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Population Fluctuation and Dispersion Patterns of Apple Snails, *Pomacea* spp. (Gastropoda: Ampullariidae) in a Rice Ecosystem

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ABSTRACT

A field study was conducted for two consecutive rice-growing seasons from August, 2013 to May, 2014 to understand the population dynamics of exotic apple snails, *Pomacea* spp. (Ampullariidae), as affected by ambient weather and aquatic weeds. A one-acre rice field was divided into four blocks and eight samples per block were taken using a 0.5x0.5m quadrat. Collected snails were recorded as numbers of egg clutches, juveniles, adult females and males. Average rainfall, relative humidity, temperature and water pH, along with number of aquatic weeds and seedlings, were also recorded. Results confirmed the presence of only *Pomacea maculata*. The numbers of egg clutches, juveniles and adults were relatively high during the off-season as compared to the main-season. Meanwhile, relative humidity had a significant effect on the number of egg clutches, and rainfall affected the densities of juveniles and adults. Among the weeds, *Limnocharis flava* (Alismataceae) had significant effect on the densities of different snail stages. Different stages showed uniform dispersion pattern during both seasons due presumably to continuous availability of water and abundant food. Thus, results obtained could be helpful in understanding the population dynamics of *P. maculata* and devising appropriate management strategy.

Keywords: Apple snail, rice, weeds, population fluctuation, dispersion, weather, *Pomacea*

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INTRODUCTION

Alien freshwater species often impose threats to lakes, streams, ponds, rivers and other freshwater bodies by altering their natural habitats and interacting with

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native fauna (Sala et al., 2000; Carpenter et al., 2011). Although the presence of such species can easily be recognised, quantifying and explaining their successful establishment along with their temporal population dynamics are difficult tasks (McCann, 2014). However, understanding patterns of population density dependence is important for forecasting the establishment and maintenance of an alien species population because some species have significant ability to regulate their growth and reproduction or both (Courchamp et al., 1999; Taylor & Hastings, 2005).

Invasive apple snails, *Pomacea* spp. (Ampullariidae), are one of the most successful invaders of freshwaters and this signifies their invasions because of the negative impacts on aquatic bodies and macrophytes, especially rice in Southeast Asia and taro in Hawaii and Florida in the continental USA (Hayes et al., 2008; Horgan et al., 2014). Apple snails were introduced in Malaysia around 1991 and spread to all rice growing areas of the country (Teo, 2003; Yahaya et al., 2006). Severe infestation of the snails can cause complete loss of rice crop in the field at an early growth of rice. In Malaysia, these snails are more devastating than in other countries due to the large scale direct seeding and flooded conditions in rice fields, either because of irrigation water or heavy rains. In case of severe snail damage, growers can lose more than RM425/hectare, either due to replanting of missing crop or application of control measures (Yahaya et al., 2006).

Many factors can contribute towards successful invasions of these *Pomacea* spp. in new regions such as high adaptability to stressful environmental conditions, high reproductive potential and lack of potential natural enemies (Cowie, 2002; Yusa et al., 2006). Considering the importance of *Pomacea* spp. as a major pest of rice, studies have been conducted on their population dynamics (Martin et al., 2001; Burlakova et al., 2010; Byers et al., 2013; Yoshida et al., 2013, 2014). However, studies on the population patterns of *Pomacea* spp., the role of environmental factors and rice weeds on their distribution in farmer-managed rice fields in the tropical regions are still lacking. Moreover, in currently available studies, none has focused on the dispersion patterns of *Pomacea* spp. in rice fields; an important factor in the application of any management strategy.

Therefore, considering the importance of *Pomacea* spp. to rice, this study was undertaken in a farmer-managed rice field to estimate the patterns of population fluctuation and dispersion patterns of different stages of *Pomacea* spp., as well as the effects of major aquatic-weeds and environmental factors on their population's fluctuation. The results obtained could be helpful in understanding the population dynamics of various life stages of *Pomacea* spp. in rice fields and the same could be helpful in the appropriate management of snails to reduce damages and improve rice productivity.

