


Why do shrimps leave the water? Mechanisms and functions of parading behaviour in freshwater shrimps

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Abstract

An understanding of the mechanisms and functions of animal migratory behaviour may provide insights into its evolution. Furthermore, knowledge about migration may be important for conservation of rare species and may help to manage species in a rapidly changing world. Upstream migration is common in riverine animals, but little is known about proximate cues and functions of the upstream migration in aquatic macroinvertebrates. In Ubon Ratchathani, Thailand, locals have observed a synchronous mass migration of freshwater shrimps on land. This so-called 'parading behaviour' occurs annually during the rainy season and has become a large ecotourism event. Yet, we know little about the natural history, proximate causation and function of this extraordinary behaviour. Here we describe the natural history of parading behaviour and report the results from a series of experiments and observations to address its mechanisms and functions. Parading behaviour is not associated with breeding and spawning; rather, shrimps leave the water to escape strong currents. Conditions promoting shrimps to leave the water include low light, high water velocity and low air temperature. In addition, there is variation explained the specific location. River topology that creates hydrological variability and turbulence plays a role in triggering the shrimps to move out of water. Furthermore, turbidity and water chemistry were associated with shrimp activity. Finally, our results support that parading behaviour in freshwater shrimps is a mass movement upstream due to hydrological displacement. This study highlights the mechanisms that stimulate parading behaviour; a common activity in *Macrobrachium* and other decapod crustaceans.

Introduction

How animals move through their habitat plays a critical role in shaping ecosystems, and influences all levels of ecological organization from individuals to the community (Holyoak *et al.*, 2008; Nathan, 2008). Investigation of movement patterns in different groups of animals may help to understand the role of movement in generating and maintaining biodiversity as well as its influence on population and species evolution (Holyoak *et al.*, 2008; Duckworth, 2009). The field of movement ecology studies both proximate and ultimate causes of movement, ranging from individual to group movement, and aims to understand how movement is influenced by environmental heterogeneity (Nathan & Giuggioli, 2013). Three major areas of movement ecology research consist of: (1) investigating internal and external factors driving motion, (2) understanding mechanisms of navigation and orientation and (3) examining the physiology and motivation of movement (Holyoak *et al.*, 2008). However, due to the limitation in technology and field study (Katzner & Arlettaz, 2019), we still

lack the understanding of the movement ecology in many species (Nathan *et al.*, 2008), especially invertebrates — organisms that play major roles in their ecosystems.

The knowledge from movement ecology studies also sheds light on conservation and management. For example, flying-fox bats (*Pteropus* spp.), a reservoir for Nipah virus, can migrate over 1000 km across Southeast Asia and Australia. An understanding of bats' spatial and temporal dynamics may inform management to control disease dispersal (Robert *et al.*, 2012). Similar to flying-foxes, mass migration of locusts has destroyed food crops since the Ancient Egyptians (2470 BC) until now (Krall *et al.*, 1997; Zhang *et al.*, 2019). By studying the mechanisms and functions of locust migration, we may be able to better control future locust outbreaks (Buhl *et al.*, 2006; Bazazi *et al.*, 2008). Similarly by increasing of our knowledge about migratory behaviour in iconic species that are associated with tourism, such as monarch butterflies (*Danaus plexippus*), grey whales (*Eschrichtius robustus*) or birds provides vital information on their conservation and management (Fraser *et al.*, 2018; Lemelin and Jaramillo-López, 2019).

The Crustacea is one of the subphyla in the phylum Arthropoda. Members of this subphylum can be found from deep seas (e.g. benthosid prawns (*Benthosicymus crenatus*) (Jamieson *et al.*, 2009)) to alpine peaks (e.g. freshwater copepods (Manca *et al.*, 1994)) illustrating remarkable adaptability. Many crustaceans engage in mass migrations after hatching (*Macrobrachium ohione* Bauer, 2011a, 2011b), or during mating (Christmas Island red crabs *Gecarcoidea natalis* Adamczewska & Morris, 2001). However, the mechanisms underlying crustacean aggregation, cues that trigger group formation, and how individuals navigate during migration are poorly known. Moreover, due to an extreme diversity of crustacean lifestyles (Bauer, 2004; Benvenuto *et al.*, 2015), the pattern of migration and group movement of many crustaceans, traits crucial for their survival, requires substantially more study.

Macrobrachium (Crustacean: Decapoda: Palaemonidae) is a genus of freshwater shrimp comprised of more than 200 species (Zheng, Chen & Guo, 2019). Even though some species can be found in estuaries or marine habitats, most of their life cycle occurs in freshwater habitats (hereafter referred to as 'amphidromous species'). Many amphidromous *Macrobrachium* species engage in round-trip migration in which the gravid females migrate downstream from a river to the ocean to spawn at a river mouth or the gravid females spawn at the upstream area and the larvae drift downstream to the ocean. After larvae develop to the juvenile stage in the marine environment, juveniles migrate back upstream by swimming against the current to settle in freshwater habitat (Bauer, 2013). Some aspects of the proximate causation of migration, such as what environmental cues stimulate the migratory behaviour, have been studied (Bauer & Delahoussaye, 2008; Kikkert, Crowl & Covich, 2012), but much remains to be known.

A long time ago, a group of indigenous people in northeastern Thailand discovered synchronous mass terrestrial migration of 'completely freshwater shrimps' in the genus *Macrobrachium* (Fig. 1; Video S1). Called 'parading behaviour', it is a phenomenon in which freshwater shrimps collectively leave the water and walk upstream on land for a distance before returning to the river. This phenomenon occurs annually during the rainy season (the end of August to early October) and only at night.

