UNIVERSIDADE DE ÉVORA

ESCOLA DE CIÊNCIAS E TECNOLOGIA

DEPARTAMENTO DE PAISAGEM, AMBIENTE E ORDENAMENTO

Estudo da capacidade de dispersão de um decápode exótico (*Eriocheir sinensis*) em águas interiores Portuguesas

Dispersal capacity of the Chinese Mitten crab (*Eriocheir sinensis*) in Portuguese inland waters

Cristina Isabel Garcia Fialho

Orientação: Professor Doutor Pedro Anastácio

Mestrado em Qualidade e Gestão do Ambiente

Dissertação

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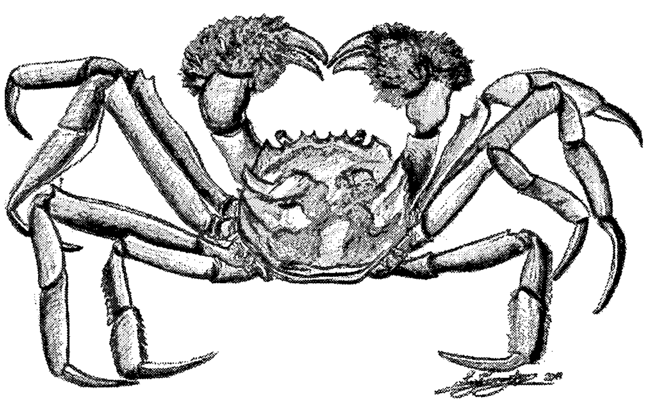

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Resumo

O caranguejo-peludo-chinês (*Eriocheir sinensis)* é um crustáceo decápode invasivo com uma larga distribuição no mundo. Nos locais em que se torna uma espécie invasiva, esta espécie causa grandes impactos negativos, tanto ecológicos como económicos. Neste trabalho estudou-se a velocidade de movimentação do caranguejo-peludo-chinês dentro e fora de água, o tempo de sobrevivência sob condições de dessecação e também a interacção com outra espécie exótica (*Procambarus clarkii*) a fim de determinar se esta última condicionaria a sua dispersão. Experiências de dessecação demonstraram que a 16^0C o LT_{50} é de 70 horas, com uma perda média de peso de 20%, e a 24^0C o LT_{50} é de 31 horas, com uma perda média de peso de 22 %. Experiências demonstraram que pode deslocar-se dentro de água em média 13.28 m em 3 minutos, com uma velocidade de 0.074 m/s^2 e fora de água em média 2.91 m em 3 minutos, com uma velocidade média de 0.016 m/s^2. Verificou-se que o Lagostim vermelho da Louisiana *P. clarkii* não condiciona a dispersão do caranguejo-peludo-chinês. Com este estudo concluiu-se que o caranguejo tem uma grande capacidade para dispersar-se sob diferentes condições, sendo a densidade, temperatura da água, humidade relativa, comprimento dos animais e sua condição (índice de Fulton), as variáveis condicionantes no deslocamento. Ainda se verificou que esta espécie possui uma grande capacidade de resistência à dessecação. Estas capacidades adaptativas conferem-lhe todos os requisitos para invadir e adaptar-se a novos locais com sucesso.

Palavras- chave: *Eriocheir sinensis*, dessecação, competição, dispersão, velocidade, *Procambarus clarkii.*

Abstract

The Chinese mitten crab (*Eriocheir sinensis*) is an invasive decapod crustacean with a widespread distribution in the Earth biota. In invaded areas, this species has strong ecological and economic negative impacts. We studied the movement speed of the Chinese mitten crab in and out of water, the survival time out of water under desiccating conditions and also its interaction with the red swamp crayfish (*Procambarus clarkii*) during dispersal. Results demonstrated that at 16^{0}C the LT_{50} was 70 hours, with a mean weight loss of 20%, and at 24^{0}C the LT_{50} was 31 hours, with a mean weight loss of 22%. A dispersal experiment showed that in the water these crabs dispersed on average 13.28 m during 3 minutes, with a mean velocity of 0.074 m/s^2. Out of water they moved on average 2.91 m during 3 minutes, with a mean velocity of 0.016 m/s^2. Our experiments demonstrated that *P. clarkii* does not affect the dispersion of *E. sinensis*. This study confirmed that the crab has a great capacity for dispersal under different conditions, being density, temperature, relative humidity, carapace length and condition of the individuals (Fulton index) the variables conditioning its displacement. Moreover we found that this species has a great capacity to resist desiccation. These characteristics give them all the requirements to successfully invade and adapt to new areas.

Keywords: *Eriocheir sinensis,* desiccation, competition, dispersal, velocity, *Procambarus clarkii.*

Introduction

The accidental introductions of non-indigenous species are largely the result of increased movement of human populations between countries and continents (Eiswerth and Jonhson, 2002; Pimentel *et al.*, 2004). The number and variety of introductions show that it is not extreme to say that biological invasions are breaking down geographical barriers (Hulme *et al.*, 2007) occurring at an unprecedented rate that not only affect the natural process of ecosystems but also cause impacts in the economy (Vitousek *et al.*, 1996; Mack *et al.*, 2000; Eiswerth and Jonhson, 2002; Hulme *et al.*, 2007). Similar to what happens in terrestrial ecosystems, aquatic ecosystems are greatly affected by biological invasions. In recent years there was an increase of aquatic invasions by invertebrates in marine, estuarine and freshwater ecosystems (Leppäkoski *et al.*, 2002). Biological invasions promote disturbances and alterations on the natural cycles, changing habitats, (e.g. altering siltation rates in estuaries and along shorelines (Mack *et al.*, 2000) and changing native species reproduction patterns (Moyle and Light, 1996). Some authors claim that after an invasion in a new habitat, exotic species are devoid of predators, which give them a competitive advantage enhancing its rapid dispersal (Eiswerth and Jonhson, 2002). However the view may not be entirely correct (Colautti *et al.*, 2004). Another important hypothesis regarding biological invasions is that sometimes the previous presence of other invaders may progressively enhance new invasions in a process called invasional meltdown (Simberloff and Von Holle, 1999; Ricciardi, 2001).