MATERIALS AND METHODS

Study site

The study was conducted at MARDI Rice Research Station (N 03^{o} 27.335' E101^{o} 09.541´) located in Tanjung Karang, Selangor, Malaysia, for two consecutive rice-growing seasons from August, 2013 to May, 2014. Off-season rice cultivation depends on the irrigation system, whereas during main-season, it is not totally dependent on irrigation system; instead it depends on monsoon rains. Moreover, in main-season, fields were properly levelled as compared to off-season one, hence ensuring proper management of water. Farmer applied molluscicide (Fentin acetate) twice; one week before transplanting and one week after transplanting to remove snails from the field. Note that other agronomic practices were the same during both seasons. Transplanted 21 days old seedlings of MR 263 variety were used by the farmer during both seasons.

Sampling Procedures

A rice field of 0.405 hectare size was selected and divided into four blocks in accordance to the layout of the field. Eight random samplings were taken from each block using a0.5x0.5m quadrat. The snails falling within each quadrat were carefully collected by hand or by using strainer to avoid any damage to the rice plants. The collected snails were differentiated into egg clutches, juveniles, adult females and males for individual species. The identification was done according to the external morphology of the apple snails as described by Marwato and Nur (2012), Cowie et al. (2006) and Hayes et al. (2012), whereas males and females were distinguished by observing the testicles through the translucent shell (Takeda, 1999) along with convex operculum for males and concave operculum for females (Estebenet et al., 2006). The snails with shell length of below 2 cm were considered as juveniles.

The number of rice seedlings and major aquatic weeds in each quadrat was also counted to ascertain their effects on the distribution of apple snails. HI1991300 pH Meter (HANNA Instruments, USA) was used to measure water pH in the field. The weather parameters of mean fortnightly temperature, relative humidity and average rainfall were obtained from the Pusat Pertanian station, *Tanjung Karang,* Metrological Department, Malaysia, to understand their influence on the distribution of snails at different sampling locations. Sampling was done from the first transplanting until harvesting of rice on a fortnightly basis, resulting in eight observations in one rice growing season.

Data Analysis

Population distribution of *Pomacea* spp. Student *t*-test at 0.05 level of probability was used to determine the significant difference in the population of individual stages of *Pomacea* spp. between two rice seasons using SAS version 9.2 (SAS Institute, 2009).

Population fluctuations of *Pomacea* spp. Population fluctuation of different stages of *Pomacea* spp. in each rice season was determined by plotting the mean number of each *Pomacea* spp. stage against the population of the mean number of rice seedlings, major aquatic weeds and weather parameters of mean fortnightly temperature, relative humidity, rainfall and water pH. Meanwhile, stepwise regression was used to determine the most significant factors among weather parameters and aquatic weeds and seedlings which contributed towards the population fluctuation of different stages of *Pomacea* spp.

Population dispersion of *Pomacea* spp. In order to calculate the dispersion patterns, the simplest method of the variance to mean ratio (s^2/m) was used as all other methods basically include mean and variance. For variance to mean ratio, the value of s^2/m < 1 indicates a uniform dispersion, while s^2/m = 1 indicates random dispersion and s^2/m > 1 indicates an aggregated dispersion (Southwood & Henderson, 2000).

Moreover, Taylor's power regression, $Log\ S^2 = log\ a + b\ log\ m$ (Taylor, 1961) and Iwao's patchiness regression, $m = \alpha + \beta x$ (Iwao, 1970) were also used to assess the level of aggregation by means of slope b and β. Taylor's law is an empirical law in ecology that relates the between-sample variance in density to the overall mean density of a sample of organisms in a study area. In Taylor's power regression or Iwao's patchiness regression, the slope values (b or β) when = 1, indicates a random dispersion. When it is > 1, it indicates aggregated dispersion; and when it is < 1, it indicates regular dispersion. In Iwao's patchiness regression, α indicates the tendency to crowding (positive) or repulsion (negative) (Arnaldo & Torres, 2005; Vinatier et al., 2011).

RESULTS

Population Abundance of *Pomacea* spp.

During the two rice seasons, all the apple snails collected were identified as *Pomacea maculata* (synonym: *Pomacea insularum*) (Horgan et al., 2014) based on their shell morphology. Population distribution of different stages illustrated that a significantly higher mean number of egg clutches per m^2 (1.1 ± 0.1) was collected during off-season as compared to main-season (0.69 ± 0.07) (P<0.001). Juvenile *P. maculata* population also indicated the same trend with significantly higher (P<0.001) population recorded during off-season (5.68 ± 0.69 per m^2) in comparison to main-season (1.08 ± 0.16 per m^2). The populations of females and males recorded during main-season were 0.49 ± 0.08 per m^2 and 0.22 ± 0.04 per m^2, respectively, and they increased significantly (P < 0.001) during off-season to 1.29 ± 0.08 per m^2 and 0.85 ± 0.08 per m^2, respectively (Figure 1).

