Understanding the biogeography and ecology of marine species in such biodiversity hot spot is essential to protect our marine resources because this can allow us to understand the present biodiversity status and predict changes under the effect of global warming (Firth et al., 2009; Tittensor et al., 2010).

The life cycle of common intertidal organisms includes a planktonic larval phase and sessile or benthic adult phase. As a result, the biogeography of intertidal species is driven by the supply of larvae, their dispersal range, settlement, and subsequent recruitment into the adult population. In most cases, larvae with longer developmental periods have longer dispersal distance (Scheltema, 1988), resulting in a wider geographical distribution. Recent studies (e.g., Barber et al., 2000, 2006; Zakas et al., 2009), however, showed that the interplay between larval supply, local oceanographic currents and geographical isolation can result in retention of larvae in both regional or local scales, leading to distinct assemblage structure and geographic distribution (see Scheltema, 1988; Kojima et al., 1997; Pannacciulli *et al.*, 1997; Wethey, 2002; Dawson *et al.*, 2010; Reece *et al.*, 2010). In addition to the effects of ocean current on larval dispersal, temperature and recruitment also can affect the survival and sustainability of both cold and warm marine species, thus affecting their biogeography (Herbert et al., 2007; Jones et al., 2009).

On rocky shores, barnacles often are used as model and representative species to study the biogeography of intertidal species, as they are the major space occupiers and often have wide geographical distribution (Darwin, 1854; Southward & Crisp, 1956; Crisp & Southward, 1958; Crisp *et al.*, 1981; Southward, 1991; Chan et al. 2007a, b; Tsang et al. 2008a, b, 2011). The larval (planktonic) phase of intertidal thoracican barnacles consists of six naupliar stages and a single cypris stage prior to settlement (Walker et al., 1987). The complete larval development period of intertidal barnacles including the genus *Tetraclita* and *Chthamalus* in the Pacific ranges from 14-21 days for dispersal in the ocean (Chan, 2003; Yan & Chan, 2004).

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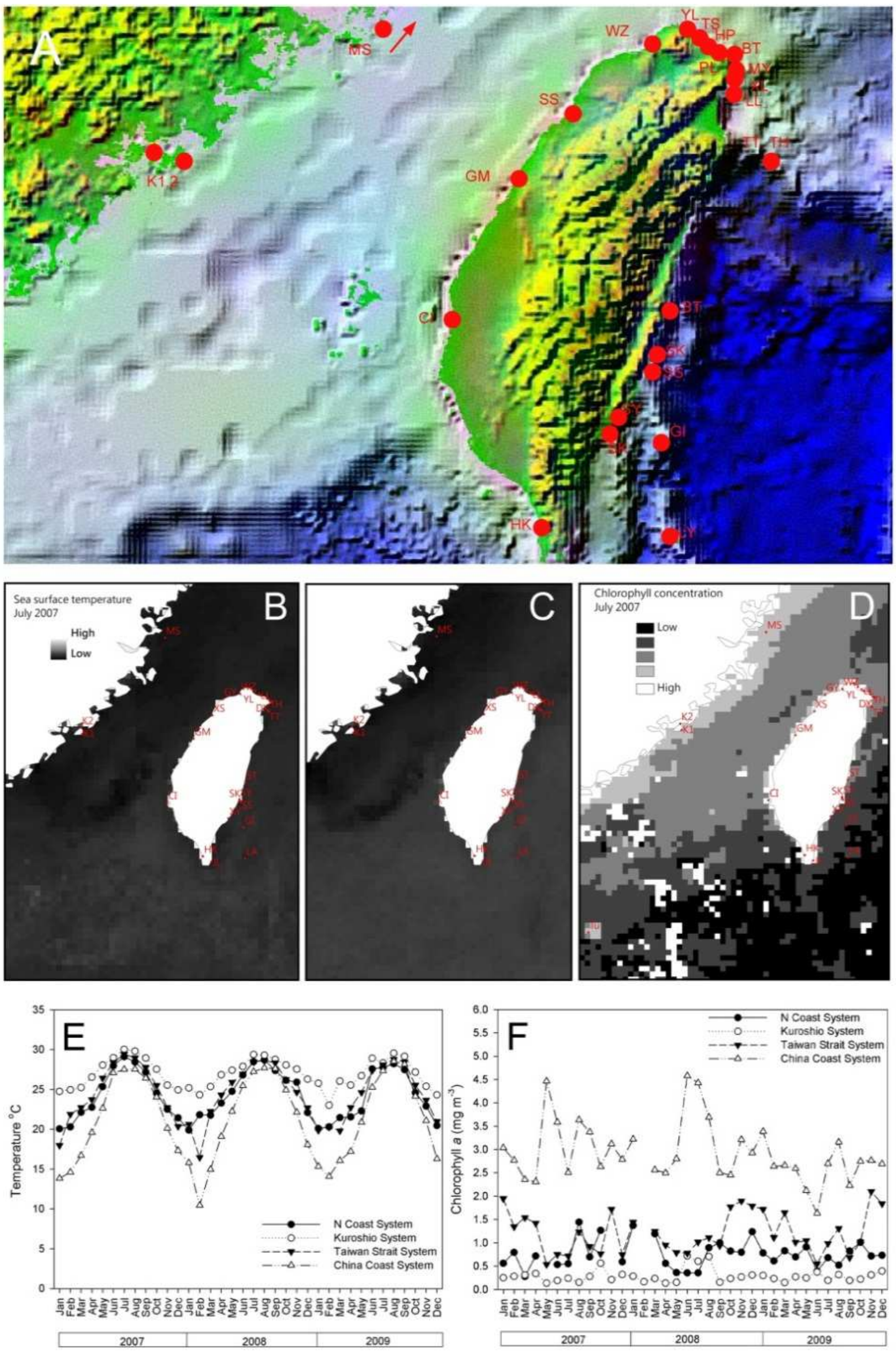