Local lore was that parading was associated with spawning and breeding (hereafter reproduction). However, this hypothesis has never been tested. To date, only three notes from Lee & Fielder (1979), Fièvet (1999), and Torkkola & Hemsley (2019) reported a similar migratory behaviour in *M. australiense* in Queensland, Australia and *M. faustinum* on Guadeloupe Island. While the behaviour was described in previous studies, causation was not formally studied. Thus, we lack a fundamental understanding of the biology of this extraordinary phenomenon.

Since 1999, shrimp parading has been promoted as an ecotourism event in Thailand and draws >100 000 visitors annually. The lack of knowledge of the shrimps is problematic because recent evidence suggests that these shrimps may be decreasing in number and body size (W. Maiphrom, 2017, unpubl. data). Alarming, there are no strategies for habitat



Figure 1 Parading shrimps synchronously walking on land at night at the Lamduan Rapids, Ubon Ratchathani, Thailand. Photo: Watcharapong Hongjamrassilp.

and ecotourism management. Thus, to conserve this natural resource that can benefit local community (in terms of food, education and business), the fundamental biology of the shrimps, including life histories and movement behaviour, requires study.

Here we study the proximate causation and functions of the parading behaviour by: (1) describing the natural history of parading, (2) investigating whether parading is associated with reproduction (breeding or spawning) and (3) identifying environmental factors and habitat structure that triggers parading. Finally, we discuss whether parading is simply upstream migration of juveniles, as seen in most amphidromous *Macrobrachium* species, or whether it is a mass upstream movement triggered by hydrological displacement.

Materials and methods

Site study

Parading shrimps were studied in Nam Yuen district, Ubon Ratchathani province, Thailand from August to September of 2018 and 2019. We surveyed nine sites along the Lamdom river where parading was observed in the past (Fig. S1). However, we only found two locations with active parading behaviour: (1) the Lamduan rapids and (2) the Yang weir.

The Lamduan rapids (14°26'07.0''N; 105°06'17.0''E) are located on the Lamdom River (Fig. 2a); a river that flows down from a headwater located in the Dânggrêk Mountains between Thailand and Cambodia. The distance from the headwater to the Lamduan rapids is about 25 km and the distance from the Lamduan rapids to the river's mouth, in the Mekong Delta in Vietnam, is about 900 km. During the summer (late March–May), the Lamduan rapids are dry, disconnecting the headwater and downstream portions. The upstream and downstream join back again during the rainy season (July–October).

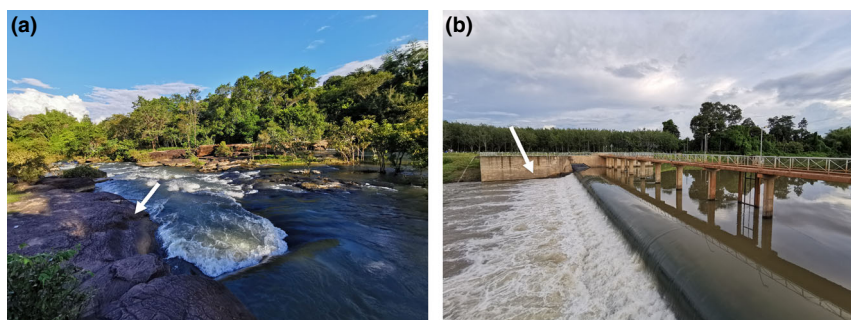


Figure 2 (a) Lamduan rapids. (b) Yang weir. White arrows indicate the area where the shrimps perform parading behaviour during the nighttime. Photos: Watcharapong Hongjamrassilp.

The highest precipitation in this area occurs in August and September (Fig. S2). The second site is Yang weir which is an inflatable rubber dam ($14^{\circ}29'35.5''\text{N}$; $105^{\circ}08'06.5''\text{E}$) (Fig. 2b). This site is located 14 km downstream from the Lamduan rapids.

Species identification

We collected 30 shrimps from Lamduan rapids and Yang Weir (almost all parading shrimps were juveniles) while they were walking on land and identified them to genus using a morphological key (Cai, Naiyanetr & Ng, 2004), and to species with molecular identification techniques. We collected abdominal muscle tissues from ten shrimps (five from each site) and extracted total genomic DNA with a PureLink Genomic DNA Mini Kit (Carlsbad, CA, USA). We sequenced 16S ribosomal RNA (16S rRNA) and Cytochrome c oxidase I (COX1) for species identification (detailed methods regarding gene amplification and sequencing are in Supplementary Material S1).

We blasted all sequences in the National Center for Biotechnology Information (NCBI) database to search for species and confirmed the results by conducting a phylogenetic analysis with eight species of *Macrobrachium*, which are found in the Lamduan river and other places in Thailand, as an outgroup (Accession numbers in Table S1). We reconstructed the phylogeny using a maximum likelihood method with rapid bootstrap algorithm using 1000 replicates under Generalized Time Reversible (GTR) model (Yang, 2006).

Study 1 Behavioural observations

We observed parading behaviour using time-lapse night cameras (Victure trail camera HC200) and *in situ* observations. The night cameras use infrared LEDs, which should minimize shrimp disturbance. To determine when shrimps moved out of the river, we set up time-lapse night cameras *c.* 30 cm from the river to take photos every five minutes within a 20 x 20 cm quadrat between 17:00 to 08:00 h the next day. We quantified (1) the time that the shrimps started and stopped parading; (2) the distance over which shrimps travelled on land; and (3) the density of shrimps every hour during which they paraded. Moreover, we observed river structure that might

be associated with parading in the two study sites by documenting hydrological variability that is a consequence of variation in river topology.

Study 2 Do the shrimps perform parading behaviour for reproduction?