Population Fluctuation of Different Stages of *P. maculata* against Weather Parameters, Rice Seedlings and Weeds

Figures 2 and 3 show the population fluctuation of different stages of *P. maculata* during the two rice seasons against weather parameters, rice seedlings and weeds. Based on the results, the population of eggs first appeared on 31 August, 2013 in main-season and showed a gradual rise through the

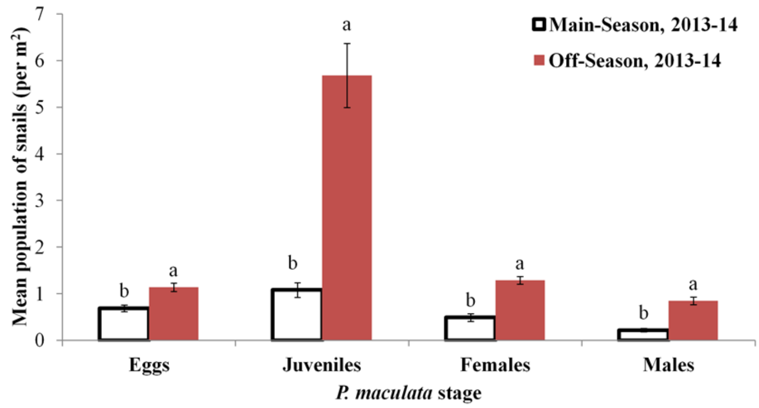

Figure 1. Mean number of different stages of *P. maculata* during two rice-growing seasons
*Means followed by the same letters against each stage are not significantly different (P < 0.001)

vegetative and reproductive growths of the rice plant. However, maximum population of egg clutches was recorded towards the maturity of rice in the month of November, 2013. During off-season, the population of egg clutches was recorded throughout the season. The egg clutch population gradually increased with rice growth with the maximum population recorded during March, 2014. Meanwhile, egg clutch population declined during the latter half of March, 2014, but it increased once again during the flowering and maturity period of rice from late April to May, 2014. The highest number of egg clutches during the two rice seasons was recorded at the ripening of rice in off-season during the month of May, 2014. The peak population of egg clutches throughout the two seasons seemed to correspond with the variation in the number of seedlings along with high relative humidity and low rainfall. Moreover, a relatively high population of aquatic weeds, particularly *Limnocharis flava* (Alismataceae), also corresponded with higher population of *P. maculata* egg clutches during the two rice seasons as females preferred these broad leaves for the oviposition. Results obtained for the population fluctuation of juvenile *P. maculata* showed that the first population of juveniles was recorded during active tillerring of rice at the end of September, 2013. The juvenile population showed a sharp rise afterwards during reproductive and ripening stages of rice in October and November, 2013. In contrast to main-season, the juvenile population was recorded since the off-season transplanting of rice. The population remained constant during the vegetative growth of the rice, i.e. during March and early April, 2014. A sharp rise in the juvenile population was observed afterwards with the peak population recorded during late April, 2014. However, the population declined slightly in May, 2014, but remained relatively high. No population of juveniles was recorded at the end of both rice-growing seasons due to the drainage of rice field for harvesting.

