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Multiple Environmental Factors Increase the Niche Complexity and Species Diversity of Brachyuran Crabs in an Intertidal Algal Reef Ecosystem in Northwestern Taiwan

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Algal reefs are one of the world's rare and poorly understood ecosystems. They are mainly distributed in the Mediterranean Sea, but one notable exception—an intertidal algal reef ecosystem in northwestern Taiwan—stretches for 27 km along the coast of Taoyuan, making it probably the largest algal reef coast found in shallow water. Despite the reef's rarity and striking characteristics, the coastal land that it is part of has undergone a series of developments and is now surrounded by industrial parks. Brachyuran crabs are one of the most abundant and visible groups of organisms in the intertidal zone. In the present study, we investigated the brachyuran crab community in this reef to provide a more detailed record of brachyuran crab species compositions in this intertidal algal reef ecosystem and illustrate the characteristics of this understudied ecosystem by comparing its species diversity and abundance with three natural variables—sampling time, tidal level, and season—in a wildlife refuge and north of the refuge. Two methods were used in the study: a qualitative method (to determine the species richness) and a quantitative method (to estimate the population density). We identified a total of 52 brachyuran species from 13 families in the habitats. The highest species richness was found in Datan G2, north of the wildlife refuge. The crab species composition in this algal reef is different from its compositions in coral and rocky reefs. Our analysis indicated that the species abundance is affected by multiple factors, and a single investigation is not enough to reflect the true population density of brachyuran crabs on this reef. In addition, we found that the sites outside the wildlife refuge were in much better condition than those in the wildlife refuge, and should therefore be included in the wildlife refuge. In particular, Datan, located north of the wildlife refuge, had the highest species richness, and the area's species composition was different from that of the nearby wildlife refuge. Thus, we strongly recommend that a) the Datan area be protected to maintain this high crab diversity and b) further research be performed to better understand brachyuran crab biology in the intertidal algal reef ecosystem.

Key words: Algal reef ecosystem, Anthropogenic disturbance, Brachyuran crabs, Coralligenous reef, Taoyuan algal reef.

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BACKGROUND

There are over 7,400 brachyuran crab species in the world; they are found in a diversity of habitats, from 6,000 meters under the sea to high mountains, and are particularly dominant in intertidal and estuarine habitats (Ng et al. 2008). Crabs play many roles in variously biological processes, such as causing bioturbation (Smith et al. 1991), maintaining and creating the microhabitats of biofilm (El-Hacen et al. 2019), supplementing nutrients (Saintilan and Mazumder 2017), and increasing local organic matter contributing to nutrient cycling and detrital decomposition (Botto et al. 2006). Their relatively sessile habits act as sensitive indicators for the anthropogenetic effects of long-term water and sediment pollution, such as organic enrichment (Lee 1998; Culhane et al. 2019) and tourism pressure (Hereward et al. 2017).

Studies are increasingly showing the important roles of crab species in habitats (Lee 1998; Boudreau and Worm 2012; Hull and Bourdeau 2017; El-Hacen et al. 2019). Coastal and estuarine regions contain habitats such as sandy beaches, mud flats, mangroves, rocky reefs, and coral reefs. The compositions of crab species in most of them have been surveyed (Ngo-Massou et al. 2018; Koyama et al. 2020; Servis et al. 2020), but only a few studies have focused on the intertidal algal reef. The algal reef ecosystem is one of the rarest ecosystems in the world (Liou et al. 2017). Algal reefs are constructed mainly of crustose coralline algae (CCA), unlike coral reefs, in which CCA is less prevalent and its calcareous deposit can cement corals and debris together (Wray 1998; Littler and Littler 2013). Algal reefs form in layers, and this creates numerous pores and crevices that provide many microhabitat types and lead to high biodiversity (Yu et al. 2020).

The best-known and most widely distributed algal reef is 20 to 120 m below sea level along a 1,000-km coast of the Mediterranean Sea (Ballesteros 2006). Intertidal algal reefs, however, are rare. In 1986, Reineck and Chang first found a massive CCA reef in the tidal flat in northern Taiwan. The Taiwanese government created the Taoyuan Guan-Xin Algal Reefs Ecosystem Wildlife Refuge in the southern part of the Taoyuan algal reef in 2014, but this did little to raise public awareness about the ecosystem, as education around the refuge focused on how exceptional and fragile the reef is. A new port is currently under construction on the seaward side of Datan, north of the refuge, that threatens the reef. However, the extent to which the construction may harm the reef is unclear, as studies have only reported general descriptions or specific groups that inhabit this algal reef (Heard et al. 2021; Kuo et al. 2019 2020; Wong et al. 2021), and the information about its benthic fauna is limited to a guidebook of species compositions (Dai et al. 2009).

The intertidal algal reef ecosystem is comprised of a sandy beach in the upper tidal area and is located at the interface between land and sea (Dai et al., 2009; Liou, 2013). Just like the intertidal areas in other ecosystems, the reef's complex physical structure can affect the zonation of its resident benthic animals. In addition, animal zonation is driven by desiccation, salinity, wave action, temperature, and species interaction (Raffaelli and Hawkins 1996). Its resident animals, such as crabs, live within the ‘zone of comfort’ depending on prey avalibility and predation pressure (Branch 2001). Therefore, comprehensive research on species compositions in this habitat should involve various sampling methods and sampling times.