Fig. 1. A. Taiwan marine topography map showing sampling sites located in different ecosystems. For sites abbreviations, refer to Table 1. B. Sea surface temperature derived from satellite images at July 2007. C. Sea surface temperature derived from satellite images at December 2007. D. Sea surface Chlorophyll *a* concentration obtained from satellite images at

July 2007. E. Average sea surface temperature and F. Chlorophyll *a* concentration (detected from Giovanni Satellite System) from 2007-2009. N Coast Ecosystem – averaged from YL, HP, TI, Kuroshio Ecosystem, averaged from ST, XG, HK, Taiwan Strait Ecosystem, averaged from SS, GM and CI , China Coast Ecosystem, averaged from MT and K1 (site abbreviation, see Table 1). Sea surface temperature map in Fig. 1C, D. was derived from NOAA/AVHRR SST images. Sea surface temperature and chlorophyll *a* data in Fig.1E, F was produced with the Giovanni online data system (developed and maintained by the NASA GES DISC).

Site name	Latitude	Longitude	Marine Ecosystem	Abbreviated site name
Tiu-shi	25.16.43N	121.36.57E	N Coast	TS
Yeliu	25.12.39N	121.41.48E	N Coast	YL
He-Ping Dao	25.09.49N	121.45.48E	N Coast	HP
Ping-Long Qiu	25.08.07N	121.48.20E	N Coast	PL
Bitou	25.07.40N	121.55.15E	N Coast	BT
Mei-Yan-Shan	25.04.15N	121.55.27E	N Coast	MY
Xiang Lan	25.01.33N	121.58.22E	N Coast	XL
Dai Xiang Lan	25.01.31N	121.58.42E	N Coast	DX
Lai Lai	25.00.08N	122.00.08E	N Coast	LL
Turtle Island - tail	24.50.39N	121.56.41E	N Coast	TT
Turtle Island - head	24.50.10N	121.57.35E	N Coast	TH
Shi Ti Ping	23.29.28N	121.30.45E	Kuroshio	ST
Siu Kang	23.09.16N	121.24.16E	Kuroshio	SK
San San Tai	23.07.25N	121.25.06E	Kuroshio	SS
Shi Yu Sha	23.10.31N	121.24.11E	Kuroshio	SY
Xiao Yeliu	22.48.56N	121.11.45E	Kuroshio	XY
Jia Ler Shui	21.59.55N	120.52.23E	Kuroshio	JL
Hai Kou	22.05.54N	120.42.57E	Kuroshio	HK
Lanyu	22.03.32N	121.30.24E	Kuroshio	LA
Green Island	22.38.49N	121.28.39E	Kuroshio	GI
Tung Sha Island	20.40.15N	116.43.01E	Kuroshio	TU
Wa Zhi Wei	25.10.14N	121.24.42E	Taiwan Strait	WZ
Xiang Shan	24.45.36N	120.53.42E	Taiwan Strait	XS
Gao Mei	24.18.57N	120.32.26E	Taiwan Strait	GM
Ciqu	23.06.49N	120.02.32E	Taiwan Strait	CI
Guan Yan	25.03.44N	121.05.29E	Taiwan Strait	GY
Ma Su Island	26.13.20N	119.59.59E	China Coastal	MS
Kinmen-Xi-Bin	24.24.32N	118.26.17E	China Coastal	K1
Kinmen-site2	24.31.34N	118.25.03E	China Coastal	K2

Table 1. Sampling locations with their correspondence marine ecosystems for the intertidal barnacles in the present study. Sites were abbreviated in figures for clarity.

In the northwestern Pacific, Taiwan is a large island located between the Philippines and Japan, and is a mixing zone of several major oceanographic currents. This current mixing has produces a great diversity of physical characteristics (including sea surface temperatures and salinities) in the marine ecosystems there. The north and north east coasts are mainly rocky shores and their hydrography is primarily subject to the East China Sea Large Marine Ecosystem (Tseng et al., 2000). The East China Sea is the largest marginal sea in the northwestern Pacific region. The East China Sea is bounded to the east by the Kuroshio Current (Chen et al., 1995), to the west by mainland China, and receives much surface runoff from Chanjiang River (Tian et al., 1993). The northeast coast of Taiwan is the eastern boundary of the East China Sea, separating from the Kuroshio Current, with its steep continental slope (> 1000 m depth, Fig. 1A) in which the Kuroshio Current flows. The Kuroshio Current intrudes from the East China Sea to the boundary region in northeastern Taiwan (Tseng et al., 2000). Between 2007 and 2009, average summer (July-September) sea surface temperature in the northeastern coast varied from 27-28°C (Giovanni database, NASA, USA; see section 2.2). In winter (December–February) the average surface seawater temperature in northeastern coast varied from 20-21°C (Figs. 1 B, C, E).