The results for population fluctuation of juveniles show that peak populations during two rice seasons are related to higher rainfall and relative humidity (Figure 2). Moreover, the peak juvenile populations during the two rice-growing seasons mainly correspond to relatively higher population of *L. flava*, along with *Monochoria vaginalis* (Pontederiaceae) and *Ischaemum rugosum* (Gramineae) (Figure 3). The population fluctuation of female *P. maculata* showed that the female population first appeared in the mid-October, 2013, i.e. in main-season. The population gradually increased through reproductive stage of rice with peak female population recorded at the ripening of rice in November, 2013. In contrast to main season, the female population was recorded with the transplanting of rice during off-season. The population then fluctuated throughout the rice-growing season, with a relatively higher population recorded at the end of February and April, and early May, 2014. During the two rice-growing seasons, no female population was recorded during harvesting of rice due to water removal from the field. Weekly rainfall appeared to contribute significantly towards the population development of females, along with higher weed populations of *L. flava* (Figures 2 and 3). Similar to the female population, the male population of *P. maculata* also appeared in the middle of October, 2013, in main-season. The male population showed a small rise with the maximum population of main-season recorded during the ripening of rice in the later half of November, 2013. However, the male population reappeared in the next season with the transplanting of rice. Their population then fluctuated throughout the remaining season with the peak populations recorded during late April and early May. Relatively higher rainfall and relative humidity seemed to contribute towards the higher male population in two rice seasons. Among weeds, *L. flava* showed significant contribution in the population fluctuation of male *P. maculata* in the two seasons, with *I. rugosum* might also have contributed in the higher male population during off-season (Figures 2 and 3).

Results showing stepwise regression of weather parameters, rice seedlings and weeds towards population fluctuation of different stages of *P. maculata* are given in Table 1. The results indicated that during both rice growing seasons, relative humidity showed significant effects on the population fluctuation of egg clutches (R^2= 0.106 and 0.239, respectively). Among the weeds, *L. flava* (R^2=0.392) and *I. rugosum* (R^2=0.0.70) showed effects on the population development of egg clutches during main and off-season, respectively. In addition, *Ischaemum rugosum* (R^2=0.174) and *L. flava* (R^2=0.326) were also the significant contributors in the population fluctuation of juveniles during main and off-seasons, whereas rainfall was the main weather parameter to influence juveniles' population during both seasons with R^2=0.241 and 0.111, respectively. During main-season, water pH (R^2=0.306) and *L. flava* (R^2=0.288) were the key contributing factors in the population fluctuation of

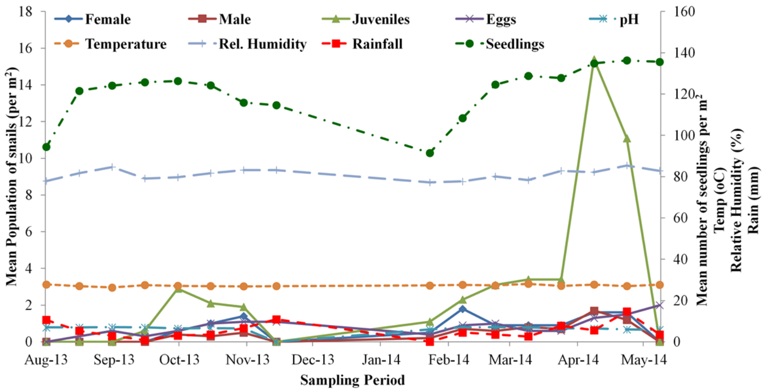

Figure 2. Population fluctuation of different stages of *P. maculata* against weather parameters and rice seedlings

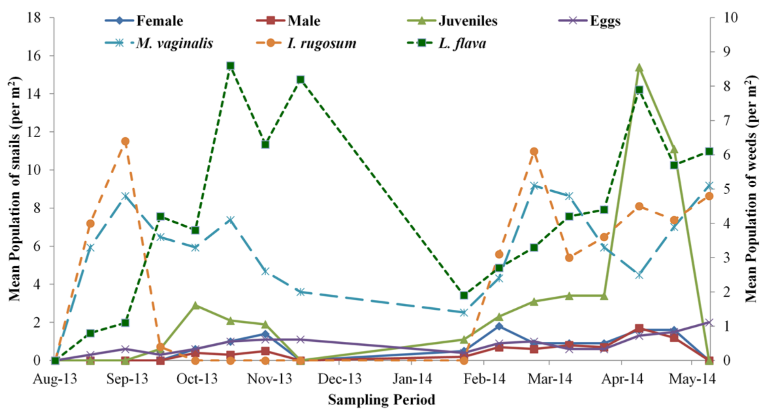

Figure 3. Population fluctuation of different stages of *P. maculata* against aquatic weeds

female snails, whereas relative humidity (R^2=0.254), rainfall (R^2=0.190) and *L. flava* (R^2=0.110) significantly affected the female population during off-season. Water pH (R^2=0.208) and *L. flava* (R^2=0.153) significantly regulated the population of male snails during main-season, whereas rainfall (R^2=0.194), temperature (R^2=0.089) and *M. vaginalis* (R^2=0.0944) were the key factors towards the population development of males.