The aim of this study was to elucidate the brachyuran crab composition of this rare and understudied intertidal algal reef ecosystem using qualitative and quantitative methods. The qualitative method was used to record the crab species. The quantitative methods focused on the crab abundance in the algal reef habitat, and crabs were sampled based on combinations of three environmental variables. Through comparing the biodiversity among sites, we try to provide the status of sites in the refuge (Baosheng, Yongxing, and Yongan) and neighboring area (Baiyu, Datan G1, and Datan G2). We also sought to compare this habitat with other hard substrate habitats to better explain how this algal reef habitat is unique.

MATERIALS AND METHODS

Study site

This study was conducted on the Taoyuan algal reef along the coastline about 50 km from Taipei City (Fig. 1). The reef is 27 km long and a superreef. According to the definition by Riding (2002), a superreef is defined as an organic reef larger than 1000 meters long. The algal reef ecosystem comprises a crevice-abundant reef and sand habitat in the intertidal zone. Currently, the most healthy and unpolluted algal reefs are mainly found in the southern part of the coastline. In 2014, the southernmost part of the Taoyuan algal reef was designated the Taoyuan Guan-Xin Algal Reefs Ecosystem Wildlife Refuge, encompassing 315 hectares along 4.2 km of coastline. North of this wildlife refuge, the adjacent 3-km Datan algal reef is less known to the public because it is less accessible and was fragmented by the construction of the cooling system of the Datan Power Plant. In spite of the construction, the entire 7.2-km reef is relatively integrated and undisturbed.

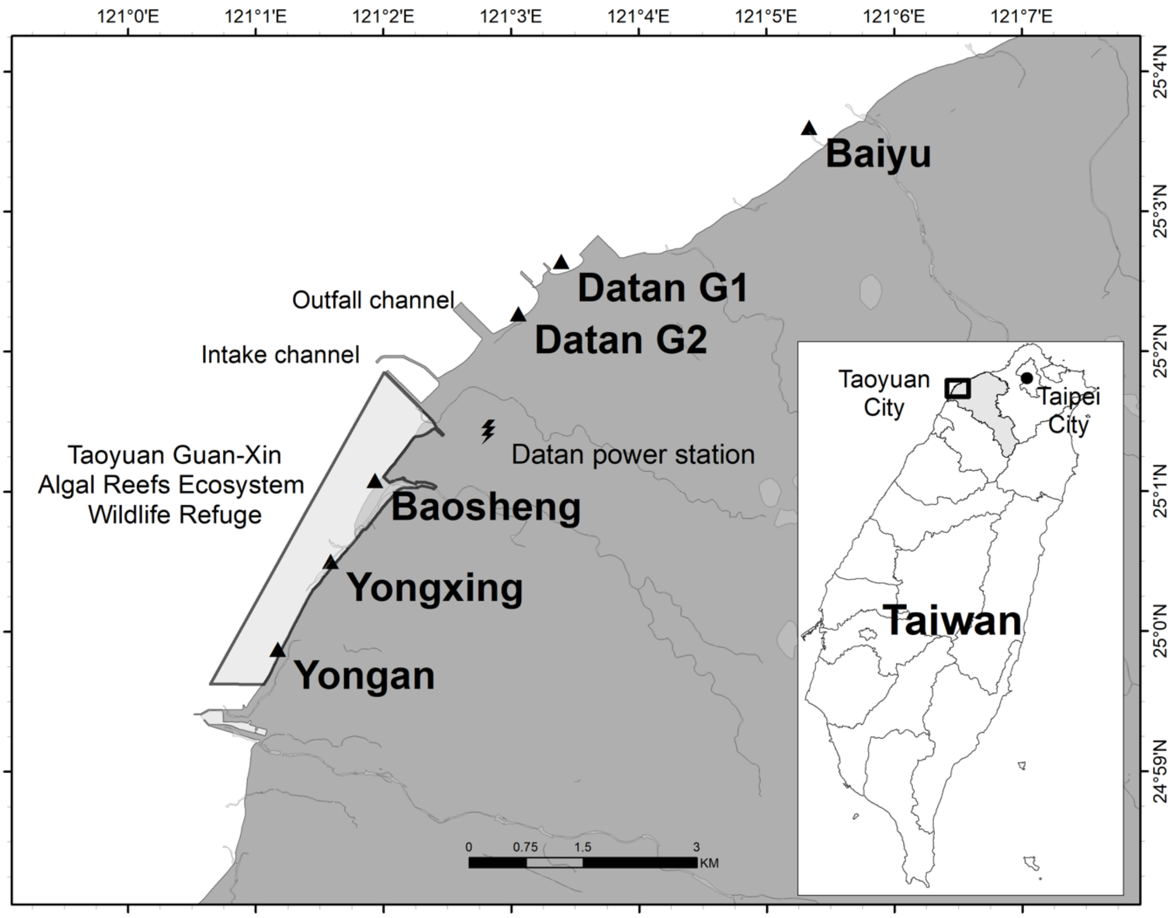

Fig. 1. The six study sites in the present study.