The eastern and southeastern coastlines of Taiwan include rocky shores and coral reefs, with hydrography affected by the warm Kuroshio Current, which has a low chlorophyll *a* concentration (Figs. 1D, F). The Kuroshio Current originates in the Philippines, flowing northward to pass through Taiwan and reaches Honshu in Japan (Muromtsev, 1970). The northward velocity of the current can reach 4 knots (Nitani & Shoji, 1970). Compared to the northeastern coast of Taiwan, the eastern and southeastern coasts sustain only small variation in annual seawater temperature. From 2007-2009, variation in the annual seawater temperature along the eastern and southeastern coasts of Taiwan ranged from 24-25°C in winter and 29°C in summer (see section 2.2; Figs. 1 B, C, E).

The western coastlines of Taiwan facing the Taiwan Strait are mainly sandy shores and mangroves. The Taiwan Strait is a wide strait between the mainland China and Taiwan, with an average depth of about 60 m (Jan et al., 2002; Fig. 1A). The hydrography of the Taiwan Strait adjacent to the Taiwan main island is affected by South China Sea Surface Current and the Kuroshio Branching Current, which arrives from the diversion of the Kuroshio Current in Basi Channel in southern Taiwan. In summer, the South China Sea Surface Current flows northward along the Taiwan Strait and enters the East China Sea, becoming the Taiwan Warm Current (Jan et al. 2010). In winter, due to the strong monsoon coming from the East China Sea Ecosystem from the north, the northward flow of Kuroshio Branch in the Taiwan Strait is blocked in the Penghu waters, because of the shallower depths in the northern part of the strait (Jan et al., 2002). Average seawater temperatures range from 19°C in winter to 28°C in summer (Figs. 1B, C, E; see section 2.2). Kinmen and Matsu are small islands located in the Taiwan Strait near the mainland China coastlines and their hydrography is mainly affected by the South China Sea Warm Current and the China Coastal Current (Tseng et al., 2000). In winter, the average seawater temperature can dropped to 14-15°C in 2007-2009 (Figs. 1B, C, E; see section 2.2). Such low temperature is due to the southward flowing of the cold China Coastal Current. The China Coastal Current also has high nutrients and productivity, resulting the waters affected by this current has a very high chlorophyll *a* concentration (Figs. 1D, F).

In addition to having high diversity of marine ecosystems, Taiwan sustains a latitudinal gradient of tropical to subtropical climate from south to north. The Tropic of Cancer bisects

Taiwan's main island approximately at the middle portion of the island. Northern Taiwan has a subtropical climate, with cold winters (average air temperature 15°C) and hot summers, while the southern part of Taiwan is tropical, having warmer winters (average air temperature 19°C) and very hot summers.

Under such diverse marine ecosystems and temperature regimes, biogeographic zones of intertidal species are distributed in relation to these different marine influences and climate zones. A gradient of warm water and cold water species appears to exist from the eastern to the northern coastlines of Taiwan. Chan et al. (2009) reviewed and reported on the distribution of 94 thoracican barnacles in Taiwan, suggesting that their distribution was related to marine currents and climatic patterns. For example, the intertidal barnacle *Tetraclita* spp. exhibited distinct distribution among different marine ecosystems. *T. kuroshioensis* and *T. japonica formosana* are distributed along the north, northeastern, and southeastern coasts of Taiwan, their presences related to the Kuroshio Current (Chan et al., 2007a, b; 2008a). *Tetraclita squamosa* is present along the coasts of the mainland China and the distribution is affected by the South China Sea Surface Current and the China Coastal Current (Chan et al., 2007a, 2008a). Along the southeastern and eastern coasts are both northern (cold water) and southern (warm water species) barnacle species. *Chthamalus moro*, *C. malayensis* and *T. chinensis* which are more abundant in the southern waters of Taiwan, are reduced in abundance towards the north (Tsang et al., 2008, Chan et al., 2009). The cold water species, *C. challengeri* are only found in Matsu and Kinmen Islands, which are influenced by the cold China Coastal Current, and these species are absent from the Taiwan main island (Chan et al., 2009).

With the anthropogenic increase in carbon dioxide production, the temperature of the earth is increasing and the recent global climate is changing, affecting the ecosystems of the world (Poloczanska et al. 2008; Hawkins et al., 2009). Among different ecosystems, the rocky intertidal zone is a harsh habitat strongly influenced by both physical (e.g., thermal stress) and biological (e.g. competition) factors. Rocky intertidal species therefore are sensitive to environmental changes, and can show rapid responses (Thompson et al., 2002, Rivadeneira & Fernandez, 2005; Helmuth et al., 2006; Hawkins et al., 2009). Increased seawater temperature has resulted in range shifts of intertidal species in northern temperate Atlantic waters (Southward *et al.* 2005; Helmuth et al. 2006; Lima *et al*., 2006, 2007a, b; Mieskowska et al., 2006, 2007; Herbert et al., 2007; Hawkins et al., 2008). In the northwestern Pacific at present there are no studies concerning the range shift of intertidal organisms, because the baseline biogeographic pattern species is still poorly known. To understand the effects of climatic change on intertidal species distributions, it is essential to understand in detail the biogeography of multiple intertidal species, particularly those in the northwestern Pacific. A comparative multispecies approach can reveal broad biogeographic patterns because different species have different reproductive seasons and larval periods, thus seasonal variation in larval survival and development will be strongly affected by current patterns and thus geographic distribution.

In this chapter, we report on the biogeography of 21 intertidal barnacles in different marine ecosystems and climatic zones in Taiwan to provide quantitative baseline biogeographic data for future temporal comparative uses. We hypothesize that the biogeography of intertidal species in Taiwan is being affected by the marine ecosystems, which differ in environmental factors, including water temperature, salinity and chlorophyll concentration (an indication on the primary production of the marine ecosystem), and along the climatic zones in southeastern and eastern coastal Taiwan.