Population Dispersion of *P. maculata*

The dispersion pattern of various stages of *P. maculata* was established in rice field by calculating different dispersion indices. The results from variance to mean ratio confirmed regular or uniform dispersion pattern for all stages of the *P. maculata* during the two rice growing seasons (Table 2). Moreover, Taylor's power law analysis for the main-season illustrated that the distribution of egg clutches and male *P.*

Table 1
Stepwise regression (R^2) of mean population of different stages of P. maculata *with rice seedlings, weeds and weather parameters*

Pomacea spp. stage	Rice season	Predictor variable	Intercept	R^2	Significance
Eggs per cluster	Main 2013-14	*L. flava*	-5.96	0.392	< 0.0001
		Relative Humidity		0.106	< 0.05
	Off 2013-14	Relative Humidity	4.78	0.239	< 0.05
		I. rugosum		0.070	< 0.05
		pH		0.142	< 0.05
Juveniles	Main 2013-14	*I. rugosum*	179.05	0.174	< 0.05
		Rainfall		0.241	< 0.05
		Temperature		0.102	< 0.05
		Relative humidity		0.095	< 0.05
		pH		0.071	< 0.05
	Off 2013-14	*L. flava*	-2.58	0.326	< 0.05
		Rainfall		0.111	< 0.05
Females	Main 2013-14	*L. flava*	24.79	0.288	< 0.05
		pH		0.306	< 0.001
		Rainfall		0.102	< 0.05
		Temperature		0.058	< 0.05
	Off 2013-14	*I. rugosum*	11.03	0.075	< 0.05
		Rainfall		0.190	< 0.05
		Relative humidity		0.254	< 0.05
		L. flava		0.110	< 0.05
		pH		0.047	< 0.05
		Seedlings		0.047	< 0.05
Males	Main 2013-14	*L. flava*	-0.37	0.153	< 0.05
		pH		0.208	< 0.05
	Off 2013-14	Rainfall	-21.69	0.194	< 0.05
		Temperature		0.089	< 0.05
		M. vaginalis		0.094	< 0.05

maculata showed significant ($P < 0.05$) relationships between their respective variance and mean, whereas no significant relationship was observed for juveniles and females. The slope values of Taylor's power law for different *P. maculata* stages (except for juveniles) were also greater than 1, indicating an aggregated or clumped distribution pattern. As compared to Taylor's power law, Iwao's patchiness regression showed a highly significant relationship between mean crowding index (m^*) and the mean (m) of all *P. maculata* stages ($P < 0.001$) during the main-season. Except for egg clutches, slope values (β) were greater than 1, indicating an aggregated disperion pattern (Table 3). Taylor's power law analysis for the off-season indicated

Table 2
Population dispersion (variance to mean ratio) of different stages of P. maculate

Fortnight	Rice-growing seasons							
	Main-Season 2013-14	Off-Season 2013-14	Main-Season 2013-14	Off-Season 2013-14	Main-Season 2013-14	Off-Season 2013-14	Main-Season 2013-14	Off-Season 2013-14
	Eggs per cluster		Juveniles		Females		Males	
1	-	0.04	-	0.61	-	0.08	-	0.31
2	0.17	0.24	-	0.41	-	0.17	-	0.20
3	0.10	0.13	-	0.23	-	0.24	-	0.18
4	0.18	0.17	0.57	0.06	-	0.06	-	0.06
5	0.30	0.17	0.79	0.00	0.11	0.11	0.06	0.33
6	0.17	0.58	0.05	0.87	0.13	0.20	0.18	0.38
7	0.25	0.11	0.09	3.85	0.07	0.14	0.08	0.12
8	0.25	0.52	-	-	-	-	-	-

Table 3
Regression data of Taylor's power law and Iwao's patchiness model analysis for different stages of Pomacea *spp. during main-season, 2013-14*

