Trends of Freshwater Crabs and Habitats in Southern Taiwan after Typhoon Morakot

莫拉克颱風過後臺灣災區淡水蟹類及棲地之時序變化趨勢

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Abstract

Natural disasters can cause severe influences on the ecosystem through different spatial and temporal scales. Decades of forest fire researches have been conducted to understand the effects of natural disaster on the ecosystem. However, the effects of typhoon upon freshwater ecosystem remain unclear, and the difficulty is exacerbated by the impacts of global warming and climate change. Furthermore, freshwater crabs are perhaps in a much difficult situation because their most important biodiversity occurs in locations where the most destructive typhoons happen, but there is still no research focusing on it. Typhoon Morakot passed through Taiwan in August 2009, and the heavy rainfall brought by the typhoon resulted in serious floods, debris flows and landslides in southern Taiwan. From spring 2010 to summer 2013, we investigated the trends of freshwater crabs and their habitats after Typhoon Morakot using systematic sampling and analyzing methods for six individual and community indicators (body size, sex, maturity, community biodiversity, community abundance and community biomass). Our results revealed highly increasing community abundance and marginally increasing community biomass in freshwater crabs, which indicated that the numbers of freshwater crabs and their habitat resources were recovering after typhoon. Interestingly, the constraints of gradually ascending community biomass and drastically rising community abundance resulted in the“side-effect” of body size decline in freshwater crabs. To reduce extinction risks in a dramatically fluctuating environment, we surmise that freshwater crabs shift their adaptive strategy toward r-selected life history to benefit their reproductive success in face of extreme catastrophes like Typhoon Morakot.

摘　要

經由數十年森林火災相關研究瞭解，偶發性大天災常造成生態系於不同時空尺度的重大影響。但於現今全球暖化與氣候變遷影響加速下，卻少有研究探討漸趨惡化的颱風天災與淡水域生態系間相關效應，而特別針對最可能遭受颱風侵襲而喪失重要生物多樣性資源的淡水蟹類，至今仍無相關研究。臺灣於 2009 年 8 月遭遇莫拉克颱風襲擊，造成臺灣歷史上最嚴重的水患、土石流及山崩災情。本研究即於莫拉克颱風過後，運用系統性取樣 22 處災區研究樣站，除於 2010 年 1 月風災後初期調查淡水蟹類的基線資料外，並自 2011 年春季至 2013 年夏季期間每季持續進行調查淡水蟹類個體及群聚的 6 項相關指標（體型、性別、成熟、群聚生物多樣性、群聚豐富度及群聚生物量），用以分析其於風災後的時序變化趨勢。研究結果發現淡水蟹類群聚豐富度顯著上升與群聚生物量近顯著增加的趨勢，顯示風災後的淡水蟹類數量與其棲地資源正在恢復，另經由時間序列分析發現，受限於緩慢增加的群聚生物量與快速上升的群聚豐富度，造成淡水蟹類體型小型化的附帶效應。我們推測在極具破壞性的天災發生後，如同莫拉克颱風所造成的巨大災難，淡水蟹類可快速增加個體數量，主動調整適應策略朝向 r 型選汰生活史模式，藉以提高其子代於更趨劇烈變化環境中的存活機率。

Key words: freshwater crab, freshwater ecosystem, Typhoon Morakot, recovery

關鍵詞：淡水蟹類、淡水域生態系、莫拉克颱風、復原

Received: August 22, 2013　　Accepted: March 21, 2014

收件日期：2013 年 08 月 22 日　　接受日期：2014 年 03 月 21 日

Introduction

Natural disasters can affect ecosystems remarkably. Forest fire is one of the best studied topics in natural disasters. Fire regime is realized not only to play a crucial role in the forest ecosystem structure (Ahlgren and Ahlgren 1960; Agee 1996), but also to influence the forest ecosystem function via chemical and physical dynamics of the environment (Johnson and Miyanishi 2001). In addition, fire enhances transformation of forest ecosystem structure and function through space as well as time (Whelan 1995). Tropical cyclone, known as hurricane or typhoon by its originating location, is another important cause of nature disasters. Tropical cyclone effects on forest ecosystem are also well documented in the literature. It can acutely and dramatically affect forest populations (Horvitz *et al.* 1995), communities (Pascarella 1998) and ecosystems (Loope *et al.* 1994). For example, defoliation is the most common effect of tropical cyclone on forest structure, and typhoon strength accounts for 82% of the litter fall variation in Fushan Experimental Forest in Taiwan (Lin *et al.* 2003).