Population demography and reproductive cycle of parading shrimps

Our hypothesis was that if parading behaviour was associated with reproduction (breeding or spawning), we would find more adults than juveniles. To test this hypothesis, we studied the population demography of the shrimps by collecting 30 actively parading shrimps, weekly, from the first week of August to the last week of October of 2018–2019 using a hand net (i.e. 12 collections/year; $N = 24$ collections). We measured carapace length, a proxy of body size, and plotted a frequency histogram of carapace length. In addition, to study the reproductive cycle of the adult shrimps, we used an underwater trap to collect female adults at the Lamduan rapids from 2018–2019. We aimed to collect 30 individuals each month. However, we caught fewer shrimps during the summer dry season. We counted the number of ovigerous females and compared them over months.

Study 3 Environmental factors associated with parading behaviour

Prior studies suggested that underwater migration in amphidromous shrimps was triggered by several environmental factors including water velocity, moonlight intensity, salinity and cloud cover (Kikkert *et al.*, 2009). Therefore, we collected six environmental variables: (1) water velocity, (2) moonlight intensity, (3) air temperature, (4) water temperature, (5) humidity and (6) cloud cover (in okta units) in the vicinity of the parading site from the end of August to early October in 2018 and 2019. We measured all environmental variables at 20:00 h which is about one hour after the shrimps start to migrate from both the Lamduan rapids and the Yang weir site. We measured water velocity using a digital flow metre fitted with 60 mm impellers (Flowwatch, JDC Electronic, Switzerland). We used a

hygrometer and thermometer to measure humidity and temperature, respectively. To quantify cloud cover, we estimated it using eight sector square grids following Llusia *et al.* (2013). We obtained the moonlight illumination data from an online source (<https://www.mooncalc.org>). To estimate a number of shrimps that paraded each night, we counted shrimps in 180 photographs per day collected at each location using the time-lapse cameras as described above.

We conducted all statistical analyses using R 3.5.3 (R Core Team, 2019). We regressed environmental variables (including water velocity, moonlight intensity, air temperature, water temperature, humidity, cloud cover and site study) against the number of parading shrimps to explain variation in a number of shrimps per night. Prior to fitting the model, we calculated correlation coefficients among all environmental variables; only humidity and the air temperature were highly correlated ($r = -0.694$, $N = 95$, $P < 0.001$). Therefore, we omitted humidity from our model. Since the independent variable (number of parading shrimps) is a count, we fitted a negative binomial regression model using the function *glm.nb* in package MASS (Venables & Ripley, 2002). We calculated the model's pseudo R^2 with the likelihood-ratio-based method for the generalized linear model (Maddala, 1983; Cox & Snell, 1989; Magee, 1990) using *rsq.lm* function in package rsq (Zhang, 2018). To estimate partial pseudo R^2 of each independent variable, we subtracted Pseudo R^2 of the full model from Pseudo R^2 of the full model without the specific independent variable and used this value to explain effect size of each environmental variable.

Study 3.1 Does water velocity cause the parading shrimps to leave water?

Based on results from study 3, we hypothesized that parading behaviour functions to help the shrimps escape strong water currents. To test this hypothesis, we created an artificial stream that consisted of an upper tank and a lower tank. The bottom of the upper tank contained a valve to adjust flow velocity. The upper tank and lower tank were connected by a semicircular concrete pipe (Fig. S3). We placed 106 shrimps (carapace length ranged from 4.06–16.04 mm) by putting a shrimp on the centre of the concrete pipe and turning on the water from the upper tank. To quantify the maximum water velocity that the shrimp could tolerate, we increased the water velocity by adjusting the valve until the shrimp was washed down the pipe. Following this experiment, we measured each shrimp's carapace length as a proxy of body size. Finally, we calculated the Pearson correlation between maximum water velocity the shrimps could tolerate and carapace length.

Study 3.2 Does water chemistry, turbidity or turbulence cause the parading shrimps to leave water?

Based on the results from study 1, we hypothesized that turbulence might cause the shrimps to leave the water. Moreover, Kikkert *et al.* (2009) suggested that water chemistry

(e.g. plant exudates from leaf litter and sediment) and turbidity were negatively correlated with migration activities in other freshwater shrimps (genus *Atya* and *Xiphocaris*). To determine whether turbulence, water chemistry and turbidity influenced shrimps activity and ultimately potentiated parading, we conducted experiments. However, we were not able to simulate the difference between chemical compounds in the water in the same way as Kikkert *et al.* (2009). Rather, we varied the source of our water. Groundwater was clear water that we sourced from an underground fountain, and river water was turbid water that we collected from the Lamduan rapids. Water from the Lamduan rapids was murkier, and we assumed that river water contained a greater diversity of chemicals than groundwater.

We divided the experimental aquaria into four conditions (hereafter treatment): (1) turbulence with river water, (2) no turbulence with river water, (3) turbulence with groundwater and (4) no turbulence with groundwater. To generate turbulence, we created an artificial stream where water was pumped uphill with aquarium pumps and flowed down to the holding tank (Fig. S4A). We used ToxTrac software (Rodriguez *et al.*, 2018) to track the shrimp movement speed as a proxy of migration activity. However, shrimps are transparent and could not be detected under normal conditions. Therefore, we fed shrimps with rice that was stained with black food colouring (Fig. S4B,C).