This study examined six sites (Fig. 1), three in the wildlife refuge—Baosheng, Yongxing, and Yongan—and three north of the wildlife refuge—Baiyu, Datan G1, and Datan G2. All the sites mainly comprise algal reef and sandy habitats in the intertidal zone, and the high tide zone to splash zone contain sandy flats or dunes. The other habitats—such as mudflats, mangroves, coastal shrubs, and coastal forests—were found in Baiyu, Datan G2, and Yongxing, which are located at a creek mouth. In the intertidal zone of Yongxing and Yongan, there is some pebble mixing with the algal reef. The two Datan sites are mainly surrounded by residue from the temporal port of a former industrial park building process and the water tunnel of the Datan Power Plant. The study sites displayed a mixed semidiurnal tide cycle. There are two high tide and two low tide a day and the tidal level between two high/low tide is different. The algal reef was exposed in the air twice a day. The tidal level of low tide is lower than -1 m on most days. This one-year study was conducted from March 2018 to February 2019.

The main study habitat was algal reef. However, there are other crab habitats at each study site. Hence, we used a qualitative method to investigate the species richness in all habitats of crabs to create a detailed record of brachyuran crab species compositions. For the more precise species abundance estimations in the algal reef habitat, the quantitative method was used.

The qualitative method for investigating crab species richness

We recorded crabs not only from the algal reef habitat, but also from mudflats, sandy flat, mangroves, coastal shrubs, and coastal forests. The same survey methods were used on each habitat type, and a similar amount of time was spent per unit area. We captured using by the following three methods: wandering crabs on the ground were hand-caught, individuals hidden in crevices were dug out, and crabs wandering during full tide were caught using overnight traps (opening diameter: 11 cm, trap length: 35 cm). Two to 10 individuals of each species were collected and kept in 70% ethanol solution. The approximate numbers of individuals of each species were ranked into three levels, 1) 1–10 individuals, 2) 11–100 individuals, and 3) >100 individuals.

The quantitative methods for estimating crab abundance

In each of the six sites, we set up two tidal plots at different tidal levels to determine crab abundance: one at the edge of the sand and reef, the other in the algal reef -1 m tidal level. The tidal level definitions were from the Central Weather Bureau according to the Taiwan Vertical Datum 2001 (TWVD). Sampling was conducted during the daytime and nighttime at ebb tide. We sampled each season (spring: March to May; summer: June to August; fall: September to November; winter: December to February) from March 2018 to February 2019 and used two methods to determine crab abundance according to carapace width (CW). First, for individuals with a CW larger than 10 mm (large crabs), we used the quadrat method to count the crabs within three random 1 × 1 m^2 quadrats in each plot. The second method was to count individuals with a CW smaller than 10 mm (small crabs). We used a core drill with a steel tube 11-cm in diameter and hammered to obtain algal reef cores 10 cm deep, with two replicates per plot. The reefs were fragmented into small pieces in the laboratory, and we collected the crabs from these pieces.

The sampling times for the qualitative and quantitative methods were in the daytime/nighttime at ebb tide. Sampling was performed five days per month and five to eight days per season for each method (Table S1). Individuals were identified to the species level based on their morphology (Huang and Yu 1997, Lee 2001; Dai et al., 2009; Lee et al., 2013; Li and Tseng 2015; Shih et al., 2015; Ng et al., 2017; Huang and Shih 2021). On the other hand, despite many guidebooks and taxonomic references about the identification, there could be wrong identification, especially for the smaller crabs. Hence, we kept the voucher specimens for the reexamination.

Data analyses

Data from the qualitative and quantitative methods were used to compare the differences in species compositions of the reef habitat across sites. The presence/absence data for the 18 species recorded at the reef were used to determine the local contribution to beta diversity, abbreviated as the LCBD index (Legendre and De Cáceres 2013). This index represents the local contribution to the overall beta diversity. Higher LCBD values means higher ecological uniqueness, which is based on environmental condition or community composition (Tonkin et al. 2016). The LCBD index was obtained (999 permutations) to identify the contribution of the sites to the overall beta diversity. Species richness was provided to test for significant differences across sites. Beta regression was used to test the relationship between LCBD and species richness. The similarities in species compositions across sites were examined by cluster analysis. Jaccard similarity distances were used to transform the data into presence/absence data to avoid sampling errors. The unweighted pairgroup method was applied using the arithmetic averages (UPGMA) method to cluster the data. The effects of season, site, sampling time, and tidal level on species abundance were examined by the permutation 4-way analysis of variance (5000 permutations). The Mann-Whitney U test, Kruskal-Wallis test, and pairwise permutation test were used to further analyze the differences in abundance from the significant factors, which were determined by PERMANOVA. The density data were present as mean ± standard deviation. The Jaccard similarity matrix was used to describe the species composition in three hard substrate habitats. The beta diversity analyses, cluster analysis, and PERMANOVA were conducted using the adespatial, vegan, and permuco packages in R language, respectively (v. 4.0.2; R CoreTeam, 2020).

RESULTS

Crab species richness

We recorded a total of 52 brachyuran species from 13 families in the Taoyuan algal reef (Table S2). Among them, the family Varunidae accounted for the most species (10), followed by Portunidae (9) and Ocypodidae (8).

