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Latitudinal gradient in the distribution of intertidal barnacles of the *Tetraclita* species complex in Asian waters

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ABSTRACT: Barnacles are a major space occupier in the intertidal zone and are good model organisms to study the biogeography of intertidal invertebrates. In the present study, we used quantitative transect sampling to study the geographical distribution of the common rocky shore barnacles *Tetraclita kuroshioensis*, *T. squamosa*, *T. japonica japonica* and *T. j. formosana* at 19 sites covering the 3 large Asian marine ecosystems (Kuroshio Current, East China Sea and South China Sea) from 22° 20′ to 35° 00′ N. *Tetraclita* spp. showed spatial variations in geographical distribution. Species assemblages of >60% similarity can be grouped into 4 distinct regions. On the Pacific coast of Japan *T. j. japonica*, *T. j. formosana* and *T. kuroshioensis* co-existed at the same tidal level, with *T. j. japonica* at the highest abundance. In North Taiwan and Okinawa *T. kuroshioensis* and *T. j. formosana* were common. In East Taiwan, *T. j. formosana* was the dominant species and *T. kuroshioensis* occurred in low abundance. In South China, *T. squamosa* and *T. j. japonica* were found, but they occupied different tidal levels. *T. j. formosana* and *T. kuroshioensis* were abundant in West Pacific waters, suggesting that their larval pool is associated with the Kuroshio Current. *T. squamosa* was distributed along the South China coast and it is possible that their larvae were transported mainly by the South China Sea Surface Current. *T. j. japonica* had high abundance in both Japan and South China, but with very low abundance at the Pacific shores between these 2 locations. There may be a physical and genetic boundary between the northern and southern populations in the Pacific Ocean and further studies of *Tetraclita* spp. in the Asian region should focus on population genetics.

KEY WORDS: Barnacles · *Tetraclita* · Rocky shores · Biogeography · Oceanography

INTRODUCTION

Intertidal invertebrates often have a planktonic larval phase and a benthic adult stage. The geographical distribution of intertidal communities can therefore be affected by the larval supply, larval mortality, larval dispersal range and post-settlement mortality (Morgan 2001). Larval supply and dispersal range can be influenced by oceanographic processes (e.g. oceanographic current patterns and upwelling), resulting in variation in geographical distribution (Connolly et al. 2001). Barnacles have often been used as model species to study the patterns and processes affecting geographical distribution as they are the major space occupier in the intertidal zone and have wide geographical distribution (see Connolly et al. 2001, Morgan 2001).

Tetraclita spp. are common rocky shore barnacles in the Indo-Pacific region (Pilsbry 1916, Newman & Ross 1976). In the past, *T. squamosa* was considered to consist of 3 sub-species (*T. squamosa squamosa*, *T. s. japonica* and *T. s. formosana*) in NW Pacific waters. Using morphological analysis and molecular techniques, the sub-species of *T. squamosa* were separated into 3 species: *T. kuroshioensis* (synonymous with *T. pacifica*, see

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Chan et al. 2007a,b); *T. squamosa* Bruguière 1789; and *T. japonica* (Yamaguchi 1987, Hasegawa et. al. 1996, Chan 2001, 2003, Chan et al. 2007a,b). *T. japonica* Pilsbry 1916 and *T. formosana* Hiro 1939 were previously identified as 2 species but Chan et al. (2007c) revealed no differentiation between their mitochondrial (COI, 12S) and nuclear (ITS1) DNA. They were therefore grouped into sub-species of *T. japonica* as *T. japonica japonica* Pilsbry 1916 and *T. j. formosana* Hiro 1939, based on their differences in parietes (shell) colour and geographical distribution. Major diagnostic morphological differences of *Tetraclita* spp. in the NW Pacific waters are in the colour of the parietes, shape of the opercular plates, the patterns on the tergal-scutal flaps and the setal types of the first and third maxillipeds (see Yamaguchi 1987, Chan 2001, Chan et al. 2007a,b).

The geographical distribution record of *Tetraclita* spp. in Asia has, however, often been reported qualitatively (Hiro 1939, Utinomi 1954, Ren & Liu 1979, Yamaguchi 1987), resulting in confusion as to where they can be found, and making it difficult to compare their abundance between locations; this may be related to interactions of the patterns of larval supply and oceanographic currents (see Morgan 2001). Utinomi (1949, 1954) claimed that *T. japonica japonica* were completely absent from Taiwan, whilst Yamaguchi (1987) documented the existence of *T. j. japonica* at one site on the northern coastline of Taiwan. *T. squamosa* was reported to be distributed in the Indo-Pacific, but recent studies showed that *T. squamosa* in the Pacific Ocean was a separate species — *T. kuroshioensis* (see Chan et al. 2007a). The geographical distribution of *T. squamosa* and *T. kuroshioensis* was, therefore, uncertain.

The zonation pattern and geographical distribution of *Tetraclita* spp. in the Pacific region appears to vary along the latitudes, which could result from variations in reproductive season, oceanographic currents, climate, larval supply and recruitment (Miron et al. 1999, Morgan 2001, Herbert et al. 2007). The aim of the present study was to obtain further insight into the biogeography of intertidal communities in the NW Pacific. Quantitative, stratified, transect surveys were conducted at locations along the latitudinal gradient from Honshu, Japan, in the NW Pacific to SE Asia (including the Okinawa island, Taiwan, Xiamen and Hong Kong) to test whether the geographical distributions of *T. kuroshioensis, T. squamosa*, *T. japonica japonica* and *T. j. formosana* vary across latitudes.

MATERIALS AND METHODS

Study sites and timing. We studied barnacle distribution from Japan, Taiwan and mainland China along the latitude from 22° 20′ to 35° 00′ N from 2003 to 2005 (Table 1), except in Hong Kong where the data were collected by Chan et al. (2001) (Fig. 1). A total of 19 sites, distributed in 3 different large marine ecosystems (Kuroshio Current, East China Sea and South China Sea), were surveyed (Table 1).