We collected actively parading shrimps and acclimated them in the aquarium with groundwater and no turbulence for 5 days to standardize shrimp activity. On the sixth day, we moved the shrimp into one of the four experimental aquaria (30 individuals per treatment). Then, every 12 h, we took each shrimp from each treatment to an observational aquarium and filmed it with a video camera for 3 min. After that, we took the shrimps back to the experimental aquarium and waited for the next 12 h. We ran all experiments for 24 h. After finishing the experiment, we measured swimming speed of each shrimp in each treatment using ToxTrac tracking software. We analysed the difference between mean rank of swimming speed among four treatments with Kruskal–Wallis test and compared the difference among significant groups using a Mann–Whitney U test.

Results

Species identification

The morphological analysis suggests two species of parading shrimps: *Macrobrachium lanchesteri* (Decapod: Caridea: Palaemonidae) comprised 1% of the sample ($N = 709$) and another unidentified *Macrobrachium* species that comprised 99% of the samples. We resolved this unidentified species with molecular techniques. We obtained a total of 408 base pairs (bp) from 16S rRNA and 692 bp from COXI from ten parading shrimps. After examining the protein-coding COXI, we found that every sequence consisted of several stop codons inside the sequences. This means that the sequences were pseudogenes and could not be included in the phylogenetic analysis. Thus, we only used sequences from 16S rRNA for species

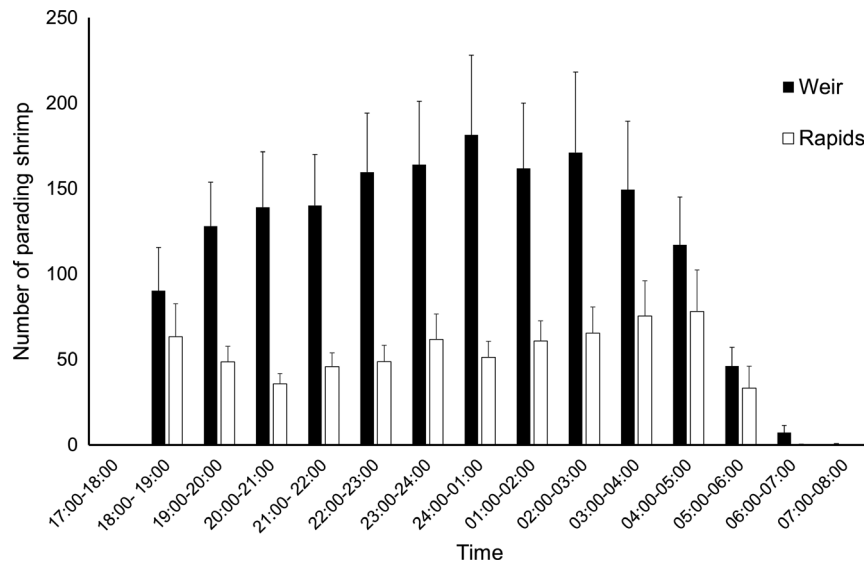


Figure 3 Estimated number (Average \pm SEM) of parading shrimps from time-lapse night cameras from 2018–2019. Migrating pattern of parading shrimps at the weir ($N = 40$ days) is represented in black bars and at the Lamduan Rapids ($N = 55$ days) is represented in white bars.

identification. The result from the phylogenetic analysis reveals that all unknown specimens were clustered inside the *M. dienbienphusense* clade with *M. eriocheirum* as a sister group (Fig. S5). De Grave & Franssen (2011) synonymized *M. eriocheirum* with *M. dienbienphusense*, but Hanamura *et al.* (2011) recognized it as valid. Even though there is some difference of the opinion on the taxonomic validity of *M. eriocheirum*, 99% of the unknown *Macrobrachium* individual belonged to a single species, *M. dienbienphusense* Đăng and Nguyễn, 1972.

Study 1 Behavioural observations

The time-lapse cameras revealed that the shrimps started to leave the river and paraded on land at around 19:00 h; ca. 30 min after dusk. We observed the shrimps aggregated underwater at the start point of the parading site around 18:00 until the sun completely set at around 18:45. After that, they climbed out of the river and continued to walk throughout the night (Fig. 3). While on land, they mostly walked inside the splash zone which was about 20–40 cm from the river's edge (Fig. 4). The movement ceased around 06:00–07:00 h when the sun started to rise. While moving, we found that most shrimps preferred to walk around 22:00–03:00 h at the weir and around 03:00–05:00 h at the rapids. Shrimps walked on land for 5–20 m depending on river velocity and riverbank structure. The average walking speed while moving on land was 85.2 ± 43.82 (Mean \pm SD) cm/min ($N = 30$).

Observations among nine locations along the Lamdom river suggested that the Lamduan rapids and the weir had unique characteristics that could not be found elsewhere. We defined four zones based on topology and hydrology: (1) downstream zone (flow velocity = 5–10 cm/s), (2) turbulent zone (flow



Figure 4 Parading shrimps migrate on land mostly in the splash zone along the Lamdom river. Photo: Watcharapong Hongjamrassilp.

velocity = 10–20 cm/s), (3) running water zone (flow velocity = 120–200 cm/s) and (4) upstream zone (flow velocity = 60–100 cm/s) (Fig. 5). After sunset, shrimps began to swim upstream underwater. They swam from the downstream zone to the turbulent zone. Shrimps aggregated there until the sky was dark. Once dark, the aggregated shrimps climbed out of the river and walked past the running water zone to the upstream zone. When the shrimps reached the end of the upstream zone where the flow velocity was sufficiently low (less than 60 cm/s), they returned to the river. The walking pattern varied depending on the number of migrants each night and the size of the splash zone. We observed shrimp walking in several rows when the splash zone was small. However, when the splash zone was sufficiently wide, the shrimps spread out and did not form a line.