Yongxing, in the middle of the wildlife refuge, had the highest species richness, with 36 species found. The four most abundant species were *Mictyris brevidactylus*, *Austruca lactea*, *Macrophthalmus banzai,* and *Pseudohelice subquadrata*. *Austruca lactea* inhabited sandy or muddy flats in the thin layer of mud that covers the reef substrate. The other sandy or muddy flat species, *Baruna sinensis*, was also found inhabiting the crevice of the algal reef in the river mouth. The second brachyuran hot spot was Datan G2, north of the wildlife refuge, and a total of 34 species were recorded there.

When only the species composition on the algal reef habitat was considered, the highest species richness among the six sites examined was in Datan G2 (north of the wildlife refuge), where

18 species were recorded, most of which were portunid crabs (Fig. 2). The second highest species richness was in Datan G1, with 13 species. Baosheng and Yongxing, in the wildlife refuge, had the lowest species richness, with only eight species recorded in each. Seven species were recorded exclusively in Datan G1 and G2 (*Atergatis integerrimus*, *Chlorodiella nigra*, *Charybdis orientalis*, *Portunus sanguinolentus*, *Epixanthus frontalis*, *Eriphia sebana,* and *Ozius rugulosus*).

Datan G2 had the highest LCBD index value, significantly higher than those of other sites ($p < 0.01$). The LCBD was significantly related to species richness (Pseudo $R^2 = 0.98$, $p < 0.05$), and Datan G2 had the highest ecological uniqueness when it came to the species compositions of all the studied crab sites (Fig. 3). Based on the cluster analysis, the crab species compositions in Datan G1 and G2 were more similar to each other than they were to the other four sites (Fig. 4).

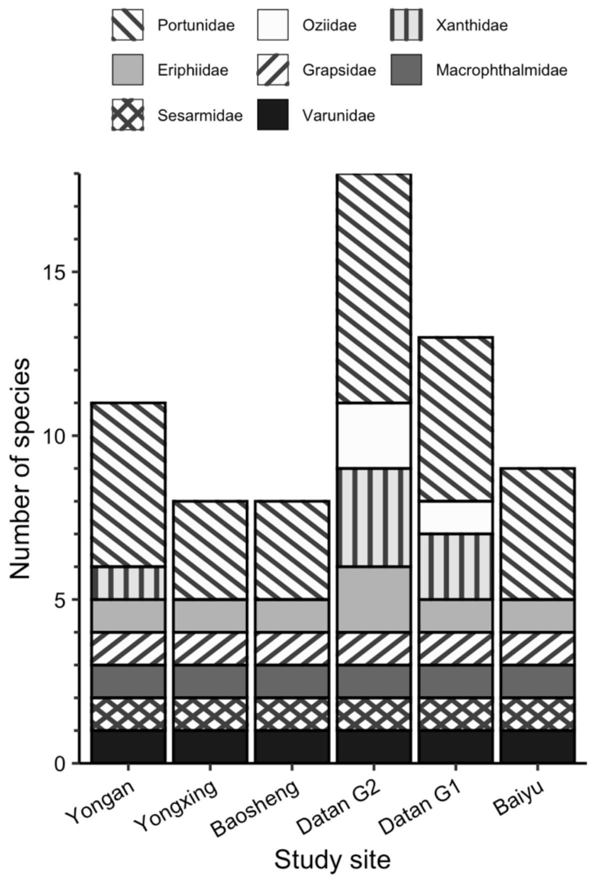

Fig. 2. The species compositions in all six study sites in the algal reef habitat. Each bar represents the total number of species recorded at each site. Family is the lowest taxonomic category in this figure.

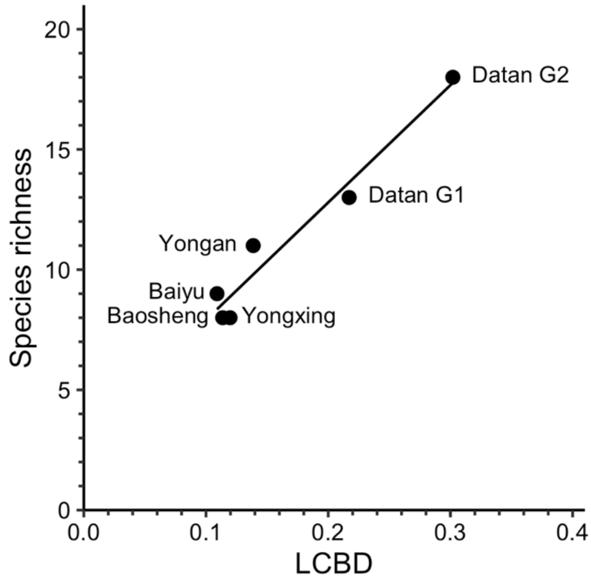

Fig. 3. Relationship between the species richness and local contribution to beta diversity (LCBD) indexes among the six sites in the algal reef habitat.