Progressive invasions in costal zones, rivers and lakes are irreversible and can displace native species with results that are impossible to predict (Rodriguez and

Suárez, 2001). In aquatic ecosystems, the crustaceans are the most invasive and prolific group (Rodriguez and Suárez, 2001). Many decapod crustaceans are a source of food and are frequently processed alive, which implies the risk of escape to natural ecosystems (Rodriguez and Suárez, 2001). Most introduced crustaceans have been reported in marine and estuarine environments (Carlton, 1996, Ruiz *et al.*, 1997; Rodriguez and Suárez, 2001). These organisms usually have an adapted life cycle, which appears to facilitate its dispersal, in some cases with humans as potential vectors (Colautti, 2004; Panov, 2006). The species we are studying is the Chinese Mitten Crab-*Eriocheir sinensis* (H. Milne Edwards, 1854) which is considered the most invasive non-indigenous crab (Rodriguez and Suárez, 2001). The Chinese mitten crab is native from waters in temperate and tropical regions between Vladivostock (RU) and South-China (Panning, 1938). It can be found in the west coast of North America (Cohen and Carlton, 1997; Rudnick *et al.*, 2003), with established populations in San Francisco Bay and its watershed (Rudnick *et al.*, 2003). Peters and Panning (1933) reviewed the available evidence for the first introduction of the Chinese crab *Eriocheir sinensis* in the North Sea, via ballast water. In fact, in continental Europe, the first reports of the Chinese mitten crab were in a tributary to the river Weser in northwest Germany in 1912 and in the Elbe in 1914 (Herborg *et al.*, 2005). In Portugal, according to local fishermen, the mitten crab appeared in the Tagus basin during the late 1980's and from 1988 to 1990 the species was abundant but the population has decreased (Cabral and Costa, 1999). In spite of this, recent distribution modeling studies both for the Iberian Peninsula and for the world demonstrate that large areas are at risk of invasion (Capinha and Anastácio, 2011; Capinha *et al.*, 2011).

The Chinese mitten crab has different morphological characters from other crabs and therefore it is easy to identify. In adult crabs, the carapace is nearly square-shaped showing slightly more width than length and has four spines in the anterior lateral margins (Rudnick *et al.*, 2000; Rudnick *et al.*, 2003). The crab also presents a frontal notch between the eyes, flanked by two small spines (Rudnick et al., 2000). In adult specimens the carapace can reach a width of 80 mm, but some larger crabs up to 100 mm have been reported (Rudnick et al., 2000). A morphological character, that clearly distinguishes it, is the dense patch of setae on the white-tipped chelae (claws) and for this it is named Chinese mitten crab (Veilleux and de LaFontaine, 2007). The "Mittens" occur in adult males and females (Rudnick et al., 2000) but in males they cover a larger area (Hoestlandt, 1959). Like many other species Chinese mitten crab have sexual dimorphism. After reaching a width greater than 10-20 mm males and females can be distinguished by the shape of the abdomen, which is rounded and large in the female and in male it is narrow and has a funnel or V-shaped (Rudnick *et al.*, 2000; Gollasch, 2006). The pigmentation of the carapace varies from brownish-yellow, mainly in juveniles, to greenish-brown in adult crabs (Hymanson *et al.*, 1999).

In freshwater ecosystems shipping activities facilitate the introductions of euryaline and marine species of crustaceans and the transfer of their diapause stages (Collauti, 2004). Economic factors such as aquaculture and fish industry have resulted in crustacean transport, outside their original range (Holdich and Pockl, 2007). In the majority of the places where *E. sinensis* is found, two main introduction pathways are considered: ballast water (Cohen and Carlton, 1997) and escapes or releases as aquaculture species (Herborg *et al.,* 2005). The most common transported life stage is the pelagical larval and it is considered the most likely form of spread by this crab (Cohen and Carlton, 1997).

As an invasive species that lives in vulnerable ecosystems, this species can promote negative ecological and economic impacts. The major impact of this crab is associated to its river bank burrowing habits that may endanger flood defenses and even endanger navigation (Holdich and Pockl, 2007). Recreational and commercial fishing is also affected (Herborg *et al.*, 2003; Herborg *et al.*, 2005). Invasive crustaceans also have an impact on native fauna by generating competition for food and shelter (Holdich and Pockl, 2007). Since this is a catadromous species, it affects estuaries which are vulnerable ecosystems combining freshwater and brackish water (Herman, *et al.*, 1999) and have a high productivity (McLusky, 1999). Chinese mitten crabs can compete with other estuarine decapod crustaceans, such as reported in the case of its juveniles which can exclude similar sized native *Carcinus maenas* from shelters (Gilbey *et al.*, 2008). Internationally, the Chinese Mitten Crab is included by the World Conservation Union, in the worst invaders list species (Lowe *et al.*, 2000). In Portugal this species is mentioned in the Decreto Lei n. º 565/99 of December 21 of the Diário da República, that forbids the introduction exotic species, being included in the annex I (non-indigenous species) and the annex III (Invasive and Ecological Risk Species).

The Chinese mitten crab is omnivorous, feeding on algae, detritus and benthic invertebrates, being an opportunistic (Rudnick *et al.*, 2000). This crab represents one of the most extreme cases of transitions from marine to freshwater habitats. It is euryhaline, eurythermic (Rodriguez and Suárez, 2001) and catadromous, spending most of the time in freshwater and only returning to estuaries to reproduce (Herborg *et al.* 2005). Chinese mitten crabs exhibit an r- selected strategy characterized by short life cycles, high fecundity and fast growth (Van der Velde *et al.*, 2000). Like other decapod crustaceans, the Chinese mitten crab is adapted to travel long distances and to colonize new sites (Green, 1961 *in* Rodriguéz and Suárez, 2001). Its life cycle also provides some resistance and adaptation to different environments because they produce planktonic larvae which act as resistant propagules (Panov, 2006). Their fecundity is remarkable, producing numerous (hundreds of thousands) of larvae which, under native conditions, are regulated by predation or loss in the environment, but in invaded areas may have a high rate of survival (Rodriguéz and Suárez, 2001). During reproduction, mature males and females migrate downstream during fall and winter to reproduce in brackish water (Anger, 1991). After reproducing, Chinese mitten crab return to the costal banks and die (Panning, 1938; Zhao 1999 *in* Rudnick *et al.*, 2000; Rodriguez and Suárez, 2001; Herborg *et al.*, 2005; Veilleux and de LaFontaine, 2007). In the marine life cycle phase, after hatching, larvae go through several developmental stages: a brief non-feeding pre-zoea stage, five zoea stages and one megalopea stage (Anger, 1991; Montú *et al.*, 1996). The upstream migration into rivers to complete the life cycle in fresh water begins after the megalopal stage when larvae metamorphose into juvenile crabs, usually in late summer or early fall (Rudnick *et al.*, 2005; Veilleux and de LaFontaine, 2007). Migrations of juveniles are enormous journeys taking them as far as 1.250 km from the cost in freshwater streams (Dan *et al. in* Rudnick *et al.*, 2000). In spite of all this general information regarding the movement of adults and juveniles, the timings for these migrations and for the life cycle processes have never been studied in the Tagus River. However, it is also known that during *E. sinensis* migrations some overland occurs (Panning, 1938; Hanson and Sytsma, 2005; Bouma and Soes, 2010) and this provides opportunities for invasion of new areas. Our purpose is to analyze the dispersal capacity of *E. sinensis* under different environmental conditions. We studied its average speed in and out of the water and its survival under desiccation conditions. Since some authors mention that previous invasions may interfere with the establishment of new invaders we also studied the dispersal interactions of *E. sinensis* with *P. clarkii,* which is a previous invader in the area.