Honshu, Japan: Sampling was conducted at Katsuura (KAT) (March 2004) and Kominato (KOM) (March 2004) in the Boso Peninsula (Table 1); at Shimoda (SHI) (October 2005) in the Izu Peninsula; and at Shirahama (SHA) (June 2005) in the Kii Peninsula (Fig. 1, Table 1). The rocks at all these study sites are sedimentary. Inshore seawater is oceanic with a high salinity of 30 to 33‰. Tides are semi-diurnal with a tidal range of ~2 m. The climate around the Boso and Izu Peninsulas is temperate and the hydrography is influenced by the cold Oyahio Current from the north and the warm Kuroshio Current from the south (Ishizaka et al. 1992). Waters at the south of Kii Peninsula are mainly influenced by the Kuroshio Current. Mean air temperature at KAT and KOM ranged from 7°C in winter to 28°C in summer.

Okinawa: At Okinawa Island, Japan, sampling was conducted in Sedake (SED) and Yaka (YK) (November 2003) (Table 1), in the Pacific Ocean, with a salinity of 33‰ all year round. Okinawa has a sub-tropical climate with semi-diurnal tides (max. tidal range can reach 2.5 m). Hydrography in Okinawa Island is mainly influenced by the Kuroshio Current from the south (Fig. 1) (Ito et al. 1995).

Table 1. Site names and their abbreviations names and positions sampled for *Tetraclita* spp.; see also Fig. 1

Site name	Abbrev.	Latitude and longitude
Honshu, Japan		
Katsuura, Boso Peninsula	KAT	35° 08′ N, 140° 18′ E
Kominato, Boso Peninsula	KOM	35° 07′ N, 140° 11′ E
Shimoda, Izu Peninsula	SHI	34° 39′ N, 138° 57′ E
Shirahama, Wakayama, Kii Peninsula	SHA	33° 40′ N, 135° 20′ E
Okinawa, Japan		
Sedake	SED	26° 32′ N, 128° 05′ E
Yaka	YK	26° 27′ N, 127° 51′ E
Taiwan		
Yeliou	YL	25° 12′ N, 121° 41′ E
Badoutz	BAD	25° 09′ N, 121° 45′ E
Bitou Cape	BTC	25° 07′ N, 121° 54′ E
Sandiu Cape	SDC	24° 59′ N, 121° 59′ E
Lai Lai	LL	24° 58′ N, 121° 57′ E
Beiguan	BQ	24° 54′ N, 121° 52′ E
Three Fairy Platforms	TFP	23° 07′ N, 121° 24′ E
Hsiao Yeliou	HYL	22° 49′ N, 121° 11′ E
Lanyu	LY	22° 01′ N, 121° 32′ E
Mainland China		
Baiyu, Xiamen	BY	24° 22′ N, 118° 08′ E
Wuyu, Xiamen	WY	24° 21′ N, 118° 07′ E
Shek Mei Tau, Hong Kong	SMT	22° 16′ N, 114° 18′ E
Cape d'Aguilar, Hong Kong	CD	22° 12′ N, 114° 15′ E

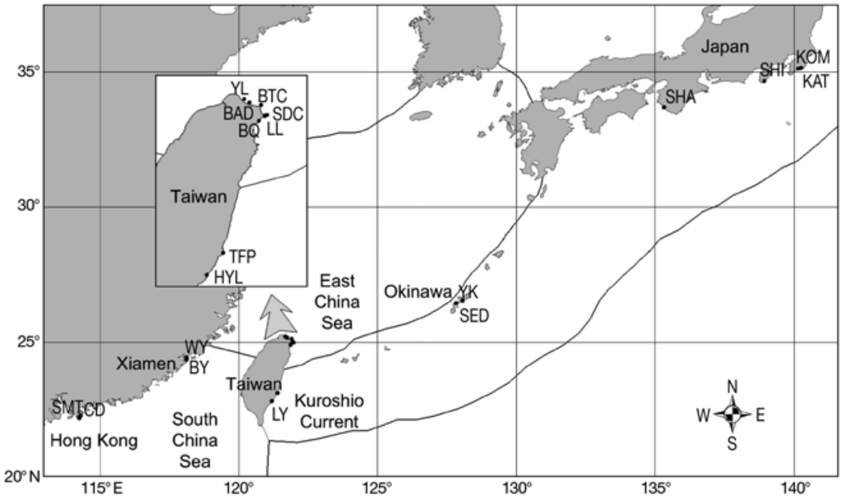

Fig. 1. Sampling locations of *Tetraclita* spp. in the NW Pacific and SE Asian waters. These localities are distributed among 3 large marine ecosystems, i.e. East China Sea, Kuroshio Current and South China Sea. See text for further description and Table 1 for abbreviations of each site

North Taiwan: North Taiwan is located in the subtropical region with mixed semi-diurnal tides of maximum range 2.5 m. Sampling was conducted in June 2004. Waters around the north coast (Yeliou [YL], Badoutz [BAD], Bitou Cape [BTC] and Sandiu Cape [SDC]) are under the influence of the cold, upwelling eddy from the East China Sea Shelf generated by the Kuroshio Current and the warm waters from the Taiwan Strait (see Chiang et al. 1997) (Fig. 1, Table 1). Sampling was not conducted on the west coast of Taiwan, as the major habitats there are mangroves and estuarine soft shores.

East Taiwan: The east coast (Lai Lai [LL], Beiguan [BQ], Three Fairy Platforms [TFP], Hsiao Yeliou [HYL] and Lanyu [LY]; sampled during June 2004) faces the Pacific Ocean, which is influenced by the warm Kuroshio Current (Fig. 1, Table 1) (Liang et al. 2003). The rocks are both sedimentary and volcanic. All the shores are oceanic and the salinity of the inshore seawater ranges from 30 to 33‰.