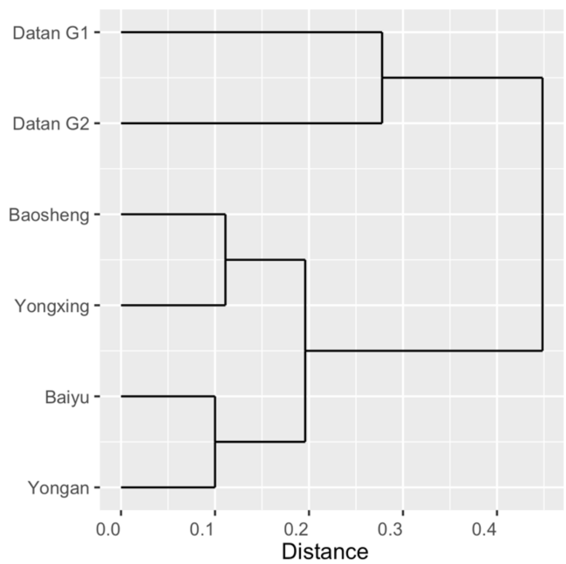

Fig. 4. The clade tree representing the similarities in species compositions among the six sites in the reef habitat.

Crab abundances

A total of 288 one-m^2 quadrates (6 sites × 2 tidal plots × 2 sampling times (day/night) × 4 seasons × 3 quadrats) were collected to count the large crabs and 192 cores (approximately 182,400 cm^3) (6 sites × 2 tidal plots × 2 sampling times (day/night) × 4 seasons × 2 core drills) were collected for the small crabs. However, almost half of the quadrates and cores did not contain any individuals (156 quadrates and 105 cores). A total of 286 and 201 large and small crabs were counted, respectively. The highest abundance of large individuals in a quadrate and small individuals in a core was seven and nine crabs, respectively.

Five large crab species were recorded: *Eriphia ferox*, *Eriocheir japonica*, *Metopograpsus thukuhar*, *Thalamita crenata,* and *Thalamita danae*. *Eriphia ferox* was the most abundant, with 185 individuals recoded (64.7% of the crabs at all six sites). The second most abundant species was *T. danae*, with 74 individuals recorded. The result of the permutational analysis of variance showed that abundance was significantly different among sites, seasons, sampling times, and tidal levels (Table 1). Almost all of the two- and three-factor interactions were significantly different. Hence, the six combinations of two-factor comparison were conducted to further explain the interactions. Four of the interactive combinations were not significant: 1) sites with tidal levels, 2) season with sites, 3) season with sampling times, and 4) season with tidal levels (Table S3). The two combinations that showed significant interactions were tidal level with sampling times and site with sampling times. Among the four factors studied, season was the only one that did not interact with any others, and the highest abundance was found in summer and fall (Fig. 5A). On the other hand, we found that the abundance was higher at the medium tidal level (Fig. 5B, density: 2.42 ± 1.59 per square meter) at night and in Datan G2 at night (Fig. 5C, density: 3.08 ± 1.5 per square meter).

Table 1. The results of permutational analysis of variance (PERMANOVA) on the abundance of crabs with a carapace width larger than 10 mm. The independent variables are season (summer, fall, and winter in 2018; and spring in 2019), site (Yongan, Yongxing, Baosheng, Datan G2, Datan G1, and Baiyu), sampling time (daytime and night), and tidal level (the edge between sand and reef, and the algal reef 1 m below sea level)

	d.f.	SS	F	parametric P	permutation P
Season (Se)	3	33.71	38.52	< 0.01	< 0.01
Site (Si)	5	55.40	37.99	< 0.01	< 0.01
Sampling Time (ST)	1	206.72	708.76	< 0.01	< 0.01
Tidal Level (TL)	1	26.89	92.19	< 0.01	< 0.01
Se × Si	15	20.04	4.58	< 0.01	< 0.01
Se × ST	3	11.44	13.08	< 0.01	< 0.01
Si × ST	5	31.86	21.85	< 0.01	< 0.01
Se × TL	3	2.72	3.11	0.03	0.03
Si × TL	5	7.19	4.93	< 0.01	< 0.01

ST × TL	1	21.13	72.43	< 0.01	< 0.01
Se × Si × ST	15	22.14	5.06	< 0.01	< 0.01
Se × Si × TL	15	14.36	3.28	< 0.01	< 0.01
Se × ST × TL	3	1.15	1.32	0.27	0.26
Si × ST × TL	5	6.63	4.54	< 0.01	< 0.01
Se × Si × ST × TL	15	18.60	4.25	< 0.01	< 0.01
Residuals	192	56			

We recorded six species of small crab (CW smaller than 10 mm) from the core sampling: *Chaenostoma orientale*, *Eriphia ferox*, *Gaetice depressus*, *Metopograpsus thukuhar*, *Nanosesarma minutum,* and *Leptodius affinis*. *Nanosasema minutum* was the most abundant species, both overall (159 individuals collected; 79.1% of the crabs at all six sites) and at each site. The second most abundant species was *L. affinis*, with 25 individuals recorded. The results of the permutational analysis of variance showed that abundance was significantly affected by site and season (Table 2). Two combinations had significant interactions: 1) site with season and 2) season and sampling times with tidal level. Further analysis of pairwise permutation tests showed that two factors had a significant effect on abundance: site and season (Table S4). Baosheng (density: 1.91 ± 2.43 per core) and Datan G2 (density: 1.72 ± 2.02 per core) had the highest abundance of the six sites (Fig. 6A). The most active seasons were summer and fall (Fig. 6B).