Tropical cyclone effects on distinct ecosystems such as forest and freshwater ecosystem, however, are not interchangeably applicable without supporting evidence. The relationship between tropical cyclone and freshwater ecosystem is still unclear, and this is made all the more difficult to understand due to the impacts of global warming and climate change. Ongoing global warming (IPCC 2007) can accelerate the happenings of more intense and frequent tropical cyclone (Emanuel 2005; Webster *et al.* 2005; Elsner *et al.* 2008), and the phenomenon will amplify the ecological impacts on freshwater ecosystem. Along with this impact, freshwater ecosystem is particularly vulnerable to climate change because of its isolation and fragmentation within a largely terrestrial landscape (Woodward *et al.* 2010). Thus, further research is needed to understand tropical cyclone effects on freshwater ecosystem to reduce the double threats.

Furthermore, freshwater crabs of the freshwater ecosystem are highly probable in a much difficult situation because their most important biodiversity occurs in locations where the most destructive tropical cyclones happen, but there is no research focusing on it. Asia, including Taiwan is the biodiversity global center and hotspot of freshwater crabs (Cumberlidge *et al.* 2009). As such, it has not only the most abundant but also the most endangered freshwater crab species in this area. At the same time, the highest number of tropical cyclones in the world are formed in western tropical Pacific Ocean (Chan *et al.* 2004), and their paths follow three general directions that majorly affect Southeast and East Asia (Elsner and Liu 2003) where the most important biodiversity of freshwater crabs occurs. Therefore, it becomes urgent to study the responses of freshwater crabs to tropical cyclone in order to determine if these catastrophic events would threaten the survival of freshwater crabs.

Typhoon Morakot, equivalent to category 1 on the Saffir-Simpson Hurricane Scale (Simpson and Riehl 1981), passed through Taiwan in August 2009, and it was the most devastating typhoon in Taiwan's historical records due to the tremendous amount of rainfall it brought from August 6 to 11. The extremely heavy rainfall induced lots of serious floods, debris flows and landslides in southern Taiwan in places where many unique freshwater crabs exist. Hence Typhoon Morakot might have rapidly increased the risk of extinction of freshwater crabs in Taiwan.

This study is the first research discussing the effects of typhoon on freshwater crabs. Using systematic sampling and analyzing methods for six individual and community indicators (body size, sex, maturity, community biodiversity, community abundance and community biomass) of freshwater crabs from spring 2010 to summer 2013, this study aimed to investigate the recovery trends of freshwater crabs and their habitats after Typhoon Morakot.

Materials and Methods

Study sites

Typhoon Morakot induced floods and debris flows in most major water systems in southern Taiwan. Our study sites were all selected in different affected water systems where crabs could be found alive or defunct. These sites were divided into three types according to different sampling methods (Fig. 1).

I. Historical Study Sites

Sites where crab surveys had been conducted in previous studies. First, Haiqian NO.2 Bridge, located in estuary of Zhongni Stream, Hengchun, Pingtung. Second, Maolin Suspension Bridge, located in northern upstream tributary of Gaoping River, Maolin, Kaohsiung. Third, Jixiang Bridge, located in upstream Gaoping River, Namaxia, Kaohsiung.

II. Monitoring study sites

Sites were selected by their unique freshwater crabs fauna and used to evaluate the species effect on crab indicators. First, South-Link Highway 458K, located in upstream Fenggang River, Shihzih, Pingtung. Second, Laiyi Village, located in upstream Linbian River, Laiyi, Pingtung. Third, Taiwu Village, located in upstream Donggang River, Taiwu, Pingtung. Fourth, Yila Waterfall, Yila Community and Wutai NO.2 Bridge, located in southern upstream tributary of Gaoping River, Wutai, Pingtung.