Material and Methods

All *E. sinensis* used in the experiments were captured with 20 mm mesh fyke nets in the Tagus River estuary, near Vila Franca de Xira, Portugal (38.95537º N, 8.98069º W), from November 2010 to May 2011 (see the appendix for exact dates). Individuals were captured as necessary according the experiments and the crab's population structure at each date was not evaluated. However, since there was no intentional selection of the individuals inside the nets, our sample should correspond to the structure present in the area. After being captured, crabs were maintained in the laboratory inside acclimation tanks at 17^{0}C for 5 days in dechlorinated tap water, for a minimum period of 48 hours and were fed carrots during this period.

Five crabs were placed in each tank (65 cm long, 45 cm wide and 40 cm deep). *P. clarkii* used in the experiments on interactions with *E. sinensis* were captured in the Divor stream (38.88210º N; 8.17323º W) and similarly to crabs these were transported to the laboratory and acclimated in tanks, under the same conditions. Before each experiment crustaceans were numbered with a Dykem type marker (Ramalho *et al.*, 2010), weighted and measured. All statistical analysis was performed using SPSS-

PAWS Statistics 20. In accordance to the national legislation, i.e. Decreto Lei nº 565/99, no specimens were returned to nature.

- **Desiccation experiment**

An *E. sinensis* desiccation survival experiment was made at 16^{0}C and at 24^{0}C (51% and 40% relative humidity, respectively) at a photoperiod of 12L/12D. These were the minimum and the maximum temperature, of the acclimated room attainable during that period. A total of 60 crabs were used, with 30 in each experiment randomly divided into 6 groups of 5 individuals, with densities interspersed. We allocated to each group a period of time (0, 20, 40, 60, 80 or 100 hours). In addition, crabs were monitored every hour and the time of death was recorded. After each death, the final weight was recorded in order to calculate the percentage of water that was lost. A Probit Analysis was used for the calculation of the LT_{50} and LT_{90} values, i.e. the time for death of 50 or 90% of the animals, respectively. Crabs used at 16^{0}C had a mean width of 60. 54 mm (± 7.55 S.D.), mean length of 54.17 mm (± 6. 81 S.D.), mean weight of 110.98 g (± 45.78 S.D.) and a mean Fulton condition index (Ricker, 1975) of 0.47 (± 0.06 S.D.). Crabs used at 24^{0}C had a mean width of 62.65 mm (± 6.15 S.D.), mean length of 58.17 mm (± 5.79 S.D.), mean weight of 146.8 g (± 46.54 S.D.) and a mean Fulton condition index of 0.73 (± 0.13 S.D.). In each experiment the crabs were individually placed into plastic containers (15 cm long 15 cm wide and 12 cm deep) without water. These experiments were performed between November 2010 and February 2011[1].

- Dispersal experiment

To determine the dispersion velocity of *E. sinensis* in and out of water we made an experiment in the Mitra hydraulic canal (Évora, Portugal). The canal was 50 m long, 20 cm wide and when water was used, we filled it with freshwater to a 10 cm depth. 30 crabs were used for each experiment and these were randomly allocated into three densities: 1 crab, 5 crabs and 10 crabs, in a total of 49 trials. The time limit used was 3 minutes because after more than 3 minutes, crabs could reach the end of the canal. After the time limit, the distance traveled by each crab was recorded. We performed two sets of experiments, one set with water in the canal and another set without water. The same group of crabs was used in each experiment in the water and out of the water although treatment allocation was random. These experiments (with and without water) assessed the speed as well as the possible influence of environmental variables such as temperature, relative humidity, wind speed, pH and availability of oxygen in the water. In the dispersal experiment in the water we registered water temperature, pH and dissolved O_2 while in the dispersal experiment out of water we registered air temperature, relative humidity and wind speed. This experiment was performed between December 2010 and May 2011 to test the effect of different environmental conditions.

Crabs used in these dispersal experiments in the water had a mean width of 60.16 mm (±7.26 S.D.), a mean length of 54.71 mm (± 6.12 S.D.), a mean weight of 113.20 g (± 45.02 S.D.) and a mean Fulton condition index of 0.49 (± 0.07 S.D.). In the experiments in the water, mean water temperature was 12.49^0 C (± 2.35 S.D.), pH was 7.74 (± 0.18 S.D.) and dissolved O_2 was 12.45 mg/l (± 1.85 S.D.). Crabs used in dispersal experiments out of the water had a mean width of 60.60 mm (± 6.81), a mean length of 54.77 mm (± 6.06 S.D.), a mean weight of 113.73 g (± 40.96 S.D.) and a mean Fulton condition index of 0.49 (±0.06 S.D.). In the experiments out of water, mean air temperature was 16.20 C^0 (± 7.11 S.D.), relative humidity was 53.57 % (± 15.64 S.D.) and wind speed was 2.01 m s^{-1} (± 0.83 S.D.).