2. Materials and methods

2.1 Study sites and sampling

Barnacles were surveyed at 29 locations distributed around the Taiwan main island and on outlying islands in 2007 and 2008 (Fig. 1A). Sampling locations covered all the marine ecosystems of Taiwan (Fig. 1). Eleven sites were located on the north and northeastern coasts of Taiwan, hereafter named as North Coast (NC) ecosystem for clarity (Table 1). Nine sites were located in the eastern and southeastern coasts of Taiwan, including the outlying Turtle, Lanyu, and Green Islands, which are influenced by the warm Kuroshio Current, hereafter referred to as the Kuroshio Ecosystem (KS; Table 1). One site was selected as a reference site: Pratas Island (Tung Sha or Dongsha), which is located in the South China Sea and close to the Luzon Strait, and which receives the Kuroshio Branch and the South China Sea Currents. Five sites were selected on the west coast of Taiwan and are part of the Taiwan Strait Marine Ecosystem. Three sites were selected in Kinmen and Matsu Islands, which are located in close proximity to the coastline of mainland China, and are affected by the South China Sea Warm Current and the China Coastal Current, hereafter named as China Coastal Ecosystem.

At each site, 30-50 m stretches of the shoreline were chosen based on accessibility and covered high diversity of habitats including sloping platforms, vertical rocks and large boulders. All intertidal barnacles species distributed from the highest tidal level to the lowest shore stages (1 m above Chart Datum, C.D.) were identified and recorded. Additionally, specific searching was conducted on shaded rocks and in cracks to detect stalked barnacles, including *Capitulum* and *Ibla* species, and the Tetraclitid barnacle *Tetraclitella* species. The abundance of each species of barnacles was scored using a semi-quantitative scale, modified from Herbert et al., 2007 (Table 2).

Frequency	Description	Abundance Score
None	None found	0
Rare	<10% cover on the shore, only a few found in 30 minutes searching.	1
Occasion	>10% to < 30% cover on the shores	2
Common	30 - 50% cover on the shore.	3
Abundant	Rocks well covered (>50% cover on the barnacle zone)	4

Table 2. Semi-quantitative scale to measure the abundance of barnacles, modified from Hebert et al., 2007.

2.2 Environmental factors

Variation in monthly seawater temperature and chlorophyll *a* concentration were obtained from the Giovanni database, NASA, USA (see web link in reference section) at Yeliu, He

Ping Dao, Turtle Island (located in the N Coast Ecosystem; site details, see Table 1), Shi Ti Ping, Xiu Gang, Hai Kou (located in the Kuroshio Ecosystem), Sheung Shan, Gaomei and Ci Qu (located in the Taiwan Strait Ecosystem) and Kinmen and Matsu (located in the China Coastal Ecosystem).

2.3 Variation in barnacle assemblages in different marine ecosystems

Variations in the barnacle species semi-quantitative abundance among different marine ecosystems in Taiwan (N Coast Ecosystem, Kuroshio Ecosystem, Taiwan Strait Ecosystem and the China Coastal Ecosystem) were investigated using multivariate analysis (PRIMER 6, Plymouth Routine in Multivariate Analysis, PRIMER-E Ltd; Clarke, 1993). The species abundance data were square root transformed prior to analysis and the matrix of similarity between each pair of sites was calculated using Bray-Curtis similarity index (Bray & Curtis, 1957). Non-metric multidimensional dimension scaling (nMDS) was used and we plotted the two dimensional ordinations of the ranked orders of similarity among the species composition at sites (Clarke, 1993). One-way analysis of similarity test (ANOSIM; Factor: marine ecosystem) and global R test (Clarke & Green, 1988) was calculated to test the significant differences in the assemblage structure among the marine ecosystems in Taiwan. SIMPER analysis was conducted to examine the diagnostic species between each pair of marine ecosystems (Clarke, 1993).

2.4 Variation in barnacle species composition and environmental factors

For representative species that exhibit diagnostic distribution among the marine ecosystems, the distribution and semi-quantitative abundance of the species was plotted on the satellite image ocean sea surface temperature and chlorophyll *a* concentration (NOAA/AVHRR SST images, 7/2007 and 12/2007). Through this approach we attempted to detect environmental factors responsible for the variation in species abundance among different marine ecosystems

3. Results

3.1 Species composition in relation to marine ecosystems

A total of 21 species of intertidal barnacles were recorded from all marine ecosystems in Taiwan. Fifteen species were recorded in the N Coast Ecosystem. The Kuroshio Ecosystem includes 17 species. Overlap of species occurred between the N Coast Ecosystem and the Kuroshio Ecosystem, with 13 species (except *Pseudoctomeris sulcata* which is only present in the N Coast Ecosystem) detected in the N Coast Ecosystem also recorded in the Kuroshio Ecosystem; however, abundance values varied between the two ecosystems (Table 3). The barnacle *Octomeris brunnea* and *Yamaguchiella coerulescens* were only recorded in the Kuroshio Ecosystem. The mangrove barnacle *Fistulobalanus albicostatus* was recorded only in the Taiwan Strait Ecosystem: this species is absent from all other marine ecosystems. In the China Coastal Ecosystem, 10 species were recorded, of which 3 species were unique to the China Coast Ecosystem: including *Chthamalus challengeri*, *Tetraclita squamosa* and *Tetraclita japonica japonica* (Table 3).