III. Other study sites

Sites were selected by their habitat difference and used to evaluate the habitat effect on crab indicators. First, CSIST Dormitory, located in downstream Xuhai River near estuary, Mudan, Pingtung. Second, Chunri Village, located in downstream Beishi River, Chunrih, Pingtung. Third, Liangshan Waterfall, located in upstream Donggang River, Majia, Pingtung. Fourth, Sandimen Bridge, located in southern upstream tributary of Gaoping River, Neipu, Pingtung. Fifth, Majia NO.3 Bridge, Majia NO.5 Bridge and Majia Waterfall, located in southern upstream tributary of Gaoping River, Majia, Pingtung. Sixth, Wutai Watersource, located in southern upstream tributary of Gaoping River, Wutai, Pingtung. Seventh, Guanshan NO.1 Bridge and NO.6 Bridge, located in upstream Gaoping River, Jiasian, Kaohsiung. Eighth, NO.15 Bridge, Minzu Bridge and Nacilan Bridge Upstream 1k, located in upstream Gaoping River, Namaxia, Kaohsiung.

Fig. 1. Geographic distributions of the study sites in this study. Study sites were distributed in different affected water systems in southern Taiwan after Typhoon Morakot and labeled as Historical, Monitoring and Other ones.

Study methods

We conducted surveys in study sites from spring 2010 to summer 2013 to collect freshwater crab data of six individual and community indicators. In each survey, we made exhaustive search but with least harm to collect crabs in 50 meters along riparian upstream from the fixed point of study sites and set six traps overnight. After identifying species and measuring the traits of carapace breadth, carapace length, wet weight, sex and maturity, the captured crabs were released to their native habitats, but ones with doubt in species identification were needed for confirmation in the laboratory. The data were transformed into individual Indicators (body size, sex and maturity) for each crab data and community Indicators (biodiversity, abundance and biomass) for each study site data. Habitat intactness and water quality of the study sites were also recorded for further study.

It is necessary to mention that community biomass of freshwater crabs, one of the community indicators, can indicate the status of the habitat resource. It can be illustrated by the hypothesis of habitat resource supply and consumption. Total resource consumption by all communities in the habitat is proportional to total resource supply of the habitat, and specific community accounts for particular ratio of total resource consumption. In addition, specific community biomass is proportional to its resource consumption because there is an allometric relationship between individual biomass and its resource consumption (Ernest and Brown 2001; Ernest *et al.* 2003, detailed discussion in the Results). Freshwater crabs, moreover, also comprise a large proportion of the overall biomass of all invertebrates in the tropical streams (Abdallah *et al.* 2004). It was supposed that these relationships would not change after Typhoon Morakot. Thus, the community biomass of freshwater crabs was taken as an indicator of the habitat resource for evaluating its recovery trend.

Data analysis

Individual indicators (body size, sex and maturity) and community indicators (biodiversity, abundance and biomass) of freshwater crabs were mainly analyzed in multiple linear and logistic regression models by JMP 9.0. Using six crab indicators as dependent variables (Y) and time series as independent variable (X), we could evaluate the time effect on crab indicators, and thus obtained the recovery trends of crab indicators after Typhoon Morakot. These factors are listed in Table 1.

Besides major independent variable (X) of time series, we also considered the influences of minor independent factors on crab indicators. These factors included seasons, species, habitat types, time series interaction with habitat types, reciprocal interactions among individual indicators and autoregression of community indicators, which are not further discussed in this study. By setting these minor factors as covariates in the multiple linear and logistic regression models to control their influences, we could confirm the true time effect on the six crab indicators.

If the potential time relationships among crab indicators (Y) exist, time series analysis of panel data is suggested for analyzing these reciprocal relationships. Panel Data Analysis (PDA) or time-series-cross-section (TSCS) data analysis is one of the most popular analyses in econometric research, and it has become popular in other research fields. The advantages principally lie in capacity for modeling cross-sectional and longitudinal (time series) data (Hsiao 2007). Our data of freshwater crab community indicators were fit for panel data analysis, and thus we attempted to progress the analysis in EView 7.2 for better understanding of the temporal relationship among crab indicators.