South China: In Xiamen, mainland China, sampling was conducted at 2 islands near Baiyu (BY) and Wuyu (WY) (June 2005) (Fig. 1, Table 1), facing the Taiwan Strait. The hydrology of Xiamen waters is influenced mainly by the South China Sea Surface Current from the south and the China Coastal Current from the north (Hu et al. 2002). The oceanographic currents affecting the waters in the Taiwan Strait are also influenced by the seasonal monsoons. Under the southwest monsoon, the water in the Taiwan Strait is mainly from the South China Sea Surface Current (summer) and the Kuroshio Current (spring), which enter the strait from the Penghu Channel (Jan et al. 2002). In winter, the water in the strait is influenced by the China Coastal Current, which flows southward under the effect of the northeast monsoons. The entry of the South China Sea Surface Current and the Kuroshio Current is blocked at the Penghu Channel during the winter months (Jan et al. 2002). The shore at Xiamen is composed of volcanic rocks.

Hong Kong is within the tropics (Table 1), but with a seasonal climate. Mean air temperature ranges from 35°C in summer to 10°C in winter. Mean seawater temperature is around 28°C in summer and 15°C in winter. The water of the east coast of Hong Kong is oceanic, with a salinity of 33‰ in winter and 25‰ in summer. Hydrography is influenced by the South China Sea Surface Current in summer, and by a combination of the Taiwan Current and the Kuroshio Current in winter (Fig. 1). Rocky shores are mainly composed of granite or volcanic rocks. Tides are semi-diurnal with maximum tidal range 2.5 m. Sampling was conducted at Shek Mei Tau (SMT) and Cape d'Aguilar (CD). Data were also taken from Chan et al. (2001), which covered 10 rocky shores in Hong Kong using the same sampling method as that used in the present study (Table 1).

To study the variation in seawater temperature and upwelling intensity of the study sites, monthly seawater temperature and upwelling indexes (from 2004 to 2006) were obtained from the NOAA Fisheries server (http://las.pfeg.noaa.gov/), which provides satellite environmental data on seawater temperature, and energy recovery device (ERD) derived upwelling indexes for Honshu (KOM, KAT, SHI, SHA), Okinawa, North Taiwan, East Taiwan and South China (Xiamen and Hong Kong). Due to resolution limitations, separate single sets of data were used to represent sites within Okinawa, Taiwan, Xiamen and Hong Kong. Variation in the seawater temperature and upwelling index from each site was analysed using multivariate analysis by PRIMER 6 (Plymouth Routines In Multivariate Ecological Research, PRIMER-E). A similarity matrix of the seawater temperature and upwelling index between locations was assessed using Euclidean Distance similarity test, followed by non-metric Multi-Dimensional Scaling (nMDS) plots.

Distribution pattern. At each study site, a 30 m stretch of coast was chosen. Four horizontal transects (30 m) were conducted at vertical intervals of 50 cm from 1 to 2.5 m above chart datum (CD), which covered the whole vertical range of *Tetraclita* spp. At each tidal level, 10 random 25 × 25 cm quadrats were photographed using a photoframer (Chan et al. 2001).

The percentage cover of all barnacle species in each quadrat photograph was identified and scored using the image analysis software SigmaScan (SPSS). From the photographs *Tetraclita* could be identified and sorted into species based on the colour differences on the parietes (Chan 2001, Chan et al. 2007a,b). Additional samples were collected from each site and dissected to examine the opercular plates for species identification and confirmation (see morphological identification of *Tetraclita* spp. in Chan 2001, Chan et al. 2007a,b,c). Vertical distribution patterns of *Tetraclita* spp. were studied by calculating the mean abundance of each species at different tidal levels (n = 10, ±1 SD). Geographical variation in the mean abundance of each *Tetraclita* species from each site (taking the average of the abundance at the 2 tidal levels which showed highest abundance, i.e. n = 20) was analysed using multivariate analysis by PRIMER 6. Due to the limited quantity, we excluded the data collected from LY in the multivariate analysis. All sampling sites were surveyed once only because the present study focuses on comparing the latitudinal differences but not on temporal variations. The 18 geographical locations were used as samples, and the abundance of the *Tetraclita* spp. at each location were used as variables. The square root was determined for all data and the similarity matrix of the *Tetraclita* spp. abundance between locations was assessed using the Bray-Curtis similarity test, followed by cluster analysis and NMDS plots. Bubble plots were generated to show the abundance pattern of *Tetraclita* spp. among the geographical locations. Analysis of similarities (ANOSIM) was conducted to investigate the variation in species composition between the hydrographic regions including Honshu (KAT, KOM, SHA, SHI), Okinawa (SDK, YK), North Taiwan (YL, BAD, BTC, SDC), East Taiwan (HYL, TFP, LL, BQ) and South China (CD, SMT, WY, BY). Similarity percentage (SIMPER) analysis was conducted to test the percentage contribution of each *Tetraclita* species to the total difference in species composition between the paired hydrographic regions.

RESULTS

Oceanographic variations in the study sites

Summer seawater temperatures (August to September) of all sites ranged from 26 to 30°C. KOM and SHI, located in Honshu, Japan, had lowest summer temperatures among all sites studied (Fig. 2A), ranging from 26 to 27°C. Xiamen and Hong Kong, located in South China, had highest summer seawater temperatures, reaching 30°C (Fig. 2A). In winter, KOM and SHI had the lowest seawater temperature, reaching 14°C in January and February (Fig. 2A). Winter seawater temperature in Taiwan, Hong Kong and Xiamen ranged from 16 to 18°C (Fig. 2A). Okinawa, however, had the highest winter seawater temperature of 23°C (Fig. 2A). In the nMDS ordination plot of the seawater temperature in the study sites, ordinations of Honshu were clustered together (Fig. 3A). The ordinations of Hong Kong, Taiwan and Xiamen were also grouped together, while the ordination of Okinawa was separated from the other groups (Fig. 3A).