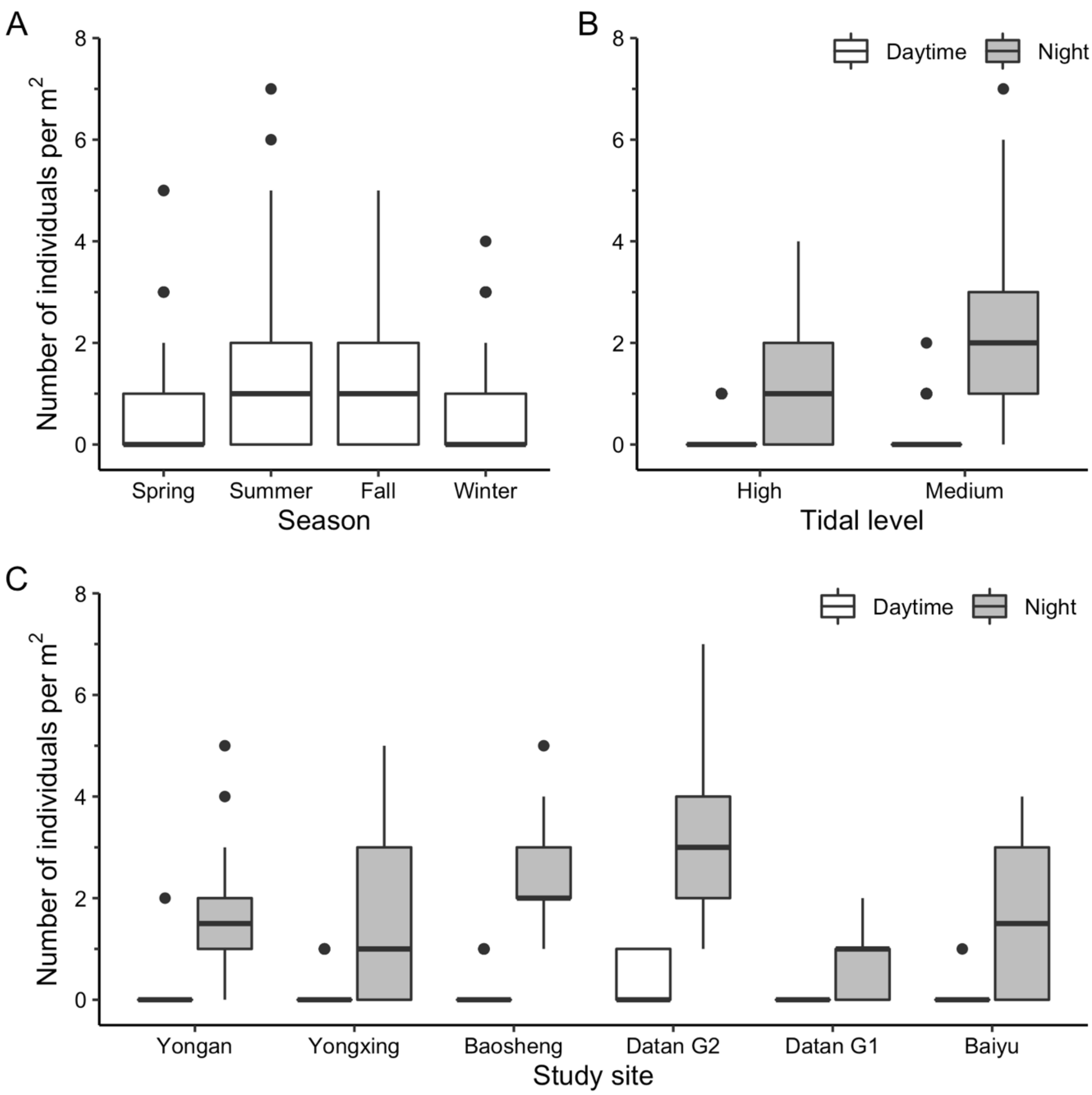

Fig. 5. The box plot of abundance of all crab species with carapace width larger than 10 mm for three factors: A: season; B: tidal and sampling time; C: study site and sampling time. The gray bar is daytime; the dark gray bar is night. The high tidal level is the edge between the sand and reef; the medium tidal level is at the algal reef 1 m below sea level.