Crab velocity was calculated for each experiment and ANCOVA (Analysis of Covariance) was applied to determine which variables had an effect on the distance traveled. In the ANCOVAs, density was considered a fixed factor and the covariates were the values of the environmental variables (temperature, oxygen and relative humidity...) and of the biological traits of the animals (size, weight, length). We excluded from the analysis potential covariables presenting a high and significant correlation with a biologically significant variable already included in the ANCOVA. ANCOVA assumptions, including the homogeneity of regression slopes, were tested prior to analysis.

- ***Procambarus clarkii* interaction with *Eriocheir sinensis***

Another dispersal experiment (in the water) was made in the canal, this time with the presence of *P.clarkii*. The purpose was to test whether the presence of *P. clarkii* influences or not the dispersion velocity of *E. sinensis*. 20 crabs were used with a mean carapace width of 60.86 mm (± 7.00 S.D.), a mean length of 54.25 mm (± 6.21 S.D.), a mean weight of 113.34 g (± 47.08 S.D.) and a mean Fulton condition index of 0.48 mm (± 0.04 S.D.). 20 crayfish were used with a mean CT of 48.74 mm (± 3.03 S.D.) and a mean weight of 23.3 g (± 5.51 S.D.). We used 26 replicates without crayfish, as controls and 26 replicates with crayfish and crabs. At each 2.5 m interval a crayfish was fixed to the bottom of the hydraulic canal with a lead weight (140 g), bound with rubber bands. After the time limit (3 minutes) for each replicate in each density the distance traveled by individual crabs was recorded and the average velocity was calculated. The results of the experiments were analyzed using a chi-square test on a contingency table.

In a laboratory experiment we tested if the presence of *P. clarkii* influenced the choice of a path by crabs. We used a tank (60 cm long, 40 cm wide and 30 cm deep) with a longitudinal division (20 cm) and a transversal gate. 20 crabs were used, with a mean width of 61.07 mm (± 6.96 S.D.), a mean length of 54.49 mm (± 616. S.D.), a mean Fulton condition Index of 0.47 (± 0.04 S.D.) and a mean weight of 114.06 g (± 46.83 S.D.). 20 crayfish were also used, with a mean CT (cephalothorax) of 46.92 mm (± 8.26 S.D.) and a mean weight of 23.3 g (± 23.09 S.D.). In the experiments, a crab was placed at one end of the tank, separated from the available paths by a gate. After one minute we removed the gate with the help of 2 strings and a webcam placed at the top of the tank recorded the path taken by the crab. Each time a replicate without crayfish was performed another run was then performed placing a crayfish in the path previously chosen by the crab. Crayfish were anchored to the bottom of the tank with a 140 g lead weight. Controls and treatments were replicated 20 times.

Results

Desiccation Experiment

The results of the desiccation experiments show that *E. sinensis* has a great ability to survive desiccation at the studied temperatures. At 16^0C the first death occurred only after 34 hours and the average percentage of weight decrease by water loss at the time of death was 20% (± 2.8 S.D.). At 24^0C there was a lower capacity for survival and a higher percentage of water loss, which was 22% (± 5.55 S.D.). The first death occurred after 9 hours.

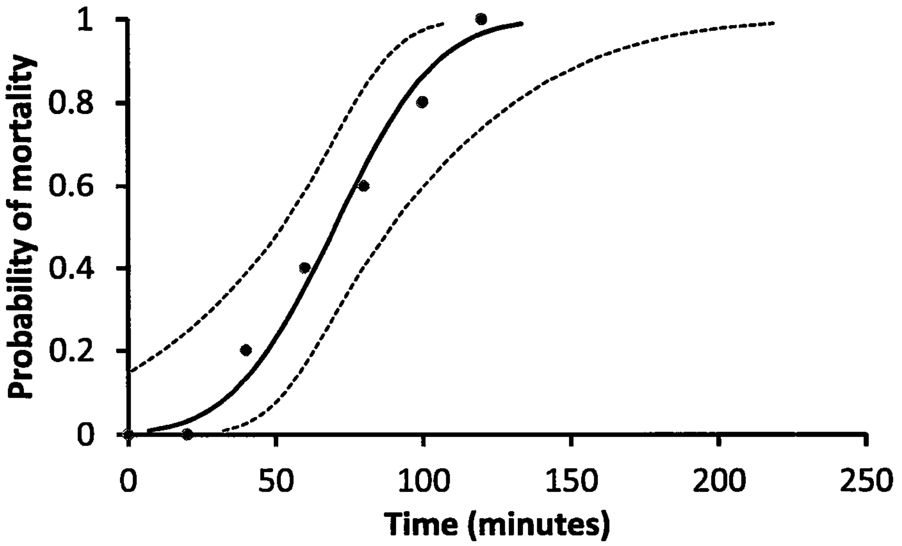

Figure 1- Probability of *Eriocheir sinensis* mortality out of water as a function of time, under laboratory conditions at 16^0C and 51 % relative humidity. The curve was obtained by probit analysis and the 95% confidence limits are presented.

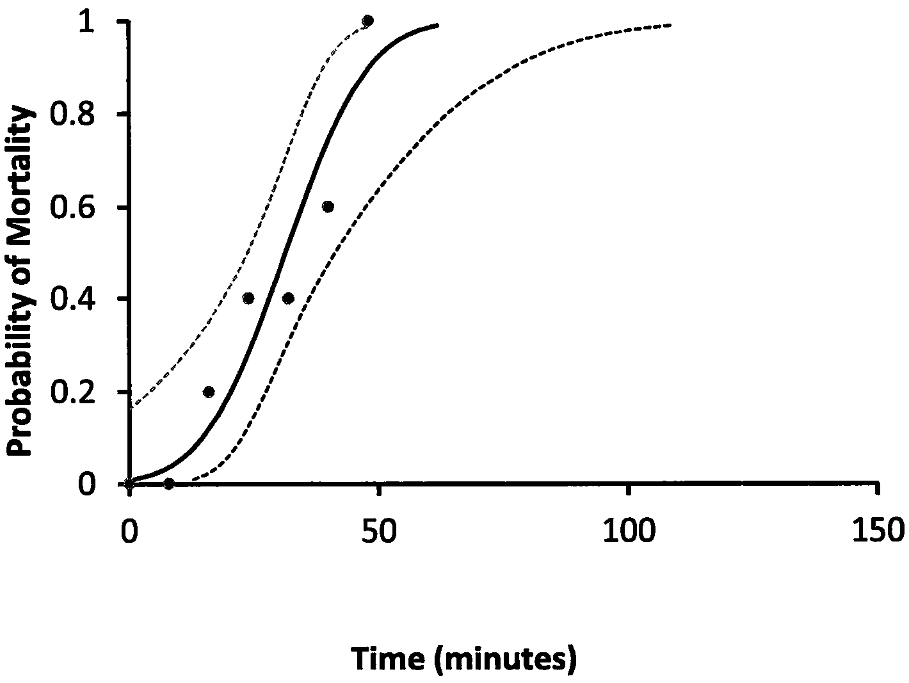

Figure 2- Probability of *Eriocheir sinensis* mortality out of water as a function of time, under laboratory conditions at 24^0C and 40 % relative humidity. The curve was obtained by probit analysis and the 95% confidence limits are presented.