Species	N coast	Kuroshio	Taiwan Strait	China Coastal
Tetraclita kuroshioensis	+	+	-	-
Tetraclita japonica formosana	+	+	-	-
Chthamalus challengeri	-	-	-	+
Tetraclita squamosa	-	-	-	+
Tetraclita japonica japonica	-	-	-	+
Chthamalus malayensis	+	+	-	-
Chthamalus moro	+	+	-	-
Hexechamaesipho pilsbryi	+	+	-	-
Megabalanus volcano	+	+	-	-
Tetraclitella divisa	+	+	-	-
Tetraclitella karandei	+	+	-	-
Tetraclitella chinensis	+	+	-	-
Capitulum mitella	+	+	-	+
Pseudoctomeris sulcata	+	-	-	-
Octomeris brunnea	-	+	-	-
Newmanella sp.	+	+	-	-
Fistulobalanus albicostatus	-	-	+	+
Chthamalus sp.	-	+	-	-
Ibla cumingi	-	+	-	-
Yamaguchiella coerulescens	+	+	-	-
Megabalanus tintinnabulum	+	+	-	-

Table 3. Summary of presence and absences of intertidal barnacle species surveyed in the marine ecosystems of Taiwan

From nMDS ordination plots of the species abundance, the ordinations of the sites in each marine ecosystem formed distinct clusters (Fig. 2A). The clusters of the N Coast Ecosystem and the Kuroshio Ecosystem are closer together (Figs. 2B, 3A) and, except the Tung Sha Island, which is located in the South China Sea, were distinct from all main clusters. The clusters of Taiwan Strait Ecosystem and the China Coastal Ecosystem separated clearly from the other ecosystems (Figs. 2A, 2B, 3A). The pattern of the nMDS ordination plot was further supported from the ANOSIM analysis, which showed significant differences in the species abundance among the marine ecosystems ($R = 0.78$, $P < 0.001$). From cluster analysis, the similarity of the assemblages between the East China Sea and the Kuroshio Ecosystems was 60%, showing these two ecosystems have similar species composition (Fig. 2B). Similarity of the China Coastal Ecosystem from the East China Sea and Kuroshio Ecosystems was 20%, showing strong differences in assemblage composition. The Taiwan Strait Ecosystem had < 10% similarity from other ecosystems, with little overlap of species from the Taiwan Strait Ecosystems to the other ecosystems (Fig. 2B). From SIMPER analysis, *Tetraclita kuroshioensis*, *Chthamalus moro*, *Yamaguchiella coerulescens*, *Chthamalus malayensis* and *Hexechamaesipho pilsbryi* contributed a total of 60% differences between the N Coast and Kuroshio Ecosystems. *T. kuroshioensis* is more abundant in the N Coast Ecosystem and is reduced abundance in the Kuroshio Marine Ecosystem. *Chthamalus moro*, *C. malayensis*, *Hexechamaesipho pilsbryi* are more abundant in the Kuroshio ecosystem, and a gradient of decreasing abundance to the north existed (Figs. 3B, C, D). Comparing the China Coastal