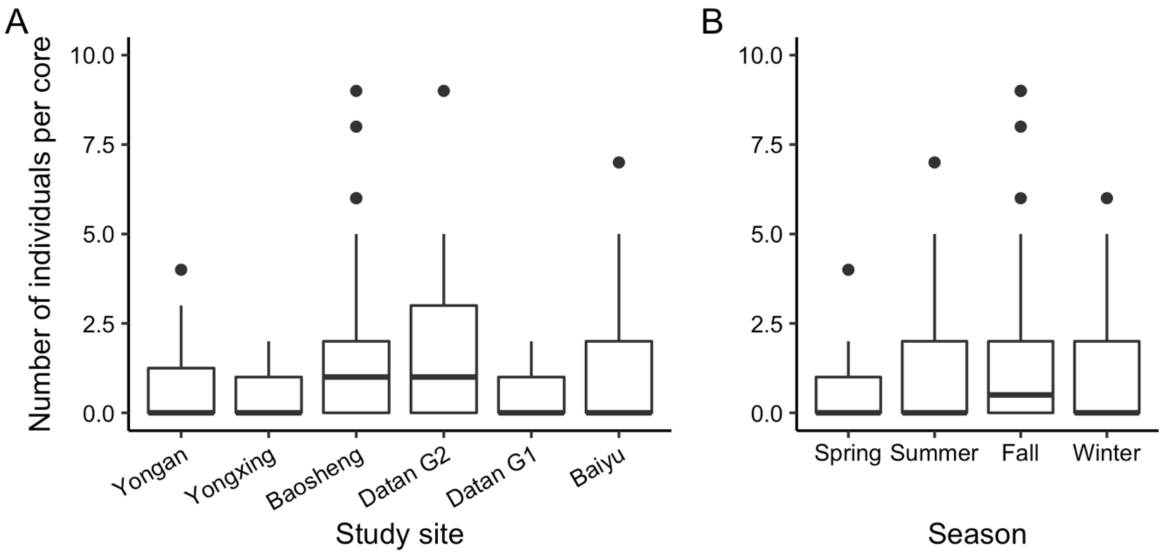

Fig. 6. The box plot of abundance of all crab species with a carapace width smaller than 10 mm across the six sites (A) and seasons (B) in the reef habitat. The core volumes are 950 cm^3.

Table 2. The results of permutational analysis of variance (PERMANOVA) on the abundance of crabs with a carapace width smaller than 10 mm. The independent variables are season (summer, fall, and winter in 2018, and spring in 2019), site (Yongan, Yongxing, Baosheng, Datan G2, Datan G1, and Baiyu), sampling time (daytime and night), and tidal level (the edge between sand and reef, and the algal reef 1 m below sea level)

	df	SS	F	parametric P	permutation P
Season (Se)	3	31.68	5.35	< 0.01	< 0.01
Site (Si)	5	69.61	7.05	< 0.01	< 0.01
Sampling Time (ST)	1	7.13	3.61	0.06	0.06
Tidal Level (TL)	1	2.30	1.16	0.28	0.28
Se × Si	15	56.66	1.91	0.03	0.03
Se × ST	3	0.89	0.15	0.93	0.93
Si × ST	5	12.03	1.22	0.31	0.31
Se × TL	3	1.89	0.32	0.81	0.82
Si × TL	5	6.98	0.71	0.62	0.62
ST × TL	1	4.38	2.22	0.14	0.13
Se × Si × ST	15	50.33	1.70	0.06	0.07
Se × Si × TL	15	40.70	1.37	0.18	0.18
Se × ST × TL	3	22.56	3.81	0.01	0.01
Si × ST × TL	5	13.28	1.35	0.25	0.26
Se × Si × ST × TL	15	32.66	1.10	0.36	0.37
Residuals	96	189.5			

DISCUSSION

Brachyuran crab studies in the algal reef ecosystem

The present study is the most detailed record of brachyuran crab species compositions in the intertidal algal reef ecosystem in northwestern Taiwan. Furthermore, we surveyed the adjacent habitats to compare them with previous studies. A total of 52 crab species were recorded based on both qualitative and quantitative data at the six sites on the Taoyuan coastline (Table S2). Among these, 18 were from the algal reef habitat alone. The most abundant species were portunid crabs. On the contrary, the best-known algal reef (coralligenous habitat) is in the Mediterranean Sea; it is mostly distributed at the deep sea level (20–140 m deep) and could be a superreef based on the criteria of Riding (2002). Numerous bryozoans on the surface of the reef (such as corals and sponges) and crevices inside the reef create micro habitats for biota such as decapods (Ballesteros 2006). However, due to its depth and habitat complexity, the reef could be hiding organisms that are yet to be recorded. Bakir and Katagan (2005) investigated the crustacean diversity of the algal reef (40-65 m deep) in Turkey and found 17 crab species. Another study reported 10 crab species on the algal reef (35 m deep) in Italy (Bedini et al. 2014). The crabs were mostly members of Dorippidae, Majidae, and Pilumnidae based on the depth of their habitats. On the other hand, most studies of the algal reef in Brazil and Norway were related to the coralline algae biology and descriptions of its ecological structure (Freiwald and Henrich 1994; Villas Bôas et al. 2005). Hence, no study has been conducted at the same depth and latitude as the Taiwan system.

Dai et al. (2009) provided the first survey of the Taoyuan algal reef. In their handbook for ecological tours, they outlined the geology of the algal reef and how it was formed; however, only 11 crab species were recorded in this survey (Table S5). Later, in 2013, 39 brachyuran species were recorded by Liou (2013) (Table S5). These two ecological handbooks showed the crab composition not only from algal reef habitat, but from other habitats such as sandy flat, mudflat, and coastal forest. Hence, in the present study, we applied various methods to collect crabs during the daytime and nighttime for all four seasons in all habitats and found 24 species that had not previously been recorded. Nine species were shared among these three studies (Table S5). However, 11 species reported from the above two studies were not found in the present study. *Thalamita picta* is one (Dai et al., 2009; Liou, 2013). The other 10 species belong to Grapsidae, Ocypodidae, Plagusiidae, Portunidae, and Xanthidae and were found by Liou (2013). In total, these three studies recorded 64 brachyuran species and provide a thorough list of brachyuran species in the Taoyuan algal reef ecosystem.