Table 1. The factors analyzed in multiple linear and logistic regression models in this study

Variables			Explanations
Y / X	Types	Name	
Dependent	**Individual Indicators**	**Carapace Breadth (CB)**	The widest distance from the opposite ends of anterolateral margins of a crab's carapace, measured in minimeter.
	Body Size traits	**Carapce Length (CL)**	The longest distance from the frontal margin to posterior of a crab's carapace, measured in minimeter.
		Weight (W)	The wet weight of a crab, measured in gram.
		Sex	Differentiate the male and female from the shape of the abdomen and/or gonopod.
		Maturity	Differentiate the adult and juvenile from the body size comparison with smallest hatching adult female of the same crab species.
	Community Indicators Biodiversity	**Shannon H'**	Habitat's biodiversity was measured through Shannon diversity index (H') in each habitat survey.
	Abundance	**Crab Individuals number (N)**	Habitat's abundance was measured through the counts of crab individuals in each habitat survey.
	Biomass	**Total Crab Weight (TW)**	Habitat's biomass was measured through the sum of total crab weights in each habitat survey.
Independent	**Trend**	**Time Series (TS)**	Time Series was sequentially coded from the first quarter after Typhoon Morakot. Surveys were taken quarterly to examine the trend.
Covariates[a]			The influences of seasons, species, habitat types, time series × habitat types, reciprocal interactions among individual indicators and autoregression of community indicators were controlled as covariates.

Note : a The effects of covariates were controlled in the multiple linear and logistic regression models, but they would not be further discussed in this study.

Results

Summaries of survey frequencies and crab data in each study site are listed in Table 2, and crab faunas are listed in Table 3.

Descriptive statistics of six indicators of freshwater crabs after Typhoon Morakot

The means ± SE of individual and community indicators of freshwater crabs were listed as follows: body size (CB: 18.356 ± 0.155 mm, n=2,797; CL: 15.365 ± 0.130 mm, n=2,797; W: 4.033 ± 0.103 g, n=2,792), sex (male: 55.3 %, female: 44.7 %, n=2,758), maturity (juvenile: 59.6 %, adult: 40.4 %, n=2,539), community biodiversity (Shannon H_e': 0.505 ± 0.036 , n=153), community abundance (N: 15.915 ± 1.234 , n=177) and community biomass (TW: 63.703 ± 6.363 g, n=177).

Time effects on six indicators of freshwater crabs after Typhoon Morakot (Table 4)

I. Individual indicators

Firstly, three body size traits of freshwater crabs, carapace breadth, carapace length and weight, were highly correlated (CB and CL: r_s=0.990, p<0.0001; CB and W: r_s=0.989, p<0.0001; CL and W: r_s=0.987, p<0.0001). It would be adequate for applying principal component analysis to acquire the single indicator representing three body size traits. Principal component 1 (PC1) accounted for the most variance (λ=2.882, variance %=96.078) and had the same pattern with three traits in multiple linear regressions. We used PC1 as the body size indicator in the analysis and found that body size was highly negatively influenced by the time series. Secondly, the time series had no effect on the likelihoods of sex and maturity of freshwater crabs.

II. Community Indicators

Firstly, the time series had no effect on the biodiversity (Shannon H’) of freshwater crab communities. Secondly, community abundance of freshwater crabs (N) was highly positively influenced and community biomass of freshwater crabs (TW) was marginally positively influenced by the time series.