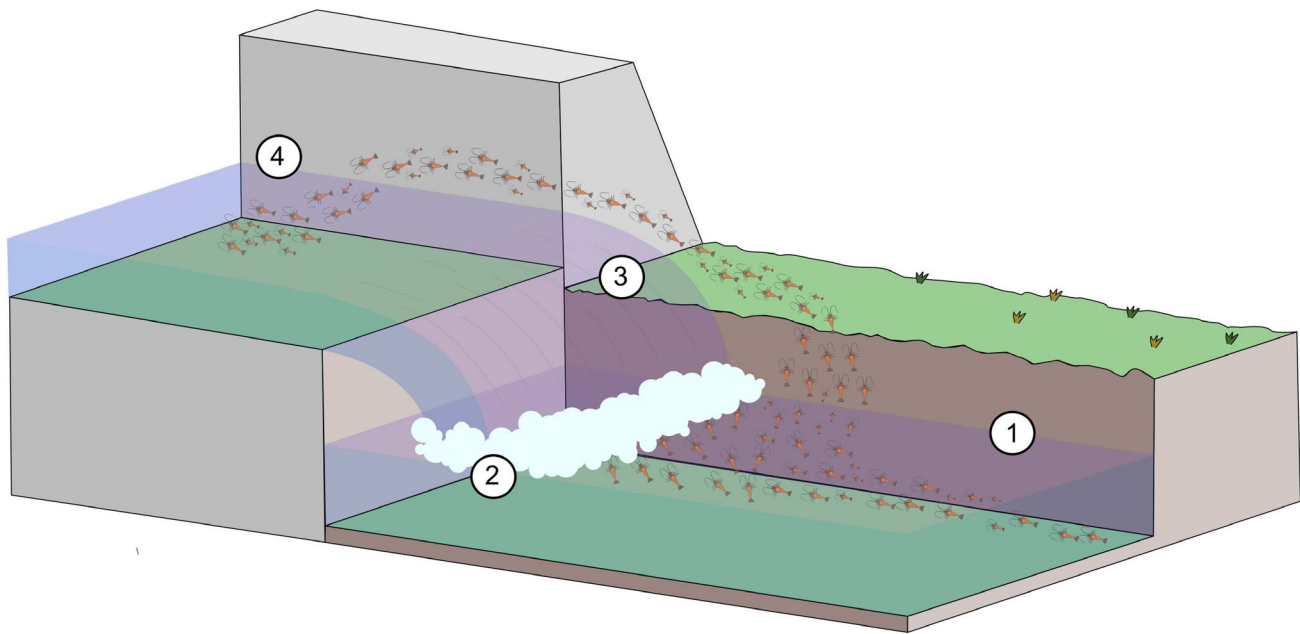


Figure 5 Four unique zones at the Yang weir, which are also found in the Lamduan rapids. Zone 1 is a downstream zone (flow velocity = 5–10 cm/s). Zone 2 is a turbulent zone (flow velocity = 10–20 cm/s). Zone 3 is a running water zone (flow velocity = 120–200 cm/s). Zone 4 is an upstream zone (flow velocity = 60–100 cm/s). Graphic credit: Boontigan Kuhasubpasin and Watcharapong Hongjamrassilp.

Study 2 Do the shrimps perform parading behaviour for reproduction?

Population demography and reproductive cycle of parading shrimps

Parading shrimps varied in their carapace length (CL) from 1.72–12.55 mm (Mean \pm SD: 6.0 ± 1.439 , $N = 706$) (Fig. 6) (relationship between CL and total length is in Fig. S6). 92% of the shrimp (CL = 1.72–7.80 mm) did not have an enlarged chela (a secondary sexual characteristic, Fig. 7a) and we did not observe eggs inside their abdomen. From this, we conclude that 92% of the parading shrimps were juveniles. Moreover, year-round data collection of adults *M. dienbienphuense* in the Lamdom River revealed that most ovigerous females were found in June to September with the peak number of ovigerous females in June (Fig. 7b). Finally, we found that within ovigerous females, eggs in their abdominal cavity were not at the same developmental stage. Some eggs already had eyes developed inside while some did not. Together, these observations suggest asynchronous spawning of *M. dienbienphuense* and suggest that parading was not associated with spawning.

Study 3 Environmental factors associated with parading behaviour

In 2018 and 2019, we quantified data from a total of 55 days at the Lamduan rapids and 40 days at the weir. More shrimps paraded at high water velocities ($P < 0.001$) and at low air

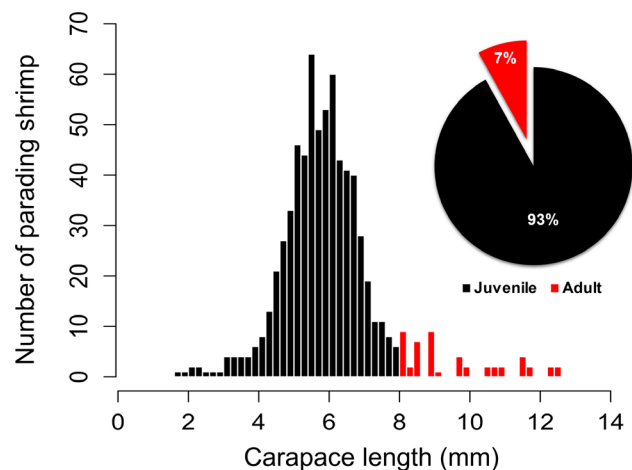


Figure 6 Histogram illustrating the frequency of parading shrimps with different carapace lengths ($N = 706$). Pie chart represents proportion of juvenile and adult *Macrobrachium dienbienphuense* which were collected while parading.

temperatures ($P = 0.006$; Table 1), and more shrimps paraded at the weir than at the Lamduan rapids ($P = 0.002$). Even though the shrimps tended to parade more with high precipitation, low moon illumination, low cloud cover and low water temperature, these independent variables were not statistically significant.