Examining the species that only inhabit the algal reef habitat, these three studies record a total of 29 species labeled as reef in the habitat type column in Table S5. The present study found 18 such species, seven of which were not found before. In addition, this is the second record that *Eriphia sebana* coexists with *E. ferox* (the first being Chen (2015)). However, only two individuals of *E. sebana* were observed at Datan G2 during the study. Despite this, the present study did not find 12 species recorded in the previous studies. On the contrary, our study found more species in the other habitats (such as sandy beach, mudflat, and coastal forest) than did Liou (2013).

Overall, these three studies (Dai et al, 2009; Liou, 2013; this study) showed different crab compositions across the years 2009, 2013, and 2018. The species richness increased with study effort. This could be because a) the species sampled did not reach its climax number of species and b) the anthropogenic effect may have changed the local condition during the past 10 years. The high habitat complexity makes sampling difficult in the algal reef habitat. Anthropogenic effects, such as heavy metal pollution, could also affect the species composition in the area (Liou, 2017).

Species compositions in the different algal reef habitats and limitations of our methods

The algal reef is made of hard substrate, and its formation process gives the habitat a different character from coral and rocky reefs. The higher surface rugosity, fractal dimensions, and numerous crevices inside the algal reef create a complex and diverse structure. The coral reef also has a high habitat structure complexity. However, the turbid water means that few corals can reach this environment (Kleypas 1996). Therefore, we selected two habitats on Taiwan's coast to compare to our study, rocky reef (Chang 2008) and coral reef (Tseng 2015). We found that the species composition is very different from those in the coral and rocky reefs (Table 3). In coral reefs, the most abundant species are members of Portunidae, Xanthidae, and Grapsidae (Tseng 2015). The crab species composition in the algal reef is more similar to that in the rocky reef—*e.g.*, Eriphiidae, Grapsidae, and Portunidae (Chang 2008)—than to the coral reef.

Table 3. The similarity matrix among habitats

	Rocky reef *1	Coral reef *2
Coral reef	0.19	
This study	0.19	0.08

*1: Chang, 2008; *2 Tseng, 2015.

The species compositions in the two Datan sites (G1 and G2) are similar (Table 4). They also have both a higher crab species richness (Fig. 3) and higher abundance (Datan G2, Figs. 5C and 6A) than the other four sites, including the three sites in the wildlife refuge. This was also found for fish diversity on the reef, and both the crab and fish diversities may be explained by the area's high niche complexity. The Datan area has the highest fish diversity in the Taoyuan algal reef (Heard et al. 2021). In the stomatopod study, two new record species were found in Datan (Wong et al. 2021). Moreover, Datan is the important habitat for the critically-endangered caryophyllid coral *Polycyathus chaishanensis* (Kuo et al. 2020). We therefore suggest that the habitats in Datan, especially G2, are in better condition than those of the Taoyuan Guan-Xin Algal Reefs Ecosystem Wildlife Refuge.

The quantitative method shows that site, season, tidal level, and sampling time and their interactions significantly affect crab abundance (Tables 1 and 2). The various combinations of interactive effects among these environmental factors at each site are good evidence for niche complexity in the algal reef ecosystem. The crevice inside the algal reef is a complicated 3-dimensional structure. Algae could grow on the surface of the algal reef and micro-benthic invertebrates could inhabit the tiny cracks. The macro-benthic invertebrates, such as crabs, could easily feed inside the reef. On the other hand, the large crabs are generally most active at night. Based on our observations, the large crabs are more sensitive to moving objects than the small ones and will hide when an observer gets within 10 meters during the daytime, but at night they were easier to observe due to their weak night vision (Powers et al. 1991). Due to the various habits of crabs, we suggest that getting a better description of the status of the crab population in the algal reef requires multiple visits and sampling methods.

CONCLUSIONS

The present findings contribute to a better understanding of the brachyuran crab species composition in the algal reef ecosystem. We provide the most detailed data on crab compositions in this area to date. The species composition in the algal reef habitat is similar to that of the rocky reef. In addition, we found that the Datan area, which is outside the wildlife refuge, has both a similar crab species composition to that of the refuge and a higher species richness. This suggests that Datan also has the highest habitat niche complexity in the Taoyuan algal reef ecosystem. However, the results of the species richness data from this and previous studies show that some species remain unrecorded. Further research is needed on the population dynamics of various taxa to better describe this unique algal reef ecosystem.

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Supplementary Materials

Table S1. The sampling dates from the quantitative methods. (download)

Table S2. The relative species abundance across sites. (download)

Table S3. The results of pairwise permutational analysis of variance (PERMANOVA) on the abundance of crabs with a carapace width larger than 10 mm. (download)

Table S4. The results of pairwise permutational analysis of variance (PERMANOVA) on the abundance of crabs with a carapace width smaller than 10 mm. (download)

Table S5. Comparison of species occurrences among recent records. (download)