Species	Taylor's power law				Iwao's patchiness regression			
	a	b	R^2	P	α	β	R^2	P
Eggs per cluster	-0.53	1.50	0.669	< 0.05	-0.47	0.63	0.517	< 0.001
Juveniles	-0.20	-0.21	0.010	ns	-0.96	1.15	0.968	< 0.001
Females	-0.37	1.53	0.091	ns	-0.99	1.08	0.997	< 0.001
Males	0.04	3.25	0.899	< 0.05	-0.02	-1.15	0.867	< 0.001

that the distribution of different stages of *P. maculata* did not show significant (P < 0.05) relationships between respective variance and mean of the stages, except for egg clutches. The slope values of Taylor's power law for all *P. maculata* stages were also greater than 1, indicating an aggregated or clumped distribution pattern. However, Iwao's patchiness regression during the same season showed a highly significant relationship between mean crowding index (m^*) and the mean (m) of *P. maculata* egg clutches (P < 0.01) and a significant relationship (P < 0.05) between the females and males. Nevertheless, no significant relationship was observed for the juveniles during off-season. The slope values (β) for egg clutches and juveniles were greater than 1, showing an aggregated disperion and less than 1 for females and males indicating a regular disperion. Nevertheless, the constant α in the Iwao's model indicates the tendency to repulsion as its value is negative (-) and the tendency to crowding when it is positive (+); the same is defined by Iwao (1970) as the Index of Basic Contagion (Table 4). Based on the higher value of R^2 using Iwao's patchiness regression compared to

Table 4
Regression data of Taylor's power law and Iwao's patchiness model analysis for different stages of Pomacea *spp. during off-season, 2013-14*

Stage	Taylor's power law				Iwao's patchiness regression			
	a	b	R^2	P	α	β	R^2	P
Eggs per cluster	-0.73	2.31	0.775	< 0.05	-1.04	1.26	0.951	< 0.001
Juveniles	-0.72	1.34	0.286	ns	-1.80	6.50	0.400	ns
Females	-0.79	1.48	0.346	ns	0.42	0.68	0.732	< 0.05
Males	-0.62	1.06	0.395	ns	-0.50	0.75	0.696	< 0.05

Taylor's power law, we can say that Iwao's patchiness regression modal fitted the data better than Taylor's power law.

DISCUSSION

Population Distribution of *Pomacea* spp.

Results regarding population distribution of *Pomacea* spp. confirmed the presence of only *P. maculata* during both rice seasons. Previous research and genetic work confirmed the introduction of at least four apple snail species, namely, *P. canaliculata, P. maculata, P. scalaris* and *P. diffusa* in Southeast Asia, with the former two species being widely distributed and well established (Yahaya et al., 2006; Hayes et al., 2008). Moreover, studies have also confirmed the higher abundance and wide distribution of *P. canaliculata* in comparison to *P. maculata* in invaded areas including Malaysia (Yahaya et al., 2006; Rawlings et al., 2007; Hayes et al., 2008; Salleh et al., 2012). However, results of this study showed only the presence of *P. maculata* from the study site and this finding is supported by Arfan et al. (2014) who confirmed more abundance and wide distribution of *P. maculata* as compared to *P. canaliculata* in the rice fields of Peninsular Malaysia. The presence of only *P. maculata* could be due to its large scale and multiple introduction and tolerance to specific environmental stresses of Peninsular Malaysia as compared to *P. canaliculata*. This is supported by the findings of Hayes et al. (2008). Moreover, comparatively higher population of all the stages of *P. maculata* was recorded during the off-season crop as compared to main-season. The main reason identified for the low population during the main-season was proper management of water especially after the heavy rains through appropriate field levelling. However, continuous presence of water in the field by irrigation and heavy rains, along with lack of proper water management, augment the population of snails by induction of fresh population from the adjacent water channels. The same finding has also been confirmed by Salleh et al. (2012).

Population Fluctuation of Different Stages of *P. maculata* against Weather Parameters, Rice Seedlings and Weeds