At 16^0C the LT_{50} was above the value obtained at 24^0C, indicating a greater capacity to survive at lower temperatures and higher humidity (Figs 1 and 2). Probit analysis indicated a LT_{50} of 70 hours at 16^0C and a LT_{50} of 31 hours at 24^0C (table 1). The LT_{90} at 16^0C is also large (105 hours) in comparison with the LT_{90} at 24^0C (48 hours).

Table 1- Estimated time to 50% (LT_{50}) and 90% (LT_{90}) mortality of *E. sinensis* out of water at different conditions. (S.E.- Standard errors CL- 95% Confidence limits and RH- Relative humidity)

Conditions	**LT_{50}**	**CL**	**LT_{90}**	**CL**	**S.E.**
24^0C/40% RH	31.39	23.759-41.305	48.159	39.115-77.059	0.023
16^0C/51% RH	70.165	52.18-89.204	105.042	86.776-156.194	0.010

Table 2- Average weight difference before and after death by desiccation, at 16^0C and at 24^0C and average percentage of water loss by evaporation.

Conditions	**Mean initial weigth (g)**	**S.D.**	**Mean final weigth loss (g)**	**S.D.**	**Water lost (%)**	**S.E.**
24^0C/40% RH	110.98	45.01	89.12	38.02	20	0.51
16^0C/51% RH	146.8	45.75	31.95	35.91	22	1

Dispersal experiment in the water

In the dispersal experiment in the water, there were high correlations between some of the variables, namely dissolved oxygen and pH and between all the crab's body measurements (length, width and weight) and therefore only one of each was used in the analysis (Table 3). A test of the homogeneity of the regression slopes before applying an ANCOVA, showed that there was no interaction between the covariates and the density (fixed factor) (see table E in appendix). ANCOVA (Analysis of Covariance) showed that the variables that influence the dispersal distance were density, temperature, and condition (Fulton index) as we can see in Table 4.

Table 3- Pearson correlation coefficient among variables affecting dispersal distance in the water.

		Water temperature	pH	Oxygen	Fulton	Width	Length	Weight
Water temperature	Pearson Correlation	1	0.097	-.321**	0.014	.183**	0.235	0.176
	Sig. (2-tailed)		0.134	0	0.83	0.005	0	0.006
	N	240	240	240	240	240	240	240
pH	Pearson Correlation	0.097	1	.688**	.189**	0.009	0.195	0.049
	Sig. (2-tailed)	0.134		0	0.003	0.888	0.002	0.446
	N	240	240	240	240	240	240	240
Oxygen	Pearson Correlation	-.321**	.688**	1	.153*	-0.015	.087**	.018**
	Sig. (2-tailed)	0	0		0.018	0.82	0.18	0.787
	N	240	240	240	240	240	240	240
Fulton	Pearson Correlation	0.014	.189**	.153*	1	-0.102	0.16	.235**
	Sig. (2-tailed)	0.83	0.003	0.018		0.114	0.013	0
	N	240	240	240	240	240	240	240
Width	Pearson Correlation	.183**	0.009	-0.015	-0.102	1	.879**	0.921
	Sig. (2-tailed)	0.005	0.888	0.82	0.114		0	0
	N	240	240	240	240	240	240	240
Length	Pearson Correlation	.235**	.195**	0.087	.160*	.879**	1**	.891**
	Sig. (2-tailed)	0	0.002	0.18	0.013	0		0
	N	240	240	240	240	240	240	240
Weight	Pearson Correlation	.176**	0.049	0.018	.235**	.921**	.891**	1
	Sig. (2-tailed)	0.006	0.446	0.787	0	0	0	
	N	240	240	240	240	240	240	240

Table 4- ANCOVA Output using the distance traveled by *Eriocheir sinensis* in the water as the dependent variable. The density was the fixed factor and all the other variables were considered covariates.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1866.657[a]	6	311.109	8.790	.000
Intercept	1266.609	1	1266.609	35.786	.000
Water temperature	950.604	1	950.604	26.857	.000
Oxygen	67.224	1	67.224	1.899	.169
Fulton	141.568	1	141.568	4.000	.047
Length	34.541	1	34.541	.976	.324
Density	222.873	2	111.437	3.148	.045
Error	8246.909	233	35.394		
Total	52453.394	240			
Corrected Total	10113.566	239			

In the water, crabs traveled an average distance of 13.28 m (S.D. = 6.51), at an average velocity of 0.074 m/s^{-1}.

Dispersal experiment out of water

In the dispersal experiment out of water, there were high correlations between three of the environmental variables, namely relative humidity, air temperature and wind speed and between all the crab's body measurements (length, width and weight) and therefore only one of each was used in the analysis (Table 5). The test of the homogeneity of the regression slopes, performed before the ANCOVA, showed that there was no interaction between the covariates and the density (fixed factor) (see table F in appendix). The ANCOVA (Analysis of Covariance) showed that the variables influencing the dispersal distance were density, body length and relative humidity as we can see in Table 6.

Table 5- Pearson correlation coefficient among variables affecting dispersal distance out of water.