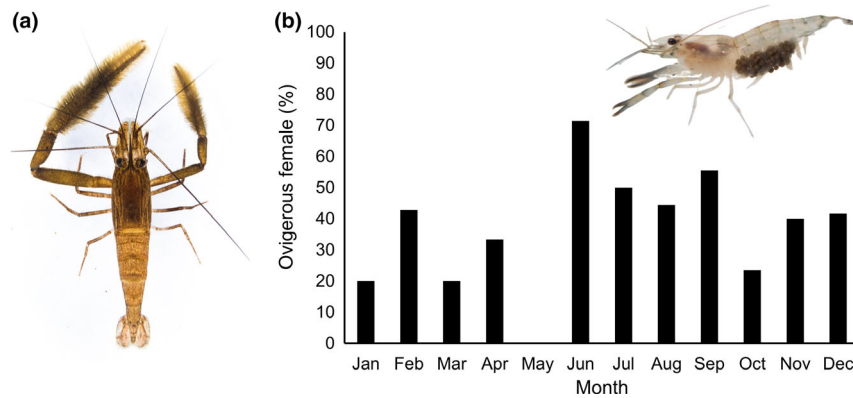


Figure 7 (a) Adult male *Macrobrachium dienbienphuense* with enlarged hairy claws. (b) The bar graph shows the percent of ovigerous females (ovigerous females in each month/ total females in each month) in different months. Top right is a female *M. dienbienphuense* with a cluster of eggs inside its abdominal cavity. Photo: Watcharapong Hongjamrassilp.

Table 1 Results from negative binomial regression describing the variation in a number of parading shrimps by environmental parameters

	Estimate	SE	Z value	P value	Partial Pseudo R^2	Pseudo R^2
(Intercept)	9.227	2.185	4.222	<0.000*		0.385
Precipitation	0.010	0.005	1.818	0.069	0.022	
Moon illumination	-0.003	0.003	-1.030	0.303	0.007	
Cloud cover	-0.008	0.026	-0.324	0.746	0.001	
Water temperature	-0.072	0.078	-0.923	0.356	0.003	
Air temperature	-0.082	0.030	-2.742	0.006*	0.042	
Water Velocity	0.012	0.002	5.417	<0.000*	0.130	
Location (Weir)	0.620	0.195	3.175	0.002*	0.055	

P-values with asterisk are considered significant.

Study 3.1 Does water velocity cause the parading shrimps to leave water?

Larger shrimps tolerated higher water velocity than smaller shrimps ($R = 0.856$, $N = 106$, $P < 0.001$) (Fig. 8). This result suggests that the small shrimps benefited from walking out of water because they could not tolerate the high flow at the rapids. However, the largest shrimps rarely walked out of water because they could tolerate the high flow in the rapids.

Study 3.2 Does water chemistry, turbidity or turbulence cause the parading shrimps to leave water?

At the start of the experiment (0 h), swimming speed of shrimps from the four treatments were not significantly different ($\chi^2 = 2.06$, $P = 0.56$, $N = 30$ in each treatment). However, by hour 12, shrimps started to behave differently as a function of treatment. After 12 h, shrimps in treatment 1 (with turbulence and river water) and 3 (with turbulence and groundwater) had higher swimming speeds than shrimps in treatment 2 (without turbulence and with river water) and 4 (without turbulence and with groundwater) ($\chi^2 = 26.73$, $P < 0.000$; Fig. 9, Table 2). This indicates exposure to turbulence increased the swimming speed of the shrimps during the first 12 h. After 24 h,

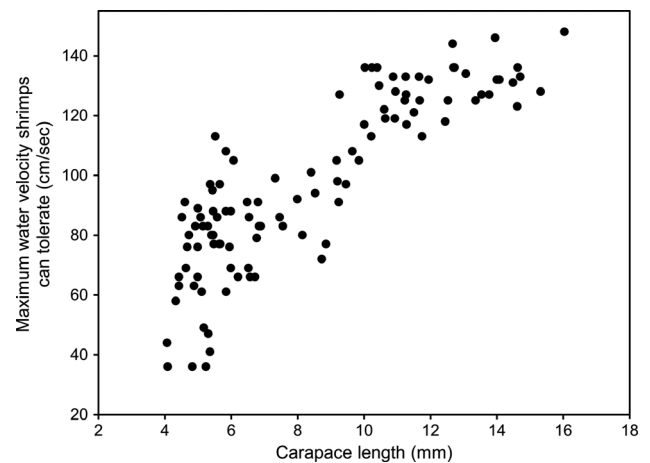


Figure 8 Relationship between carapace length and maximum water velocity that the parading shrimps can tolerate ($N = 106$).

swimming speed of shrimps in treatment 1, 2 and 3 were similar and were higher than treatment 4 ($\chi^2 = 11.25$, $P < 0.001$; Fig. 9, Table 2) suggesting that turbulence and river water increased shrimp swimming speed. However, the turbulence had a greater effect within a short period (the first 12 h)

Table 2 Results from Kruskal–Wallis test describing the difference in mean ranks of swimming speed of parading shrimps in four different treatments with Mann–Whitney U test

Time	d.f.	Chi-square	P	Mann–Whitney U test	
				Treatment	Group
0	3	2.06	0.56		
12	3	26.73	<0.000*	1	a
				2	b
				3	a
				4	b
24	3	11.25	<0.001*	1	a
				2	a
				3	a
				4	b

P-values with asterisks are considered significant.

Treatment 1 is turbulence and river water. Treatment 2 is non-turbulence with river water. Treatment 3 is turbulence with groundwater. Treatment 4 is non-turbulence with groundwater.