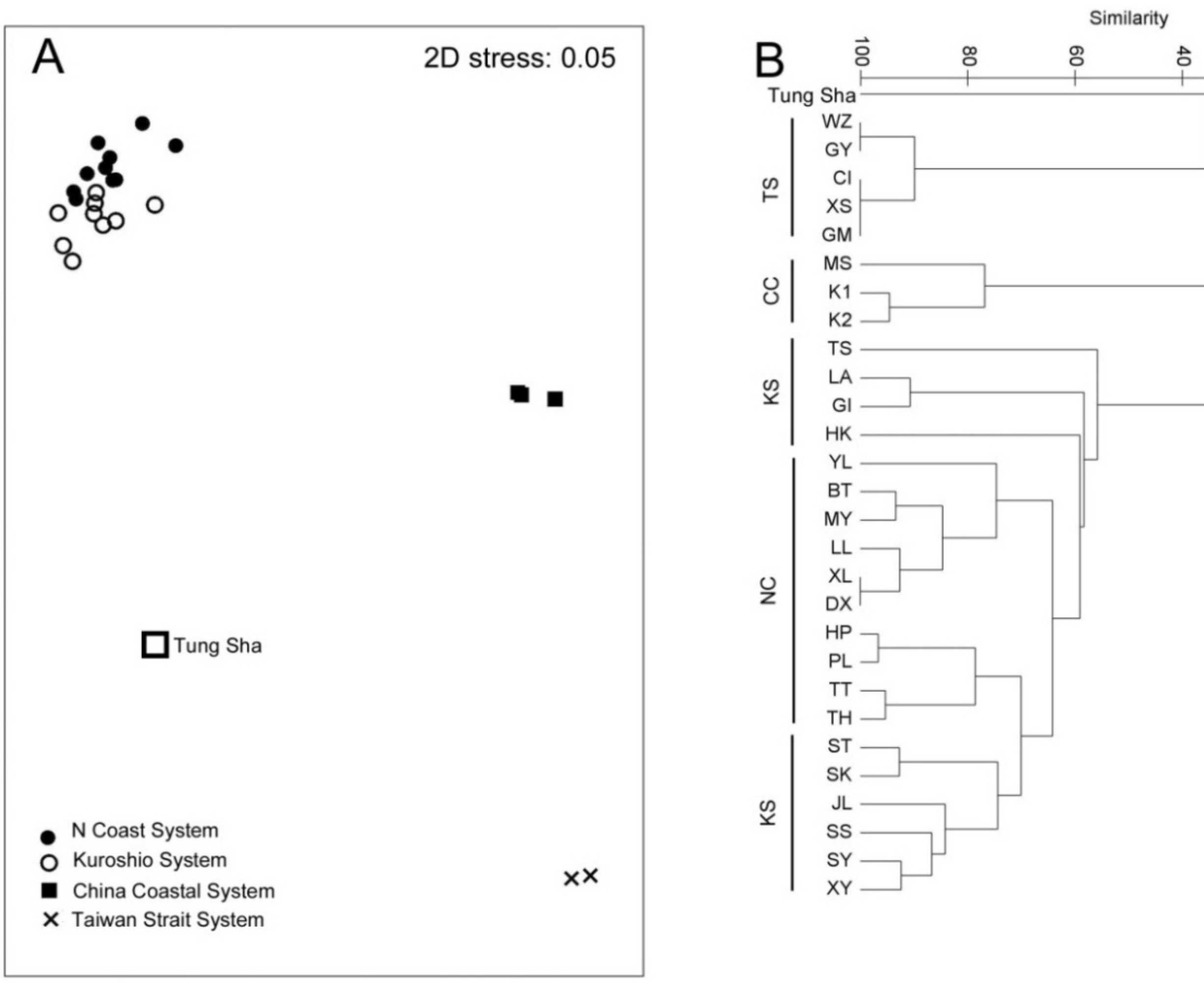

Fig. 2. A. Non-metric nMDS plots on the species composition in all sites from the N Coast Ecosystem
Strait Ecosystem and the China Coastal Ecosystem. B. Cluster plots on the species composition on al
Ecosystem (NC), Kuroshio Ecosystem (KS), Taiwan Strait Ecosystem (TS) and the China Coastal Eco
was not grouped in the ecosystem because it is located in the South China Sea. The Taiwan Strait Ec
of them overlap in the ordination plot.

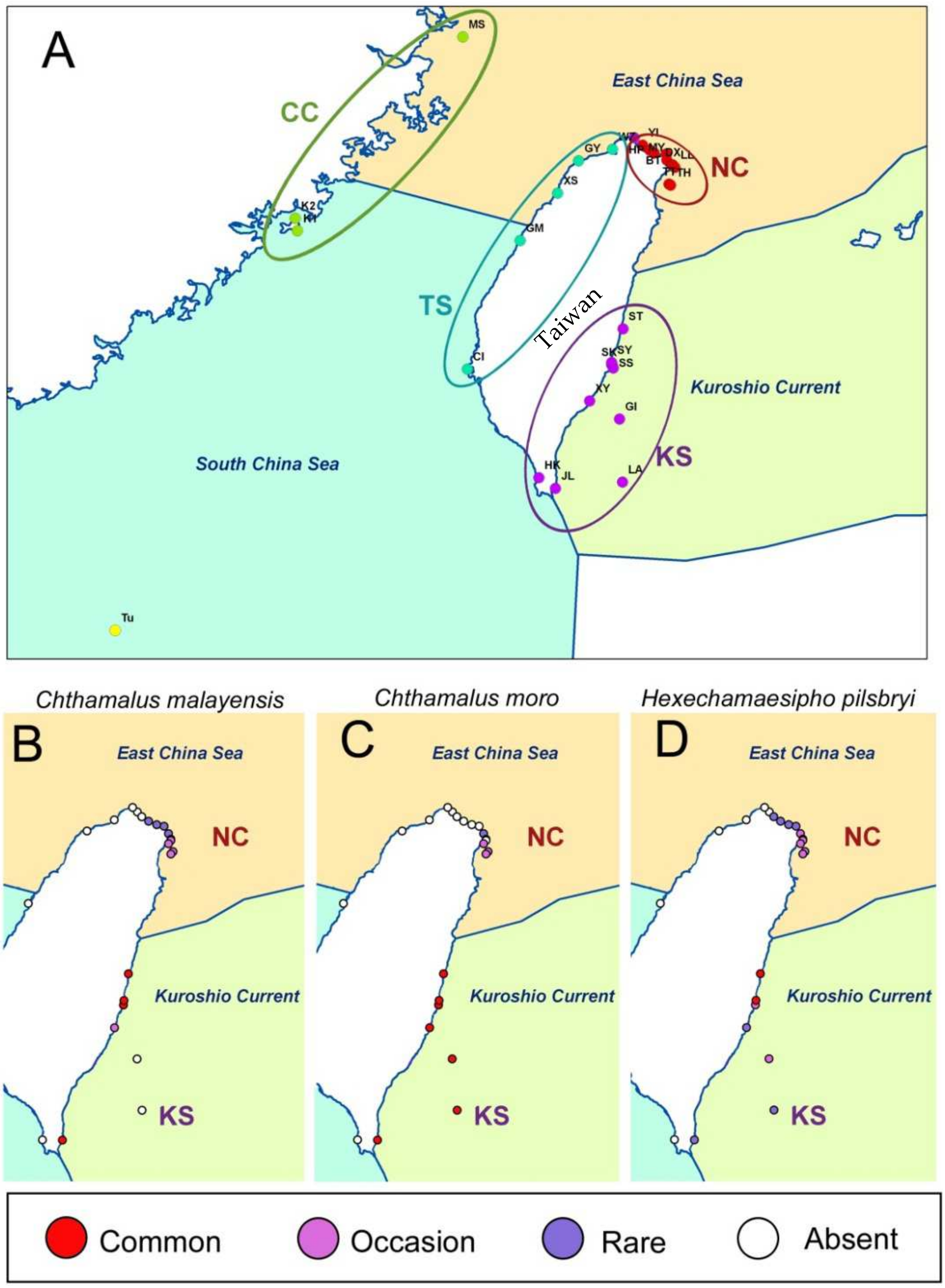

Fig. 3. A. Distribution of the large marine ecosystems of Taiwan, corresponding to the cluster distribution in the nMDS plots in Fig. 2A. Semi-quantitative distribution of B. *Chthamalus malayensis*, C. *C. moro* and D. *Hexechamaesipho pilsbryi* from the S to N coast of Taiwan main island. For details of the semi-quantitative scale, refer to Table 2.