		Air temperature	Relative Humidity	Wind speed	Fulton	Width	Length	Weight
Air temperature	Pearson Correlation	1	-.921**	.626**	-.197**	0.073	-.032**	.022**
	Sig. (2-tailed)		0	0	0.002	0.261	0.623	0.73
	N	240	240	240	240	240	240	240
Relative Humidity	Pearson Correlation	-.921**	1	-.622**	.139*	-.071**	-0.019	-.039**
	Sig. (2-tailed)	0		0	0.031	0.272	0.768	0.55
	N	240	240	240	240	240	240	240
Wind speed	Pearson Correlation	.626**	-.622**	1	-0.1	-.094**	-.145**	-0.101
	Sig. (2-tailed)	0	0		0.131	0.147	0.024	0.117
	N	240	240	240	240	240	240	240
Fulton	Pearson Correlation	-.197**	.139*	-0.098	1	-.005**	.169*	0.323
	Sig. (2-tailed)	0.002	0.031	0.131		0.937	0.009	0
	N	240	240	240	240	240	240	240
Width	Pearson Correlation	0.073	-0.071	-0.094	-0.01	1	0.911	0.928
	Sig. (2-tailed)	0.261	0.272	0.147	0.937		0	0
	N	240	240	240	240	240	240	240
Length	Pearson Correlation	-0.032	-0.019	-.145*	.169**	0.911	1	.898*
	Sig. (2-tailed)	0.623	0.768	0.024	0.009	0		0
	N	240	240	240	240	240	240	240
Weight	Pearson Correlation	0.022	-0.039	-0.101	.323**	0.928	0.898	1
	Sig. (2-tailed)	0.73	0.55	0.117	0	0	0	
	N	240	240	240	240	240	240	240

Table 6- ANCOVA results using the distance traveled by *Eriocheir sinensis* out of water as the dependent variable. The density was the manipulated factor and all the other variables were considered covariates.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	901.455[a]	5	180.291	39.144	.000
Intercept	.902	1	.902	.196	.658
Relative humidity	632.999	1	632.999	137.435	.000
Fulton	10.026	1	10.026	2.177	.141
Length	72.051	1	72.051	15.643	.000
Density	113.145	2	56.572	12.283	.000
Error	1077.761	234	4.606		
Total	4011.560	240			
Corrected Total	1979.216	239			

In the dispersal experiment out of water, crabs traveled an average distance of 2.91 m (S.D. = 2.87) at an average velocity of 0.016 m/s^2.

Procambarus clarkii* interaction with *Eriocheir sinensis

The results of the one-way ANOVA applied to canal data showed that the distance traveled by crabs is not influenced by the presence of crayfish ($p<0.965$). In the experiment without crayfish the average distance traveled by crabs was 10.528 m (S.D.

= 6.64) and the mean velocity was 0.058 m/s^{-1}. In the dispersal experiment with crayfish the average distance traveled by crabs was 10.604 m (S.D. = 5.37) and the mean velocity was also 0.058 m/s^{-1}.

The laboratory experiments in the tank showed that the path chosen by crabs was not affected by crayfish presence (X^2= 0.921; df= 1; N= 40; p= 0.337).

Discussion

This study demonstrated that adult Chinese mitten crabs are capable of dispersing fast both in and out of the water. For crabs, the most important land barrier for colonization is the dehydration (Thurman, 1998) and physiological traits for desiccation resistance such as survival time, water evaporation rate, salinity and water balance can limit colonization for different habitats (Issartel, *et al.*, 2005). In our study we found a larger resistance to desiccation when exposed to 16^0C and 51% relative humidity, under which a maximum survival time of 104 hours was obtained. At higher temperatures and lower humidity, resistance to desiccation decreases which is probably related to the larger water loss. Evaporation depends largely on two factors, temperature and humidity (Bergmann *et al.*, 2000). In marine crustaceans, evaporation during desiccation can occur from the residual water film from the body surface, through the gills (Herreid, 1969) or through permeability of the integument (Thurman, 1998). However, water may be lost from the gill chamber without compromising cellular metabolism (Thurman, 1998). Water loss by evaporation can lower body temperature and can promote the invasion of habitats that are thermally hostile to ectothermic invertebrates (Thurman, 1998). Terrestrial decapod crustaceans such as *Birgus latro, Gecarcoidea lalandii, Sudanonautes africanus africanus* lose respectively 22%, 15-18 % and 20% of body weight before death by desiccation (Tsai *et al.*, 1998). In our experiments *E. sinensis* lost 20 to 22% body weight by water evaporation which is a similar value and may indicate a physiological threshold for these animals. In our study, the effect of weight or body size variables on the survival time out of water was not explored. Nevertheless, some studies indicate a possible relationship between survival time and these variables, e.g. conditioning physiological parameters in shore crabs (Rasmussen and Andersen, 1996) and decreasing water permeability with increasing size in *Carcinus maenas* (Smith, 1970). Moreover in *Ligia exotica* and *L. taiwanensis*, the larger the body sizes the larger the survival time (Tsai *et al.*, 1998).

According to our experiments, successful and fast dispersal can occur in or out of water. Our results showed that the distance traveled is influenced by environmental and biological variables. Relative humidity, body size and density conditioned dispersion out of water. In ectotherms, changes in body temperature and dehydration can alter locomotor performance limits (Weinstein, 1998). In the dispersal experiment out of water, at densities five and ten, crabs tended to cluster, possibly to maintain the temperature or to prevent water loss by evaporation. This aggregation can occur during migrations, when *E. sinensis* move across land to get around weirs (Herborg *et al.*, 2003) and may therefore be a behavioral mechanism increasing the survival time or the performance out of water.

In the submerged dispersal experiment, temperature was crucial but density and animal condition (Fulton index) were also important for the locomotion speed of the crabs. In dispersal experiments, in and out of the water, temperature significantly influenced the distance traveled by crabs. In fact, as for many other species, niche modeling studies showed that temperature related variables have an influence on *E. sinensis* distribution (Capinha *et al.*, 2011; Capinha and Anastácio, 2011). The success of the autonomous dispersion is also enhanced by the average speed that an organism can reach. Compared with other decapod crustaceans (e.g. *Carcinus maenas* and *Hemigrapsus sanguineus*), *E. sinensis* has a high spread rate (Ruiz *et al.*, 1997). According to Panning (1938), Chinese mitten crabs migrate downstream between 8 and 12 Km per day. In one year its range expansion can reach 40 Km (Herborg *et al.*, 2005). In this study the mean velocity in the water without current was 0.074 m/s (approx. 6.4 km/day) which is a bit lower than values for downstream migration. Out of the water the mean velocity was 0.016 m/s (approx. 1.4 km/day), which can allow overland dispersion to nearby water systems and will facilitate overcoming river flow barriers.