Occurrence of upwelling followed seasonal cycles, with stronger upwelling in summer months (April to September, Fig. 2B). The locations in Honshu, Japan, had a higher upwelling index through the year (Fig. 2B), compared to Taiwan, Xiamen and Hong

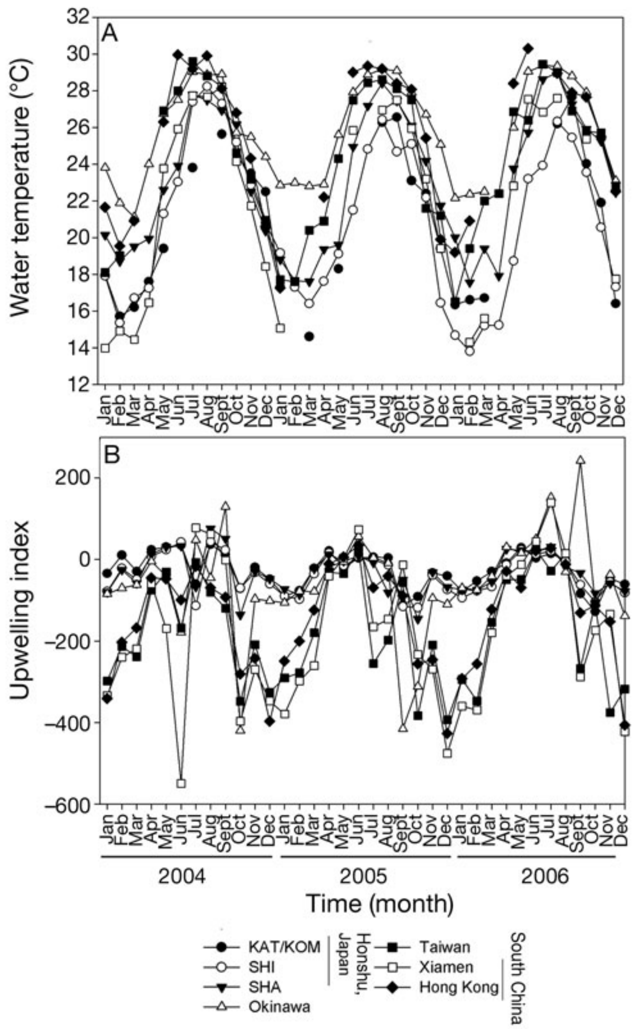

Fig. 2. Monthly variation in (A) seawater temperature and (B) upwelling index of the study sites (see Table 1 for definition of abbreviations) from 2004 to 2006. Data obtained from the NOAA Pacific Fisheries Laboratory. Gaps in lines indicate no data were available in that period

Kong (Fig. 2B). Okinawa, however, had the highest peak of upwelling during August 2004 and 2006 (Fig. 2B). From the nMDS ordination of the upwelling index of the study sites, Honshu ordinations are clearly clustered in one patch (Fig. 3B), whilst ordinations of Xiamen, Hong Kong and Taiwan are clustered in a second patch (Fig. 3B). The Okinawa ordination was separated from the other 2 patches (Fig. 3B).

Geographical and vertical distribution

Tetraclita spp. exhibited significant variation in species composition among the geographical locations studied (ANOSIM result: $R = 0.873$, $p < 0.001$, Table 2). Among the 4 taxa *T. squamosa* was only recorded in South China regions (Hong Kong and Xiamen) (see SIMPER analysis in Table 2); *T. japonica formosana* dominated in Taiwan (Table 2), *T. kuroshioensis* existed along the Kuroshio Current shoreline, and *T. j. japonica* mostly occurred in Honshu, Hong Kong and Xiamen (Fig. 4). The diagnostic species revealed from SIMPER analysis that separates paired site

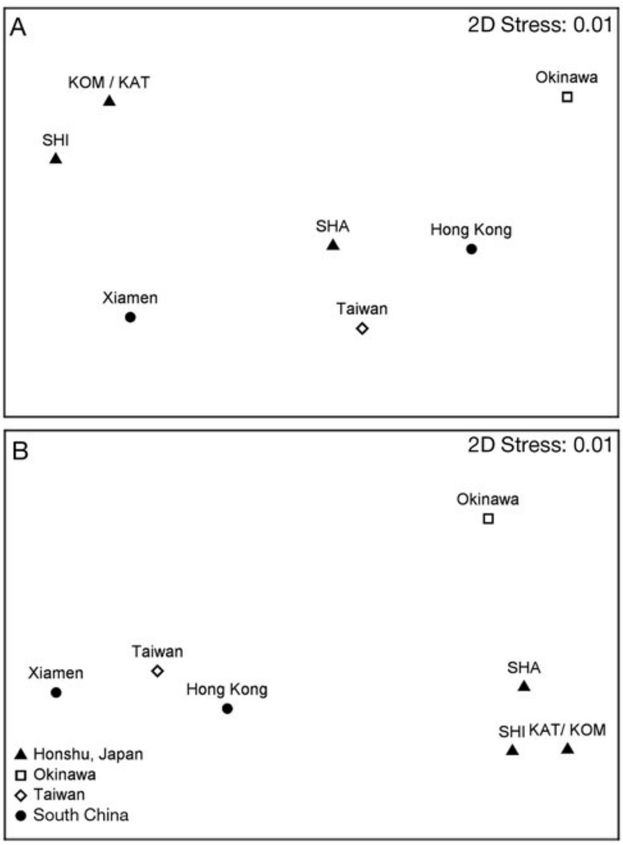

Fig. 3. nMDS plots of monthly (A) seawater temperature and (B) upwelling index of Honshu (KAT, KOM, SHI, SHA; see Table 1), Okinawa, Taiwan and South China (Xiamen and Hong Kong)

groups can be seen in Table 2. Except in Xiamen and Hong Kong where the *T. squamosa* and *T. j. japonica* showed vertical zonation, little evidence of vertical separation of *Tetraclita* spp. was found (Table 3).