Table 2. Survey frequencies and crab data among study sites in this study

Typhoon Morakot		Post - Typhoon													
Time / Year		2010				2011				2012				2013	
Season		Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer
Series		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Study sites															
Haiqian NO.2 Bridge	a									6	5	9	10	4	15
CSIST Dormitory	c						4		19	16	14	19	23	17	22
South-Link Highway 458K	b						15	17	24	20	30	34	55	55	45
Chunri Village	c					6			8	0	5	3	3	0	4
Laiyi Village	b	4				3	19	8	28	13	26	12	36	11	20
Taiwu Village	b	4				4	18	24	61	36	64	44	67	47	84
Liangshan Waterfall	c					3			36	29	20	18	15	29	26
Sandimen Bridge	c					11			23	11	13	27	16	12	19
Majia NO.3 Bridge	c					8			11	3	2	7	1	4	8
Majia NO.5 Bridge	c					1			9	3	10	16	14	21	9
Majia Waterfall	c					4			16	41	15	28	27	57	22
Yila Waterfall	b	8				11	7	12	19	12	8	13	30	54	15
Yila Community	b	3				4	9		22	17	13	6	0	////	2
Wutai NO.2 Bridge	b	12				3		4	5	3	////	8	8	13	11
Wutai Watersource	c						1		7	5	4	14	4	1	11
Maolin Suspension Bridge	a									0	0	0	0	0	0
Guanshan NO.1 Bridge	c					8			15	20	12	19	15	5	13
NO.6 Bridge	c					15			12	36	7	21	20	44	17
Jixiang Bridge	a									0	////	0	0	0	0
NO.15 Bridge	c								0	0	////	0	0	0	0
Minzu Bridge	c								0	17	////	0	1	2	1
Nacilan Bridge Upstream 1k	c					26			11	22	////	7	7	20	////

Notes：Blank rectangles denote no surveys. Rectangles with slash line denote unconducted surveys because tbese study sites were not accessible. Rectangles with gray background represent conducted surveys.

Number in rectangles denotes the crab data acquired in each survey.

[a] Historical study sites. [b] Monitoring study sites. [c] Other study sites.

Table 3. Data of freshwater crab species and individual numbers among study sites analyzed in this study

Study sites		Freshwater Crabs										Total
		C. rathbunae	*G. albogilva*	*G. caesia*	*G. ferruginea*	*G. lili*	*G. neipu*	*G. olea*	*G. shernshan*	*G. tawu*	*G. tsayae*	
Haiqian NO.2 Bridge	a	21	7	0	21	0	0	0	0	0	0	49
CSIST Dormitory	c	42	67	0	25	0	0	0	0	0	0	134
South-Link Highway 458K	b	223	0	0	0	0	0	0	0	72	0	295
Chunri Village	c	5	2	0	0	2	5	15	0	0	0	29
Laiyi Village	b	36	0	0	0	0	68	76	0	0	0	180
Taiwu Village	b	108	0	0	0	29	179	137	0	0	0	453
Liangshan Waterfall	c	18	0	0	0	2	93	63	0	0	0	176
Sandimen Bridge	c	60	0	0	0	47	5	20	0	0	0	132
Majia NO.3 Bridge	c	34	0	0	0	1	3	6	0	0	0	44
Majia NO.5 Bridge	c	57	0	0	0	26	0	0	0	0	0	83
Majia Waterfall	c	209	0	0	0	1	0	0	0	0	0	210
Yila Waterfall	b	164	0	0	0	0	0	0	25	0	0	189
Yila Community	b	0	0	0	0	0	0	0	76	0	0	76
Wutai NO.2 Bridge	b	67	0	0	0	0	0	0	0	0	0	67
Wutai Watersource	c	44	0	0	0	2	0	0	1	0	0	47
Maolin Suspension Bridge	a	0	0	0	0	0	0	0	0	0	0	0
Guanshan NO.1 Bridge	c	29	0	1	0	0	0	1	0	0	76	107
NO.6 Bridge	c	94	0	1	0	0	0	0	0	0	77	172
Jixiang Bridge	a	0	0	0	0	0	0	0	0	0	0	0
NO.15 Bridge	c	0	0	0	0	0	0	0	0	0	0	0
Minzu Bridge	c	2	0	0	0	0	0	0	0	0	19	21
Nacilan Bridge Upstream 1k	c	93	0	0	0	0	0	0	0	0	0	93
Total		1306	76	2	46	110	353	318	102	72	172	2557

Notes：[a] Historical study sites. [b] Monitoring study sites. [c] Other study sites.