This study also tested whether the presence of *P. clarkii* could influence *E. sinensis* dispersion. Eco-ethological studies testing the interference of river crabs (*Potamon fluviatile*) and crayfish (*Austropotamobius pallipes*) suggest that both choose similar food, share the same habitat and have similar temporal activity patterns (Barbaresi and Gherardi, 1997) and therefore this could constrain *E. sinensis* dispersion in our case. However, in the laboratory experiment we found that the crab's path choice was not influenced by the presence of crayfish. In fact, we observed that crayfish had a more aggressive behavior, but this did not intimidate the crabs or alter their path choice. Several factors can condition interspecific interactions, such as differential susceptibility to predation, reproductive interference (Barbaresi and Gherardi, 1997), ontogenic phase (Anastácio *et al.*, 2011) or uneven body sizes (Butler and Stein, 1985; Schroder *et al.*, 2009). Some authors also reported that experimental competition studies may be influenced by the laboratory conditions, therefore providing partial results (Butler and Stein, 1985). In spite of this, in a crab (*Potamon fluviatile)* and crayfish (*Austropotamobius pallipes*) interaction study, the crab had a more aggressive behavior and dominated over crayfish (Barbaresi and Gherardi, 1997). In laboratory conditions, mitten crab juveniles can successfully exclude similar sized green crabs (*Carcinus maenas*) from shelters (Gilbey *et al.*, 2007)." In our dispersal experiment with crayfish we also found that the presence of *P. clarkii* did not influence the movement of the crab. Therefore the previous invasion by *P.clarkii* may not have a negative impact on *E.sinensis* dispersion.

With this study we obtained information about the capacity of *E. sinensis* to spread. These findings will also be important to understand movements during the seasonal migrations, which can result in the invasion of new water bodies. Studies about the interference of biotic and climatic conditions upon the dispersal of organisms are important to predict the likelihood or the timing of new invasions.

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Appendix

Table A- Information regarding dispersal experiments

E. sinensis capture	Date	Number of individuals
1st capture	20/11/2010	97
2nd capture	20/12/2010	55
3rd capture	03/04/2011	51
4th capture t	10/05/2011	48

Table B- Information regarding the desiccation experiments

Temperature	Date	Number of individuals
24^0 C	25/11/2010	30
16^0 C	21/02/2011	30

Table C- Dates of the dispersal experiments

Experiment	Dates
Water dispersal	27/12/2010
	17/01/2012
	21/01/2011
	11/04/2011
	17/04/2011
Out of water dispersal	22/12/2010
	23/12/2010
	21/01/2011
	06/05/2011

Table D- Values of the water variables

Density	Distance (m)	Temperature (C^0)	Ph	O2 (mg/l)	Fulton	Width (mm)	Length (mm)	Weight (g)
1	5.20	14.20	7.70	12.10	.55	81.66	73.35	299.50
1	7.10	14.20	7.70	12.10	.47	66.05	58.68	136.00
1	9.60	14.20	7.70	12.10	.43	62.37	58.04	104.50
1	.0	14.20	7.70	12,.10	.54	64.82	57.17	147.50
1	1.10	14.20	7.70	12.10	.45	60.34	53.57	98.50
1	13.60	14.20	7.70	12.10	.53	60.61	53.92	118.00
1	12.30	14.20	7.70	12.10	.52	57.79	52.83	100.50
1	.0	14.20	7.70	12.10	.47	71.47	64.63	170.00
1	.0	14.20	7.70	12.10	.41	61.23	53.58	95.00
1	10.50	14.20	7.70	12.10	.52	61.66	54.89	122.50
1	22.70	14.20	7.70	12.10	.56	69.28	64.31	186.00
1	16.50	14.20	7.70	12.10	.53	68.30	60.98	168.50
1	10.30	14.20	7.70	12.10	.56	56.95	51.46	103.50
1	12.70	14.20	7.70	12.10	.46	54.16	47.38	72.50
1	16.00	14.20	7.70	12.10	.50	51.05	46.26	67.00
1	16.50	14.20	7.70	12.10	.41	66.84	59.42	122.50
1	5.50	14.20	7.70	12.10	.49	68.22	60.04	156.50
1	10.30	14.20	7.70	12.10	.45	50.82	44.98	58.50
1	16.60	14.20	7.70	12.10	.45	63.60	57.20	117.00
1	17.30	14.20	7.70	12.10	.49	54.51	49.24	79.00
1	18.20	13.10	7.98	13.57	.27	53.49	58.96	41.00
1	15.00	13.10	7.98	13.57	.63	50.56	56.06	82.00
1	10.40	13.10	7.98	13.57	.70	46.57	51.61	70.50
1	2.40	13.10	7.98	13.57	.67	48.08	50.82	74.50
1	9.90	13.10	7.98	13.57	.69	56.69	62.73	125.00
1	7.80	13.10	7.98	13.57	.72	57.19	62.72	135.00
1	3.30	13.10	7.98	13.57	.66	44.57	50.11	58.50
1	18.70	13.10	7.98	13.57	.52	65.15	57.27	143.00
1	17.40	10.00	7.48	12.54	.52	61.00	57.30	119.00
1	20.00	10.10	7.48	12.54	.52	56.80	50.40	95.50
1	13.60	10.20	7.48	12.54	.47	63.50	56.80	120.50
1	18.00	10.30	7.48	12.54	.51	56.35	50.65	91.50
1	16.50	10.30	7.48	12.54	.44	60.90	52.45	100.00
1	3.80	11.20	7.48	12.54	.56	55.70	50.75	96.00
1	16.70	11.30	7.48	12.54	.41	48.10	43.30	46.00
1	24.70	11.30	7.48	12.54	.44	58.40	51.90	88.50
1	22.80	11.40	7.48	12.54	.57	45.50	41.30	54.00
1	15.40	11.50	7.48	12.54	.50	57.00	50.85	93.00
1	17.90	8.50	7.48	12.54	.48	60.90	53.50	109.50
1	19.10	8.70	8.05	15.87	.52	48.70	43.90	60.50
1	13.50	9.00	8.05	15.87	.47	52.00	45.00	66.00
1	12.20	9.10	8.05	15.87	.50	64.20	57.70	131.50
1	17.20	9.20	8.05	15.87	.51	68.40	61.40	162.00
1	12.60	11.60	8.05	15.87	.57	70.60	64.60	199.00
1	11.20	11.70	8.05	15.87	.53	68.20	60.60	168.50
1	16.90	11.70	8.05	15.87	.48	54.40	49.40	77.00
1	15.20	11.80	8.05	15.87	.45	58.00	51.60	88.50
1	17.40	11.70	8.05	15.87	.39	58.90	52.40	79.50
1	15.90	11.80	8.05	15.87	.53	66.00	58.60	153.00
1	14.80	11.70	8.05	15.87	.54	63.00	56.60	134.50
1	11.30	11.60	8.05	15.87	.44	68.00	60.90	139.50
1	22.40	11.60	8.05	15.87	.49	65.60	57.70	137.00
1	7.80	11.60	8.05	15.87	.50	62.00	56.00	119.00
1	12.70	11.60	8.05	15.87	.43	63.00	56.80	107.00
1	9.20	11.50	8.05	15.87	.55	62.60	56.40	134.50
1	10.80	11.30	7.66	10.46	.48	49.30	44.05	57.50
1	7.00	11.40	7.66	10.46	.46	49.60	44.10	56.00
1	10.00	11.40	7.66	10.46	.46	50.40	44.85	58.50
1	7.20	11.40	7.66	10.46	.50	57.60	50.60	95.50
1	8.00	11.50	7.66	10.46	.50	62.29	55.80	120.00
1	9.20	13.40	7.66	10.46	.44	56.70	49.80	81.00
1	7.90	14.10	7.66	10.46	.47	60.70	54.06	106.00