ecosystem and the N Coast ecosystem, *Chthamalus challengeri*, *Tetraclita squamosa*, *Tetraclita japonica japonica*, *Tetraclita japonica formosana*, *Tetraclita kuroshioensis* and *Hexechamaesipho pilsbryi* contributed a total of 60% difference between these two ecosystems (Figs. 2B, 3A). *C. challengeri*, *T. squamosa* and *T. j. japonica* are only present in the China Coastal ecosystem, while the remaining representative species are absent from the China Coastal ecosystem.

4. Discussion

4.1 Biogeography, marine ecosystems and environmental factors

In this study, the species composition of intertidal barnacles in Taiwan is related to the individual marine ecosystems and to obvious biogeographical zones among the marine ecosystems. Barnacle species composition is similar between the N Coast Ecosystem and the Kuroshio Ecosystem, but abundance patterns differed between these two ecosystems. Species composition the Taiwan Strait Ecosystem and the China Coast Ecosystem are clearly distinct from the other ecosystems.

Comparing species composition between the N Coast Ecosystem and Kuroshio Ecosystem, almost all species collected in the N Coast Ecosystem were present in the Kuroshio Ecosystem, but the Kuroshio Ecosystem has additional diagnostic species. Similar species composition between the N Coast Ecosystem and the Kuroshio Ecosystem can be attributed to the intrusion and mixing of the Kuroshio Current at the N coast of Taiwan. In summer, the Kuroshio sub-surface water in the Pacific Ocean intrudes into the East China Sea in the waters around N and NE Taiwan, resulting in cold eddies in those regions (Tseng et al., 2000). In winter, the intrusion of the Kuroshio Current further shifts westwards onto the N coast of Taiwan (Tseng et al., 2000). Under the mixing of the Kuroshio and the waters in the East China Sea, the larvae of the intertidal barnacle can probably disperse between ecosystems, resulting in overlap of a considerable proportion of species. Although there are common species between the N Coast Ecosystem and the Kuroshio Ecosystem, latitudinal variation of species abundance occurs from the Kuroshio Ecosystem to the N Coast Ecosystem. *Chthamalus malayensis* and *Chthamalus moro* are warm water species common in the South China Sea region, including Hong Kong, the Philippines, and SE Asian locations (Yan & Chan, 2001; Rosell, 1972, 1986; Southward & Newman, 2003; Tsang et al., 2008). These two species had higher abundance in the southern locations of Taiwan main island and their abundance decreased from the E coast to the NE coast and were absent from the N coast locations. The decrease in abundance when approaching northwards in the east coast of Taiwan may be related to the change in seawater temperature. The seawater temperature in the N Coast Ecosystem is colder than the Kuroshio Ecosystem due to the strong NE monsoon in the East China Sea (Figs. 1B, C, E). *C. malayensis* and *C. moro* were not recorded from geographical locations (e.g., Japan) further north than Taiwan (Chan et al., 2008b; Southward & Newman, 2003), suggesting the NE coast of Taiwan may be their northern geographical limits. Decreasing abundance in cooler water species along a latitudinal gradient in Taiwan (Figs. 3B, C) is similar to barnacle distribution patterns reported in the British Isles. There, the warm water species *Chthamalus montagui* and *C. stellatus* reach range limits in the Central English Channel and fail to enter the North Sea due to reduced water temperature. By comparing the distribution pattern of *Chthamalus* in the UK from 1950 to 2004, *Chthamlaus* showed range extension in the English Channel and with extensive recruitment in warmest years (Herbert et al., 2007). Under the effect of global warming, warm water barnacle species along the east coast of Taiwan can expand northwards. The E to NE coast in Taiwan can provide excellent sites for monitoring range extension of intertidal species under the influence of the global climatic changes. Monitoring abundance and recruitment of warm water barnacle species at the NE Coast where their populations sharply decrease in abundance will clarify temporal and spatial scales of change and allow future comparative studies.

Hexechamaesipho pilsbryi is a high-shore barnacle recorded from Honshu and Okinawa in Japan and also in Taiwan (Chan et al., 2008b). The abundance of *Hexechamaesipho pilsbryi* decreased from south to north along the eastern coast (Fig. 3D). *Hexechamaesipho pilsbryi* is also recorded in the Philippines and Borneo waters (B. K. K. Chan unpublished data). From molecular analysis, it appears there are northern and southern populations of *Hexechamaesipho,* and the Taiwan populations belong to the latter (B.K.K. Chan, unpublished data). This suggests that *Hexechamaesipho* is distributed along the Kuroshio Current, but there is a physical boundary at Taiwan that blocks gene flow between the northern and southern populations.