The population fluctuation of different stages of *P. maculata* during the two rice-growing seasons showed high variation in the population density of different stages within and between two seasons. Relatively higher populations of either stage were recorded in the latter period of the two rice-growing seasons. Burlakova et al. (2010) also reported highly variable pattern in the population of *P. canaliculata* in rice fields as compared to ponds and streams. Moreover, relatively lower populations of the snails in this study during the beginning of the seasons were mainly affected by the two applications of molluscicide (fentin acetate) by farmers before and after sowing that had almost eliminated snail population in the rice field. However, it was also observed in the study that higher relative humidity and rain fall contributed significantly towards the population build-up of different stages. Studies showed that the presence of water is key for snail movement and thus towards damages as it is the habitat that the snails used for their movement and feeding (Cowie, 2002: Teo, 2003; Joshi, 2007). Accordingly, higher rainfall during both cropping seasons helped to increase the population of *P. maculata* from the adjacent fields and water channels, the finding which had also been reported by Salleh et al. (2012). However, other weather parameters did not show any significant effect on the population regulation of *P. maculata* as it could tolerate high range of pH and temperature (Estebenet & Martín 2002; Ito 2003; Albrecht et al., 2005; Matsukura & Wada 2007; Ramakrishnan, 2007; Seuffert & Martín 2009; Seuffert et al., 2010; Byers et al*.,* 2013). Moreover, constant temperature regime around 30^{o}C supported the steady population development of different stages of *P. maculata*.

A significant role of aquatic weeds especially broad leaf weeds was also identified to contribute towards the population fluctuation of *P. maculata* in the rice field. Snails were found to mostly depend on these weeds which are present at the corners of field for their survival and growth during the initial period of rice growth when famers apply molluscicides, and also during the latter period when rice crop becomes hard for their consumption. Joshi et al. (2006) also recorded the significant role of apple snails in reducing the weed density in transplanted rice when released after the early destructive period to rice. Other studies have also confirmed the significant role of *Pomacea* spp. in the management of weeds in the rice field and accordingly their role in the population fluctuation of *Pomacea* spp. (Wada et al*.,* 2002; Yusa et al*.,* 2003). High correlations of females and egg clutches of *P. maculata* with *L. flava* were also observed in the study, indicating the preference of females towards *L. flava* not only as source of food but also as a substrate for oviposition. The studies also confirmed the preference of female *Pomacea* spp. towards some particular plant species for their oviposition as compared to metal and concrete objects surrounding the water bodies (Burks et al., 2010).

Population Dispersion of *P. maculata*

The simplest dispersion index of variance to mean ratio confirmed a uniform dispersion for the different stages of *P. maculata*. However, Taylor's power law and Iwao's patchiness regression indicated the aggregated dispersion pattern for most of the *P. maculata* stages. The difference in different indices seemed to be due to the applicability of individual indices, but the variable dispersion patterns of different stages of *P. maculata* populations might also be influenced by the availability of sufficient food in the forms of rice and aquatic weeds throughout the cropping seasons. Petney et al. (2012) also suggested an aggregated dispersion pattern for the snail population of genus *Bithynia* in Thailand. Studies by Ge et al. (2015) also obtained the aggregated distribution of the girdled horn snail *Cerithidea cingulata* (Caenogastropoda: Potamididae) mainly due to availability of food. Previous studies also showed the significant contribution of different stages of rice and weeds in the population development and dispersions of different stages of *Pomacea* spp. in rice fields (Sanico et al., 2002; Joshi et al., 2005). Another significant factor in the population dispersion of snails may be the availability of sufficient water due to irrigation and continuous rainfall that facilitate the movement of different stages of *P. maculata* in variable patterns (Cowie, 2002; Teo, 2003; Salleh et al., 2012). The dispersion indices used are commonly used to estimate the dispersion patterns of insects that mostly showed aggregated behaviour, which is either due to availability of food, mates, natural enemies, seasonal changes or role of microclimate (Tsai et al., 2002; Sule et al., 2012). Accordingly, the factors mentioned above might also have contributed towards the variable population distribution of *P. maculata* in the rice field.

In conclusion, this study confirmed the presence of only *P. maculata* in the rice field during two rice-growing seasons. Comparatively higher populations of egg clutches, juvenile, female and male *P. maculata* were recorded during off-season as compared to main-season. Among weather parameters, significant effects of rainfall and relative humidity were found to influence the population development of the various stages of *P. maculata* stages, along with aquatic weeds, *L. flava* and *I. rugosum*. Other weeds and weather parameters did not show any effects on the population of snails. Different dispersion indices indicated a variable pattern of uniform and aggregated dispersions for different stages of *P. maculate*, depending upon the applicability of individual dispersion indices. The results obtained could be practically applied in the field to properly devise various control measures, keeping in view not only the distribution pattern of different stages of snails but also considering the potential role of weather parameters and associated aquatic weeds.

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