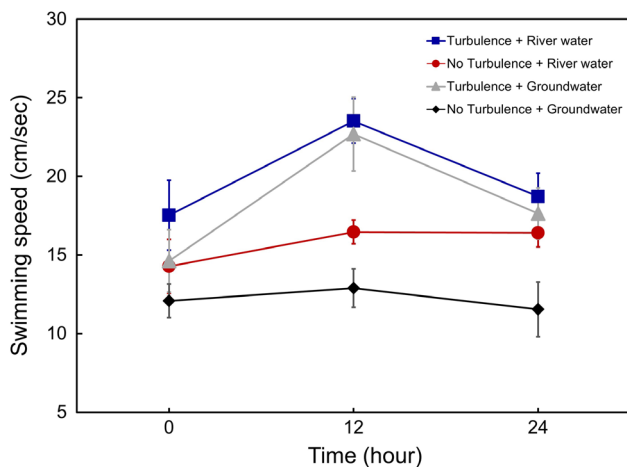


Figure 9 Temporal pattern of swimming speed (mean \pm SE) of the parading shrimps in four different treatments. Hour in x-axis is number of hours after the shrimps were placed in each treatment. $N = 30$ in each treatment.

compared to the effect of the type of water, which was only important at 24 h. Based on these results, we conclude that the type of water (high turbidity and chemically complex water) and turbulence increases shrimp activity and stimulates them to walk out of the river.

Discussion

A number of species of freshwater caridean shrimps engage in what is referred to as parading behaviour. Our research shows that small shrimps leave the river and walked on land to escape strong currents. The main factors that triggered parading were low light intensity, high water velocity, low air temperature, high

turbulence, high turbidity and (to date unidentified) chemicals in the water. We discuss these below.

Virtually all of the shrimps we identified performing parading behaviour in Ubon Ratchathani, Thailand were *Macrobrachium dienbienphuense*; 1% of them were *M. lanchesteri*. Both species are endemic to East and South East Asia (Chace & Bruce, 1993; Hanamura *et al.*, 2011). Other studies reported parading behaviour in caridean shrimps (Decapoda, Caridea) throughout the world including in Asia (*Caridina japonica*, *Paratya compressa* and *M. japonicum* in Japan (Hamano *et al.*, 1995); *M. malcomsonii* in Godvari, India (Ibrahim, 1962)), Australia (*M. australiense* in Queensland, Australia) (Lee & Fielder, 1979; Torkkola & Hemsley, 2019), and in the Americas (*Atyoida bisulcata*, *M. grandimanus* and *M. lar* in West Maui Mountain, Hawaii, USA (Benbow *et al.*, 2002); *M. ohione* in the Atchafalaya River, Louisiana, USA (Olivier *et al.*, 2013); *M. faustinum*, *Xiphocaris elongata* and *Atya innocous* on Guadeloupe Island, French West Indies (Fièvet, 1999)). These reports indicate that the ability to leave a river and climb over either natural barriers (e.g. waterfalls) or man-made barrier (e.g. dams or weirs) during upstream migration is widespread in amphidromous and freshwater caridean shrimps.

Ancestors of caridean shrimps are thought to have originated in marine habitats (Davis *et al.*, 2018) and some species evolved to exploit freshwater habitats (Bauer, 2013). Upstream migration in concert with novel reproductive strategies (abbreviated larval development (ALD) versus extended larval development (ELD)) are two main features that allow caridean shrimp to successfully colonize freshwater habitats (Bauer, 2011a; Bauer, 2013). We suggest that parading is another behavioural adaptation that facilitates colonization of freshwater ecosystem by allowing shrimps to move past barriers to upstream areas while other organisms cannot (e.g. predatory fishes). Moreover, the ability to walk on land may facilitate overland dispersal (Torkkola & Hemsley, 2019). More observations are needed to confirm this hypothesis.

Many species of amphidromous *Macrobrachium* parade while travelling to headwaters with relatively fewer predators than downstream areas (Covich *et al.*, 2009). However, until now, there have been no reports of upstream migration of the completely freshwater *Macrobrachium*. Bauer (2013) reported the upstream migration of *M. ohione*, an amphidromous species, by swimming upstream at nighttime but not at daytime. However, we did not observe *M. dienbienphuense*, which are a freshwater species (De Grave, Wowor, & Cai, 2013; WoRMS, 2020), performing upstream migration by swimming during both the day and night. We only observed them walking at night. After the parading shrimps returned to the river, we did not observe them swimming upstream. Bauer (2013) proposed that the migration between freshwater and marine system of amphidromous *Macrobrachium* was related to developmental strategy. The amphidromous species are known to have extended larval development (ELD). ELD is a type of development where adults spawn with many tiny larvae that contain a small amount of yolk (Mashiko, 1990; Walsh, 1993; Bauer, 2004). Because of less yolk, the larvae must drift downstream to the ocean where there is more food and sufficient salinity that triggers their development. In some species, gravid

females migrate downstream and spawn at a river mouth (Olivier & Bauer, 2011; Bauer, 2011a). By contrast, completely freshwater species are known to exhibit a direct or abbreviated larval development (ALD), which is the type of development whereby the adult spawn with fewer larvae, but these larvae are typically in more advanced stages or, in some species, hatching out as a juvenile (post-larvae) (Hayashi & Hamano, 1984). Because completely freshwater species hatch out in an advanced developmental stage, the juveniles need not migrate.