In Honshu, Japan, *Tetraclita japonica japonica* was an abundant barnacle on the mid shores (1.5 to 2 m above CD) of KAT and KOM (Boso Peninsula), SHI (Kii Peninsula) and SHA (Izu Peninsula), reaching ~30 to 50% cover (Fig. 4, Table 3). In contrast, *T. j. formosana* and *T. kuroshioensis* occurred in lower abundance in Honshu. All of these 3 *Tetraclita* spp. occurred in the same tidal zone and did not show distinct zonation patterns. The vertical range of *T. j. japonica* is ~0.5 m (Fig. 4, Table 3).

In SED and YK at Okinawa, *Tetraclita kuroshioensis* was the most abundant species, reaching ~20% cover on the mid shore (Table 2). *T. japonica formosana* existed in the same vertical range, but occurred at a very low abundance of <5%. No *T. j. japonica* were recorded (Fig. 4).

On the east coast of Taiwan (BQ, HYL and TFP), *Tetraclita japonica formosana* was common in the mid shore (1.5 to 2 m above CD), with ~25% cover, whilst *T. kuroshioensis* had a low abundance of <10% cover (Fig. 4). In LY, an exposed Pacific island, only a few *T. j. formosana* were sampled around the whole island. On the northeast coast (LL, SDC, BTC, BAD and YL), *T. kuroshioensis* and *T. j. formosana* were recorded (Fig. 4). *T. kuroshioensis* was the most abundant species, occupying ~25% cover on the shore (Fig. 4). The abundance of *T. j. formosana* in YL was ~10%, which was lower than the east coast population. At YL, *T. j. japonica* had a very low abundance with a cover <5% (Fig. 4) and was absent from other sites in Taiwan. The 3 species did not occupy different vertical ranges and were mixed in the same intertidal region (Fig. 4, Table 2).

Only *Tetraclita squamosa* and *T. japonica japonica* were recorded in Xiamen and Hong Kong, and the 2 species showed distinct vertical zonation (Fig. 4, Table 2). One-way ANOVA on the abundance of *T. j. japonica* along the 4 tidal levels studied (1, 1.5, 2, and 2.5 m above CD) showed that this species was common on the high shores (>1.75 m CD), reaching ~40% cover (Xiamen, WY: $[F]_{3,36} = 187$, $p < 0.05$, Student-Newman-Keuls [SNK] tests on tidal levels: 2 > 2.5 > 1.5 > 1; Xiamen, BY: $F_{3,36} = 174$, $p < 0.05$, SNK tests: 2 > 2.5 = 1.5 > 1; Hong Kong, CD: $F_{3,36} = 185$, $p < 0.05$, SNK tests: 2 = 1.5 > 2.5 = 1; SMT: $F_{3,36} = 196$, SNK tests: 1.5 > 2 > 2.5 = 1), whilst *T. squamosa* was abundant on the low shores (<1.5 m CD, 1-way ANOVA: Xiamen, WY: $F_{3,36} = 188$, $p < 0.05$, SNK tests: 1 > 1.5 = 2 = 2.5; Xiamen BY: $F_{2,27} = 17.9$, $p < 0.05$, SNK tests: 1 > 1.5 = 2 [*T. squamosa* only occurred at the 2 lowest tidal levels in Hong Kong; therefore no statistical analysis was

Table 2. *Tetraclita* spp. Percentage cover (%, mean ± SE) at the 4 tidal levels studied (1, 1.5, 2 and 2.5 m above CD), of *T. japonica japonica* (TJJ), *T. j. formosana* (TJF), *T. kuroshioensis* (TK) and *T. squamosa* (TS) in the NW Pacific and SE Asian regions. See Table 1 for location and definition of sites. –: absence of barnacles (i.e. abundance = 0). Note that *T. j. japonica*, and *T. kuroshioensis* were common on the mid shores in Japan; *T. j. formosana* and *T. kuroshioensis* were common in Taiwan and Okinawa; and in Xiamen and Hong Kong, only *T. squamosa* (low shore) and *T. j. japonica* (mid shore) were found

Site	TJJ				TJF				TK				TS			
	1	1.5	2	2.5	1	1.5	2	2.5	1	1.5	2	2.5	1	1.5	2	2.5
KAT	–	40 ± 10	33 ± 15	–	–	0.8 ± 2	1 ± 1	–	–	–	–	–	–	–	–	–
KOM	–	27 ± 6	32 ± 5	–	–	0.2 ± 1	0.4 ± 1	–	–	–	–	–	–	–	–	–
SHI	–	24 ± 14	28 ± 10	–	–	1 ± 3	–	–	–	9 ± 8	5 ± 12	–	–	–	–	–
SHA	–	25 ± 17	32 ± 12	–	–	1 ± 2	–	–	–	12 ± 13	8 ± 12	–	–	–	–	–
SED	–	–	–	–	–	2.4 ± 2	4 ± 2	–	–	13 ± 10	16 ± 12	–	–	–	–	–
YK	–	–	–	–	–	3 ± 2	2 ± 0.6	–	–	12 ± 7	20 ± 10	–	–	–	–	–
YL	–	2 ± 3	1 ± 3	–	4 ± 5	4 ± 4	4 ± 2	3 ± 2	8 ± 6	17 ± 13	20 ± 9	6 ± 7	–	–	–	–
BAD	–	–	–	–	–	7 ± 6	13 ± 11	–	–	12 ± 5	7 ± 1	–	–	–	–	–
BTC	–	–	–	–	–	22 ± 5	18 ± 6	–	–	18 ± 7	14 ± 10	–	–	–	–	–
SDC	–	–	–	–	–	31 ± 10	21 ± 10	–	–	2 ± 2	5 ± 3	–	–	–	–	–
LL	–	–	–	–	–	34 ± 22	23 ± 13	–	–	5 ± 3	3 ± 2	–	–	–	–	–
BQ	–	–	–	–	6 ± 8	21 ± 7	27 ± 10	–	3 ± 2	2 ± 3	3 ± 2	–	–	–	–	–
TFP	–	–	–	–	–	19 ± 6	18 ± 9	–	–	–	–	–	–	–	–	–
HYL	–	–	–	–	–	12 ± 9	16 ± 10	–	–	–	–	–	–	–	–	–
WY	1 ± 2	6 ± 5	39 ± 11	21 ± 7	–	–	–	–	–	–	–	–	28 ± 14	31 ± 4	4 ± 6	1 ± 2
BY	2 ± 3	8 ± 6	43 ± 5	7 ± 5	–	–	–	–	–	–	–	–	2 ± 3	9 ± 6	7 ± 5	–
CD	8 ± 6	30 ± 20	46 ± 24	7 ± 4	–	–	–	–	–	–	–	–	11 ± 4	–	–	–
SMT	3 ± 4	36 ± 20	40 ± 8	5 ± 3	–	–	–	–	–	–	–	–	24 ± 12	17 ± 8	–	–