Table 4. The effects of time on six crab individual and community indicators were analyzed in multiple linear and logistic regression models. Body size, community abundance and community biomass of freshwater crabs exhibited more dominant trends than other indicators after Typhoon Morakot

X variables	Individual indicators			Community indicator		
	Body size (Principal component 1, PC1) n=2509	**Sex** (log odds (Female / Male))[a] n=2509	**Maturity** (log odds (Juvenile/Adult))[a] n=2509	**Biodiversity** (Shannon H') n=110	**Abundance** (Total individual number, N) n=130	**Biomass** (Total crab weight, TW) n=130
Full model						
R^2adj	0.578	0.049	0.945	0.810	0.702	0.648
df	37	37	37	26	29	29
Time Series						
b ± SE	**-0.164 ±0.020**	0.036 ±0.040	-0.257 ±0.566	0.008 ±0.021	**3.876 ±0.938**	**9.242 ±5.043**
F Ratio / LR_X^2	**68.670**	0.835	0.198	0.123	**17.067**	**3.359**
*p*value	**<0.0001** ***	0.361	0.656	0.727	**<0.0001** ***	**0.070**

Notes: [a] General Equation of Multiple Logistic Regression： $G = \text{logit}(p_{event}) = \log(odds_{event}) = \log(\frac{p_{event}}{1-p_{event}}) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_i X_i + \varepsilon$

* p<0.05, ** p<0.01, *** p<0.001.

Panel data analysis of body size, community abundance and community biomass of freshwater crabs after Typhoon Morakot

The effects of time on freshwater crabs were dominant in trends of the three indicators, body size decline, community abundance and community biomass rise, from results of previous section. The relationships among body size, abundance and biomass can be illustrated by the equation of habitat resource supply and resource consumption by populations or communities (Ernest and Brown 2001; Ernest *et al.* 2003):

$$R \cong C_{total} = \sum_{i=1}^{n} C_i \qquad (1)$$

where R is the resource supply of the habitat, C_{total} is the resource consumption by all communities and C_i represents resource consumption by specific community. If we focus on crab community of the habitat, the resource consumed by crabs in a habitat can be expressed as:

$$C_i \cong aB_i = aN_i\overline{M}_i^{\,b} \qquad (2)$$

where B_i is the biomass of the crab community, N_i is the number of total individuals of the crab community (abundance), $\overline{M}_i$ is the mean body mass of the crab community (body size: mean weight), a is an allometric constant and b is an allometric exponent. If the typhoon effect will not alter the relationships in the equation 1 and 2, we believe that the community biomass of freshwater crabs can infer their habitat resource, and thus the recovery trend of habitat resource can be assessed by time pattern of crab community biomass.

In order to identify whether the trends of the three indicators resulted from reciprocal influences in equation 2, we further analyzed our data by Vector AutoRegression (VAR) Granger Causality Test of panel data analysis. This test can determine whether one time series data is useful in forecasting the others. Our results revealed that both biomass and abundance would granger cause body size of freshwater crab communities (Table 5).

Table 5. Vector AutoRegression (VAR) Granger Causality among body size, abundance and biomass of freshwater crab communities. Biomass and abundance would granger cause body size of freshwater crab communities

Indicators	**Body size (Mean weight, W)** n=24			**Abundance (Crab individuals number, N)** n=24			**Biomass (Total crab weight, TW)** n=24		
	df	χ^2	*p* value	*df*	χ^2	*p* value	*df*	χ^2	*p* value
Body size				6	2.045	0.915	6	1.889	0.930
Abundance	6	**12.791**	**0.046 ***				6	1.464	0.962
Biomass	6	**17.762**	**0.007 ****	6	0.907	0.989			

Notes: * p<0.05, ** p<0.01

Moreover, the VAR equation of crab body size could be expressed as:

$$W = -0.002\times N(-1) + 0.083\times N(-2) - 0.154\times N(-3)^{*} - 0.153\times N(-4) - 0.091\times N(-5) - 0.099\times N(-6) + 0.005\times TW(-1) + 0.006\times TW(-2) + 0.022\times TW(-3)^{*} + 0.005\times TW(-4) - 0.003\times TW(-5) + 0.026\times TW(-6) + 0.387\times W(-1) - 0.233\times W(-2) - 0.556\times W(-3) + 0.288\times W(-4) - 0.509\times W(-5) - 0.045\times W(-6) + 8.778$$

Five over six lag phases of abundances negatively affected body size, especially for most significant effect of lag 3 (asterisk labeled, χ_1^2= 4.434, *p*= 0.035). On the contrary, five over six lag phases of biomass positively affected body size, especially for most significant effect of lag 3 (asterisk labeled, χ_1^2= 4.943, *p*= 0.026).