While we do not have any direct evidence that the populations of *M. dienbienphuense* in our study sites have ALD, the distance from our study sites to the closest estuary was about 1000 km. Most of females *M. dienbienphuense* in our study sites carried eggs that were at the pigmented eye stage to pre-hatching stage indicating that they were ready to spawn. Therefore, we hypothesize that *M. dienbienphuense* in our study sites have ALD. Thus, we conclude that the function of parading behaviour in *M. dienbienphuense* is not similar to the upstream migration in amphidromous species, yet the parading behaviour helps the juvenile shrimps move past the rapids.

We observed *M. dienbienphuense* parading after sunset; light suppresses the behaviour. By contrast Fivè (1999) observed shrimps (*M. faustinum*, *X. elongata* and *A. innocuous*) leaving the water during the day when there was a sudden strong release of water over an impoundment (water current >100 cm/s). We also observed a single event in September of 2019 where *M. dienbienphuense* continued to migrate after sunrise on a day of exceptionally heavy rain and extremely rapid flow (c. 220 cm/s). These anecdotes suggest that the decision to parade involves multiple drivers including at least ambient light and water velocity.

The number of parading *M. dienbienphuense* was positively correlated with water velocity and negatively correlated with shrimp size. Lee & Fielder (1979) also reported a similar pattern of smaller *M. australiense* being more likely to parade. Together, parading behaviour is a way that small shrimps can continue to move upstream where water velocity exceeds about 120 cm/s. In addition to velocity, our experiments revealed that turbulence also potentiates parading. Since most migrating shrimps make use of positive rheotaxis during the upstream migration (Lee & Fielder, 1984), turbulence might eliminate or modify flow direction (Benstead *et al.*, 1999). The Lamduan rapids and the Yang weir have the turbulence zone following the running water zone (Fig. 5). Therefore, by moving on land, shrimps, especially small individuals, avoid turbulent areas. We also observed that while moving on land, shrimps often walked near the splash zone and put their legs into the river. We speculate that the shrimps sensed flow direction using setae on their legs. However, how the shrimps navigate while on land requires formal study.

Covich (1988) proposed that chemicals from leaf litter might contain toxic compounds that drive shrimps to migrate to another habitat, while Olsson *et al.* (2006) proposed that chemicals in the water could trigger the shrimps to collectively move because chemicals from leaf litter might be a food cue. Kikkert *et al.* (2009) demonstrated that *Atya* and *Xiphocaris* shrimps avoided swimming in a river with high leaf litter and high turbidity consistent with the hypothesis that they avoided

toxic leaf litter. While we also found that activity was increased when shrimps were in river water compared to ground water, we cannot conclude why. Regardless, our results illustrate the potential that both chemicals and turbidity stimulate parading.

Parading behaviour was not associated with reproduction in *M. dienbienphuense* because almost all were juveniles. Several riverine species such as Atlantic salmon (*Salmo salar*) and aquatic insects migrate upstream to mate (Baglinière *et al.*, 1990; Higler, 2004). Furthermore, studies in amphidromous *Macrobrachium* shows that shrimps migrate downstream to spawn in the ocean while most juveniles migrate upstream after larval development in the sea (Bauer, 2013). This suggests upstream migration in amphidromous species may not function for reproduction. Moreover, we found that the parading season was not associated with spawning because *M. dienbienphuense* has an asynchronous spawning reproductive pattern.

Information about the mechanisms and functions of parading behaviour allows us to improve conservation and management strategies for freshwater shrimps. For example, dams have been constructed throughout the world (Kaika, 2006; Zaharia *et al.*, 2016), and they affect upstream migration of many riverine species including amphidromous and freshwater shrimp. Hamano *et al.* (1995), Fièvet (2000) and Olivier *et al.* (2013) demonstrated how a fundamental understanding of climbing performance in caridean shrimps could be applied to create 'shrimp ladders', which permit shrimp to move across dams. Furthermore, an understanding of parading behaviour can be used to limit the movement of invasive species to upstream headwaters. For instance, red swamp crayfish (*Procambarus clarkii*) (Crustacea: Astacidae), a native species in the southern United States, is an invasive predator in other parts of the world (Loureiro *et al.*, 2015). By understanding crayfish climbing performance, scientists have designed a special type of roof on a dam that can prevent upstream crayfish movement (Dana *et al.*, 2011). Our results could be used to create similar structures that can facilitate or limit the movement of decapod crustaceans.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Location of surveyed sites. Parading shrimps were only detected at sites 4 and 9. Number 4 is Lamduan rapids and number 9 is Yang weir. Table on the bottom left indicates the latitude and longitude of surveyed sites.

Figure S2. Monthly average \pm SEM rainfall at Phon thong village (ca. 3 km away from out study site), Nam Yuen district, Ubon Ratchathani, Thailand. Data from <http://hydro-4.com/>.

Figure S3. Artificial stream to study the decision to parade. Yellow arrow illustrates flow direction. Shrimps were put in the lower tank. During the experiment, the shrimp walked up from lower tank to an upper tank.

Figure S4. (a) Experimental aquarium with turbulence creating system. (b) Rice stained with black food coloring (white arrow) contrasted with a shrimp in the top right which has not eaten the rice. (c) Close-up photo of shrimp fed black rice. The white arrow points its stomach stained with black color.

Figure S5. Ultrametric phylogeny of some members of shrimps in genus *Macrobrachium* found in Thailand. S1–S5 are samples collected from the Lamduan rapids and S6–S10 are samples collected from the Yang weir. The values represented on this phylogeny are bootstrap values.

Figure S6. Relationship between total length and carapace length of *Macrobrachium dienbienphuense* with regression equation.

Table S1. Accession numbers used for phylogenetic analysis.

Video S1. Parading behaviour of parading shrimps (*M. dienbienphuense*) at Lamduan Rapids, Ubon Ratchathani, Thailand.