conducted to compare with the high shore abundance]). No *T. j. formosana* or *T. kuroshioensis* was observed in Hong Kong or Xiamen (Fig. 4, Tables 2 & 3).

Based on nMDS plots (Fig. 5A) and similarity tree by cluster analysis (Fig. 5B), 4 geographical location groups separated at 60% similarity were identified: Honshu, North Taiwan and Okinawa, East Taiwan, and South China groups. *Tetraclita japonica formosana* was the most abundant species in the East Taiwan group (Fig. 5F), whilst *T. j. japonica* showed high abundance in the Honshu and South China groups (Fig. 5C). *T. squamosa* showed distribution in the South China group, whilst *T. kuroshioensis* was common in the Honshu, Okinawa and North Taiwan groups (Fig. 5D,E).

DISCUSSION

Geographical distribution

Tetraclita spp. showed distinct variations with latitudinal gradient in geographical distribution, abundance and zonation pattern. In Japan, where *T. kuroshioensis*, *T. japonica japonica* and *T. j. formosana* co-existed, they did not show different zonation patterns, whilst in the southern locations (Xiamen and Hong Kong), *T. j. japonica* and *T. squamosa* occupied distinct zones, with *T. j. japonica* in the mid to high shore and *T. squamosa* in the low shore. The vertical distribution range of *Tetraclita* spp. was also higher in Hong Kong and Xiamen than Okinawa, Taiwan and Japan.

nMDS ordination of *Tetraclita* spp. composition among the geographical locations matched with the ordination patterns of the seawater temperature and upwelling index (Figs. 2 & 5), suggesting that geographical distribution of *Tetraclita* spp. could be influenced by hydrographic regimes. Differences in oceanographic currents may result in variation in larval dispersal and hence geographical distribution of *Tetraclita* spp. along the latitudinal gradient from Japan to Hong Kong (see Morgan 2001, Herbert et al. 2007). The brooding season of *Tetraclita* spp. occurs in summer as high temperature is essential to initiate gonad development (Hines 1978, Chan & Williams 2004) (Fig. 2) and, therefore, the larvae of *Tetraclita* spp. are probably transported by the summer oceanographic currents in the Asian region. *T. kuroshioensis* and *T. japonica formosana* exist only in Japan, Okinawa and Taiwan. The highest abundance of *T. j. formosana* on the east coast of Tai-