In equation 2, our results supported the positive effect of biomass and negative effect of abundance on body size. According to the relative stable trend of biomass in result of Table 4, the former's drastically increasing abundance caused the latter rapidly decreasing body size (Fig. 2).

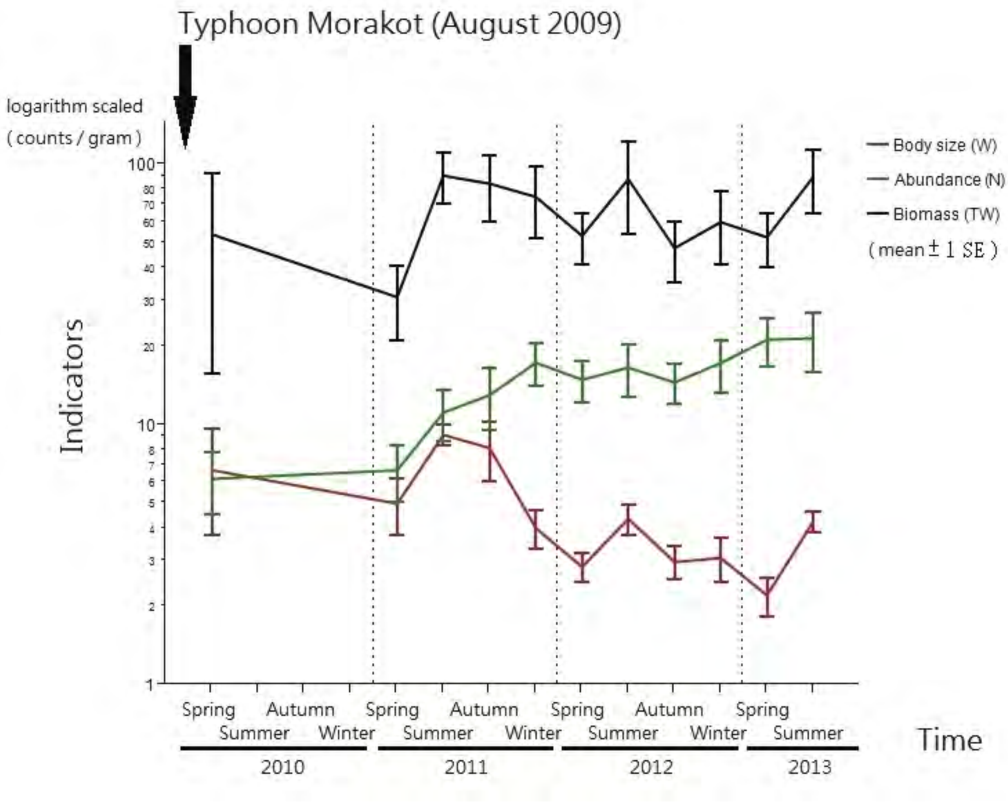

Fig. 2. Drastically rising community abundance (Crab individuals number, N) and gradually ascending community biomass (Total crab weight, TW) resulted in rapidly declining body size (mean weight, W) in freshwater crab communities.

The trend patterns of community abundance rise and body size decline of freshwater crabs were further checked by adding a square of time series as independent variable in their multiple linear regressions. The results revealed that these trends would not change through time (community abundance: $F_{1,99}$=0.323, *p*=0.571; body size: $F_{1,2471}$=1.598, *p*=0.206).