The tetraclitid barnacles *Yamaguchiella coerulescens* and *Octomeris brunnea* were present only in the Kuroshio Ecosystem and were entirely absent from the N Coast Ecosystem. *Y. coerulescens* is reported common in the waters of the Philippines (Rosell, 1972). This suggests *Y. coerulescens* is distributed by the Kuroshio Current and its larvae do not intrude into the East China Sea waters. *Octomeris brunnea* was only recorded in Hai Kou, southern Taiwan in an extensive barnacle survey by Hiro (1939). In the present study, *O. brunnea* was also recorded in Hai Kou, but was absent from all other locations in Taiwan. *O. brunnea* live in shaded habitats and the rock formations in Hai Kou contain many large crevices. High habitat specificity in *O. brunnea* may limit its distribution in Taiwan.

The barnacle species composition of Kinmen and Matsu Islands, is distinct from that on the Taiwan main island. *Tetraclita squamosa*, *Tetraclita japonica japonica* and *Chthamalus challengeri* are only present this ecosystem. *T. squamosa* and *T. j. japonica* also have been recorded from South China to the East China coastline. The distribution of these two barnacle taxa is likely related to the flow of the China Coastal Current along the mainland China continent. The influence of the China Coastal Current is pronounced as little as 50 m offshore (Tseng et al., 2000). On the N Coast Ecosystem, *Tetraclita kuroshioensis* and *Tetraclita japonica formosana* become abundant, indicating no horizontal transfer of larvae across the Taiwan Strait. This likely is due to strong longitudinal flow along the strait. A similar distributional pattern also occurs for the lobster *Palinurus delagoa* in the East Africa and Madagascar. *P. delagoa* exhibits distinct genetic divergence between Madagascan and east African populations (Gopal et al., 2006), suggesting that gene flow across the Mozambique Channel is rather limited.

Chthamalus challengeri is a northern species that is abundant on temperate shorelines, including Yellow Sea, East China and the Japanese coastline. In Kinmen and Matsu, due to the low seawater temperature of the Chiangjian runoff and the China Coastal Current (Tseng et al., 2000), the environment may favor the survival of *C. challengeri*. *C. challengeri* is absent from Taiwan main island probably because the relatively higher seawater temperature on the N Coast Ecosystem and in the Kuroshio Ecosystem prevents its survival and recruitment. Further monitoring and examination of larval composition in Taiwan is needed to reveal the arrival of *C. challengeri* larvae into the waters around the Taiwan main island.

Most of the shorelines in the intertidal of the Taiwan Strait are occupied by mangroves or are open, sandy shores, and consequently, few intertidal barnacle species were recorded. In the present study, only *Fistulobalanus albicostatus* was collected on mangrove trunks. *Fistulobalanus* is a widespread estuarine barnacle species in Pacific waters, and can be abundant in brackish waters. In the present study, *Fistulobalanus* is abundant in the Taiwan Strait Ecosystem because of its association with mangrove and soft shore habitats. The absence of *F. albicostatus* from the other three marine ecosystems (except its rare occurrence in Kinmen) may be due to the rocky intertidal shorelines of those sites, and the lack of soft benthic habitats.

4.2 Conclusions

The marine ecosystems and associated barnacle species of Taiwan provide an excellent opportunity to study and monitor the processes of climate change. The present study demonstrates that the biogeography of intertidal barnacles in Taiwan is strongly influenced by oceanographic currents and water temperature differences among the several marine ecosystem. The Kuroshio and N Coast Ecosystems share a great proportion of species in common. However, we detected a gradient of decreasing abundance of the warm water species including *Chthamalus malayensis*, *C. moro* and *Hexechamaesipho pilsbryi* along the East coast of Taiwan, and with a sharper decrease in abundance to the NE coast of Taiwan. *Yamaguchiella coerulescens* was only detected on the east coast of Taiwan. Under the effects of global warming, warm water barnacle species are expected to expand their distributional ranges, similar to the case of *Chthamlaus* spp. in the English Channel (Herbert et al., 2007). The abundance of warm water barnacle species in the E and NE coast can be used as an indicator for global warming. Further studies should conduct regular monitoring to sample the abundance and recruitment of warm water barnacle species on the NE coast of Taiwan, and be designed to detect range extensions of intertidal species under the effects of climate change.

5. Acknowledgement

This study was partially funded by the Career Development Award from Academia Sinica to BKKC (AS-98-CDA-L15) and the grant from National Science Council of Taiwan to PFL (101-2631-H-002-005- and 100-2631-H-002-019-). Analyses and visualizations used in Fig 1C, D. were produced with the NOAA/AVHRR SST images, Fig. 1E, F were produced with the Giovanni online data system, developed and maintained by the NASA GES DISC.

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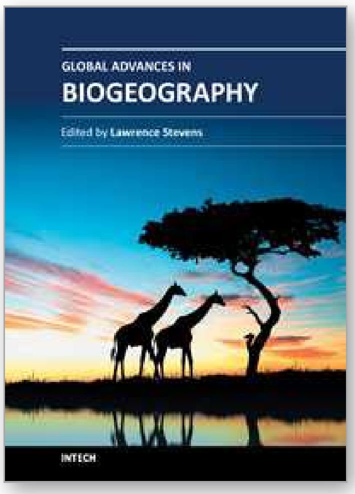

Global Advances in Biogeography

Edited by Dr. Lawrence Stevens

ISBN 978-953-51-0454-4

Hard cover, 360 pages

Publisher InTech

Published online 30, March, 2012

Published in print edition March, 2012

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