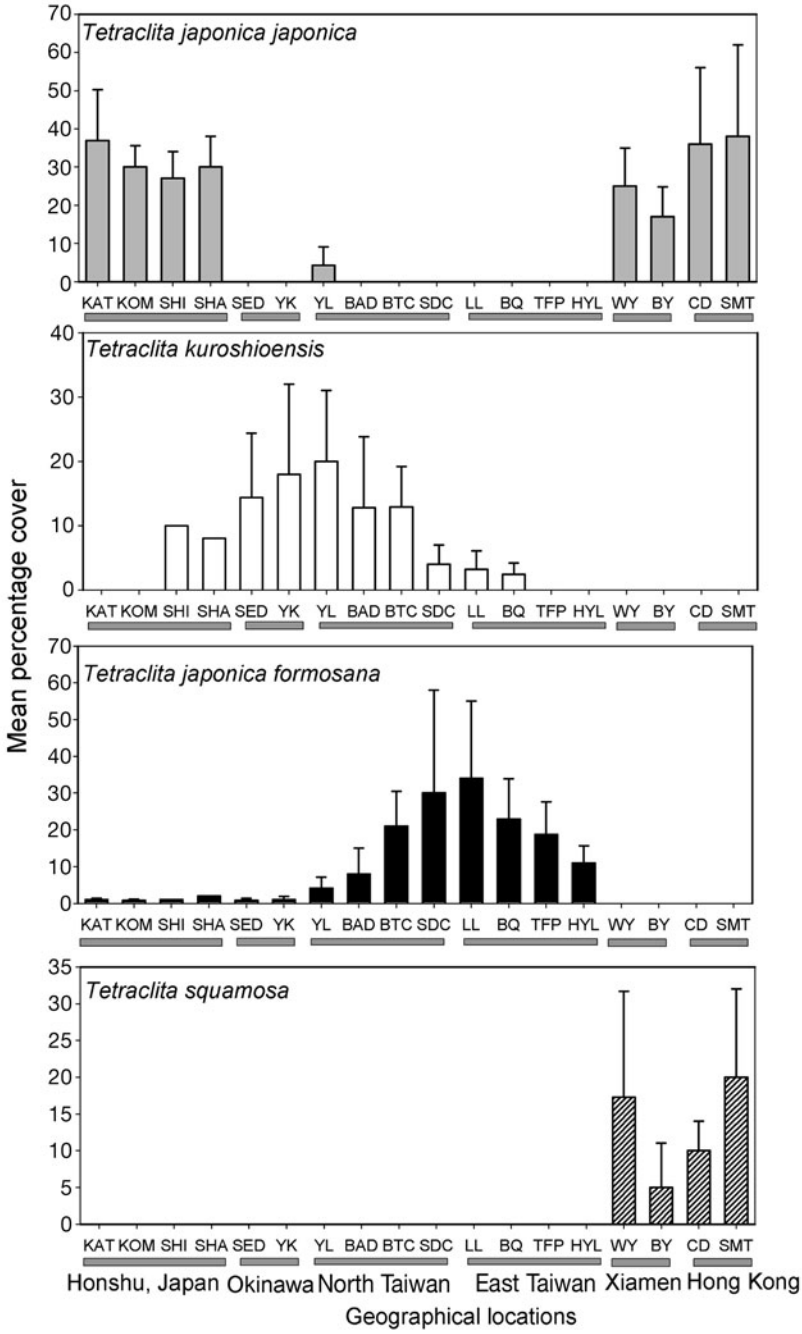

Fig. 4. *Tetraclita* spp. Geographical distribution (mean % cover ± 1 SD) of 4 species in the NW Pacific and SE Asian waters. Grey horizontal bars beneath site abbreviations represent site groupings in different hydrographic regions (see Table 1)

wan suggests that the larvae of *T. j. formosana* are transported by the Kuroshio Current flowing along the eastern coastline of Taiwan in summer (see Lee & Chao 2003, Liang et al. 2003). The complete larval development period for *Tetraclita* spp. was ~14 d under laboratory conditions (Chan 2003) and the speed of the Kuroshio Current was estimated to be ~6.4 km h^{-1} (Makoto 1989). As a result, *Tetraclita* spp. larvae could probably travel at least 2000 km (i.e. 14 d × 6.4 km × 24 h) in 14 d when transported by the Kuroshio Current. This geographical distance covers the region from Taiwan to Wakayama in Honshu, Japan (which matched with the geographical distribution of *T. kuroshioensis* in the present study). *T. j. formosana* was absent from the South China Sea and the Taiwan Strait probably because these waters are not affected by the Kuroshio Current during summer (see Jan et al. 2002). *T. j. japonica* had high abundance at Honshu, Hong Kong and Xiamen. The low abundance of *T. j. japonica* in Taiwan and Okinawa, which is in between Japan, Hong Kong and Xiamen, suggests that there may be a physical and genetic boundary between the northern and southern populations in the Pacific Ocean. The larval pool of *T. j. japonica* in Japan may be associated with the Kuroshio Current, whilst the larval pool in South China is associated with the South China Sea Surface Current. *T. squamosa* had high abundance along the southern mainland China coast, suggesting that the larval pools are related to the South China Sea Surface Currents (Jan et al. 2002, Lee & Chao 2003).

Vertical zonation and abundance

Variation in the vertical zonation patterns of *Tetraclita* spp. along the latitudinal gradient from Japan to Hong Kong could result from the interactions of the rock types, climate and post-settlement mortality (Raimondi 1988, Miron et al. 1999). The rock types in Taiwan, Okinawa and Japan are mainly fine, porous volcanic and sedimentary, whilst common rock types of Hong Kong shores are relatively smooth, hard granite and volcanic. During the summer, rock surface temperature in Japan, Taiwan and Okinawa may be lower than that on the granite and volcanic rocks in Hong Kong and Xiamen (rock surface temperature in summer in Hong Kong can reach up to 50°C when emersed and is similar to seawater temperature when submerged; Chan & Williams 2003, Chan

Table 3. *Tetraclita* spp. Global test (showing R; $p < 0.001$) and SIMPER analysis for pairwise comparison of species composition (%) between hydrographic regions (see Table 1 for site names). Diagnostic species which contributed >25% difference between regions are shown with their percentage contribution. TK: *T. kuroshioensis*; TJJ: *T. japonica japonica*; TJF: *T. j. formosana*; TS: *T. squamosa*

	TK	TJJ	TJF	TS	R
Okinawa					
Honshu	35	57	–	–	1
East Taiwan	40	59	–	–	0.93
South China	–	43	–	29	0.99
North Taiwan					
Honshu	32	41	–	–	0.97
Okinawa	33	–	58	–	0.45
East Taiwan	55	–	37	–	0.531
South China	28	33	–	30	0.99
East Taiwan					
Honshu	–	58	33	–	0.99
Okinawa	40	–	59	–	0.93
South China	–	39	30	26	0.99
South China					
Honshu	–	31	–	65	0.74
Okinawa	–	43	–	29	0.99
East Taiwan	–	39	30	26	0.99

et al. 2006). In Hong Kong, the vertical settlement ranges of *T. squa mosa* and *T. japonica japonica* are similar, and spat settled in the same vertical range. In the mid shore, *T. squamosa* settlers suffered higher mortality compared with *T. j. japonica* (Chan & Williams 2003), thus confining them to a lower shore region in Hong Kong. In northern geographical locations, *T. kuroshioensis*, *T. j. japonica* and *T. j. formosana*, which settled on the mid shores, can probably still survive, resulting in a mixture of *Tetraclita* species in the same tidal zone. Mortality could occur very early after settlement, when the settlers are still in cyprid stage (Glenner & Høeg 1993) and such mortality could vary among different barnacle species. Settlement pattern of barnacles could be affected by the variation in biofilm assemblages (Qian et al. 2003). *Balanus amphitrite*, for example, settles intensely on areas which contain biofilms that grow on the mid shores of the intertidal region (Qian et al. 2003, Thiyagarajan et al. 2006). Variation in biofilm assemblage among geographical regions could be another factor affecting the geographical variation in zonation pattern of *Tetraclita* spp. Further studies should compare the settlement patterns and post-settlement mortality of *Tetraclita* spp. among the geographical regions to test whether