Discussion

This study is the first research focusing on the responses of freshwater crabs after typhoon, and we found drastically increasing community abundance and gradually increasing community biomass in freshwater crabs after Typhoon Morakot. It indicated that the numbers of freshwater crabs and their habitat resources were recovering in short-term study period after typhoon, but the recovery in freshwater crabs was much faster than the natural recovery of habitat resource. Despite lack of pre-typhoon information for comparison, the results are consistent with the findings of McMullen and Lytle (2012). They concluded that the abundance of freshwater invertebrate reduces at least one half after flood events, and the negative effect becomes greater with increasing relative flood magnitude. Freshwater invertebrates increase in numbers in short-term period after a flood event, but these patterns vary among different taxonomic groups. They propose the variation patterns of abundance recovery arising from different life history and lifespan of taxonomic groups.

The abundance increase was a result of the higher offspring surviving rate, which involves the adaptive strategies of species. In comparisons with marine crabs, freshwater crabs will undergo direct development in which the large, yolky eggs hatch directly into juvenile crabs and extend their parental cares (Yeo *et al.* 2008). Abbreviation of larval development and extension of parent care are key features of freshwater decapoda such as freshwater crabs, which tends to be k-selected life history with parental investments for best offspring surviving in particularly varied freshwater habitats (Vogt 2013).

Our results, however, revealed an average of 97.4% (3.876 * 4 / 15.915 , Table 4 and first part of the results) increase annually in abundance of freshwater crabs after Typhoon Morakot. We suggest adaptive strategy modification toward r selected life history in freshwater crabs to rapidly recover from the catastrophic damages and reduce the extinction risk in future extreme catastrophes. Typhoon Morakot, the most devastating typhoon in Taiwan's history, induced the most serious floods in affected water systems and caused the highest reduction of abundance in freshwater crabs. If more intense and frequent typhoons or other nature disasters happen due to the impacts of global warming and climate change, the occurrence of extreme catastrophes will be in a much higher condition. Under the usual extinction pressures caused by extreme catastrophes, it will be evolutionarily advantageous to shift to r-selected life history that maximizes reproductive potential in dramatically fluctuating environments.

Interestingly, our results also showed the trend pattern of body size decline in freshwater crabs, which resulted from the constraints of gradual ascending habitat resource and drastically rising abundance. The negative relationship between body size and abundance has been widely recognized in diverse taxa and is generated by the metabolic rate (White *et al.*

2007). The negative relationship between body size and abundance, which is acquired by tracking communities through time, is called cross-community scaling relationship (CCSR). When habitat resource availability is stable through time, body size directly determining abundance is the regular pattern in CCSR as discussed by White and his colleagues. But our results supported the inverse effects of rapidly increasing abundance on significantly decreasing body size in freshwater crabs. In order to reduce extinction risks of extreme catastrophes, freshwater crabs rapidly increased their abundance with relative stable habitat resource, and thus led to the"side-effect" of body size decline in short-term study period.

Although we found the trend pattern of their rapidly increasing numbers to counteract surviving threats, specific species such as *Geothelphusa shernshan* and *G. lili*, which were restrictedly distributed in affected area with small populations, still decreased in population abundance and suffered much higher extinction risks than the others after Typhoon Morakot (unpublished data).

We depicted the adaptation strategy and the different responses of freshwater crabs and their habitats in short-term study period after extreme catastrophes, but establishing long-term datasets are important for biodiversity research (Magurran *et al.* 2010). It is crucially important for the rare, endangered (Cumberlidge *et al.* 2009) and totally endemic (Shih and Ng 2011) resource of freshwater crabs in Taiwan. Long-term monitoring, which gauges not only the background data of specific species but also the variation patterns of the ecosystem, will provide critical information for conservation policy. We continue to monitor freshwater crabs and their habitats in important study sites to collect long-term datasets.

Acknowledgements

We deeply appreciate Ming-Hua Chen, Chien-Hsiang Liao, Chih-Hsin Tsai, Shu-Hui Ke, Jen-Chuan Chang, Chuan-I Chang and Li-Hsiang Chen for their help in field and laboratory works, and we are thankful of the referees for their helpful comments on the manuscript. This research was financially supported by Council of Agriculture of Taiwan.

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