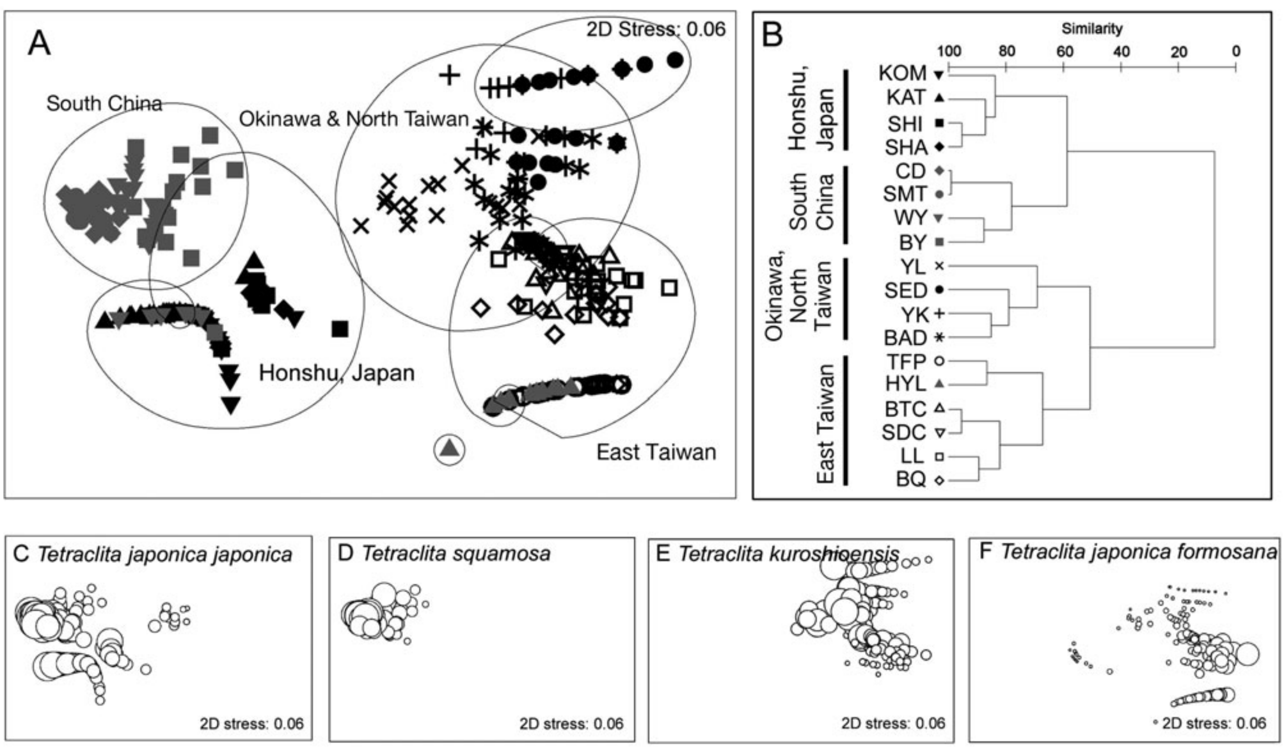

Fig. 5. *Tetraclita* spp. Multivariate analyses of the distribution pattern in the NW Pacific and SE Asian waters: (A) nMDS plot, (B) similarity tree by cluster analysis, (C–F) bubble plots of abundance patterns for each *Tetraclita* species. (LY data were excluded from the analysis due to the low abundance of barnacles). See Table 1 for location and definition of sites

Tetraclita spp. in northern locations suffer lower settlement mortality, which results in a mixture of species at the same tidal levels.

The percentage cover of *Tetraclita* spp. on the Pacific coast (Japan, Okinawa and Taiwan) is lower than the populations on the mainland China coast (Hong Kong and Xiamen). Variation in barnacle density among locations is related to upwelling and variation in predation pressure. Strong upwelling in summer months has been reported to exist along the coastline of Izu Peninsula in Japan, the northeastern coastline of Taiwan and the Okinawa Island (Ishizaka et al. 1992, Ito et al. 1995, Lee & Chao 2003) (Fig. 2B). Upwelling can carry larvae out to the open ocean and thereby reduce recruitment density and frequency (Connolly et al. 2001). Lower barnacle density on the coastline in Japan, Taiwan and Okinawa may result from the effect of upwelling (Ito et al. 1995).

Variation in barnacle abundance between geographical locations can also result from differences in predation pressures. In Hong Kong and Xiamen the major predators in the intertidal zone are the muricid gastropods *Thais clavigera* and *Morula musiva* (Morton & Morton 1983). On the NW Pacific coast, the predators in the intertidal zone include the muricid gastropods (Utinomi 1971) and, with high diversity and abundance, the porcupine fish *Diodon* spp., which can feed intensely on barnacles (Masuda et al. 1984). The lower abundance of *Tetraclita* spp. in the Pacific shores compared to the mainland China coast may result from variation in predation pressure along the latitudes.

The intertidal acorn barnacle *Tetraclita* spp. has a high diversity of species in the waters of the NW Pacific and South China. The present study indicates that the distribution of *Tetraclita* spp. varies along the latitudes, and similarity of species assemblages can be grouped into 4 geographical regions, including the Pacific coast of Japan, North Taiwan and Okinawa, East Taiwan, and South China waters. Such geographical distribution of *Tetraclita* spp. could be influenced by the oceanographic currents (Kuroshio Current and the South China Sea Surface Current) which drive the larval pools into these 4 distinct geographical regions. Variation in abundance and zonation of *Tetraclita* spp. along the latitudes may be a result of interactions of upwelling patterns, climate and settlement biology. Further studies should focus on the population genetics and phylogeography of *Tetraclita* spp. in the Asian region to reveal the connections among the geographical populations.

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