1	.0	14.90	7.66	10.46	.47	57.30	50.10	89.00
1	11.10	15.80	7.66	10.46	.46	61.20	54.25	104.50
1	16.70	16.50	7.66	10.46	.50	59.70	52.70	105.50
1	11.00	11.70	7.66	10.46	.55	78.40	69.30	264.50
1	13.50	11.80	7.66	10.46	.48	61.10	54.12	110.50
1	19.70	11.80	7.66	10.46	.45	53.80	48.20	70.50
1	21.00	11.80	7.66	10.46	.45	63.05	57.60	112.00
1	21.20	11.80	7.66	10.46	.44	60.05	53.60	94.50
1	18.80	11.70	7.66	10.46	.52	72.14	62.79	194.50
1	11.30	11.60	7.66	10.46	.44	72.05	64.40	164.50
1	14.90	11.60	7.66	10.46	.41	59.00	52.60	83.50
1	9.10	11.60	7.66	10.46	.57	64.23	56.99	150.50
1	16.40	11.60	7.66	10.46	.45	54.20	49.20	71.50
1	.50	11.50	7.66	10.46	.51	59.10	54.10	104.50
1	16.10	11.50	7.66	10.46	.48	64.40	58.60	129.50
1	1.40	11.50	7.66	10.46	.53	68.15	61.30	166.50
1	.40	11.40	7.66	10.46	.45	64.90	58.75	124.00
1	.0	11.40	7.66	10.46	.49	62.20	54.30	119.00
5	8.30	15.10	7.60	12.04	.55	81.66	73.35	299.50
5	11.90	15.10	7.60	12.04	.47	66.05	58.68	136.00
5	12.00	15.10	7.60	12.04	.43	62.37	58.04	104.50
5	16.40	15.10	7.60	12.04	.54	64.82	57.17	147.50
5	7.40	15.10	7.60	12.04	.45	60.34	53.57	98.50
5	16.30	15.10	7.60	12.04	.53	60.61	53.92	118.00
5	15.90	15.10	7.60	12.04	.52	57.79	52.83	100.50
5	11.70	15.10	7.60	12.04	.47	71.47	64.63	170.00
5	1.00	15.10	7.60	12.04	.41	61.23	53.58	95.00
5	14.40	15.10	7.60	12.04	.52	61.66	54.89	122.50
5	15.60	14.20	7.70	12.10	.56	69.28	64.31	186.00
5	18.30	14.20	7.70	12.10	.53	68.30	60.98	168.50
5	15.40	14.20	7.70	12.10	.56	56.95	51.46	103.50
5	14.62	14.20	7.70	12.10	.46	54.16	47.38	72.50
5	17.00	14.20	7.70	12.10	.50	51.05	46.26	67.00
5	19.10	14.20	7.70	12.10	.41	66.84	59.42	122.50
5	7.60	14.20	7.70	12.10	.49	68.22	60.04	156.50
5	10.70	14.20	7.70	12.10	.45	50.82	44.98	58.50
5	19.50	14.20	7.70	12.10	.45	63.60	57.20	117.00
5	5.00	14.20	7.70	12.10	.49	54.51	49.24	79.00
5	14.30	13.10	7.98	13.57	.27	53.49	58.96	41.00
5	10.40	13.10	7.98	13.57	.63	50.56	56.06	82.00
5	9.20	13.10	7.98	13.57	.70	46.57	51.61	70.50
5	.40	13.10	7.98	13.57	.67	48.08	50.82	74.50
5	9.60	13.10	7.98	13.57	.69	56.69	62.73	125.00
5	12.00	13.10	7.98	13.57	.72	57.19	62.72	135.00
5	13.80	13.10	7.98	13.57	.66	44.57	50.11	58.50
5	23.90	13.10	7.98	13.57	.52	65.15	57.27	143.00
5	13.60	9.40	7.48	12.54	.52	61.00	57.30	119.00
5	19.60	9.40	7.48	12.54	.52	56.80	50.40	95.50
5	13.60	9.40	7.48	12.54	.47	63.50	56.80	120.50
5	20.50	9.40	7.48	12.54	.51	56.35	50.65	91.50
5	14.60	9.40	7.48	12.54	.44	60.90	52.45	100.00
5	16.40	9.50	7.48	12.54	.56	55.70	50.75	96.00
5	18.90	9.50	7.48	12.54	.41	48.10	43.30	46.00
5	24.80	9.50	7.48	12.54	.44	58.40	51.90	88.50
5	23.30	9.50	7.48	12.54	.57	45.50	41.30	54.00
5	21.00	9.50	7.48	12.54	.50	57.00	50.85	93.00
5	24.50	10.50	7.48	12.54	.48	60.90	53.50	109.50
5	24.70	10.50	7.48	12.54	.52	48.70	43.90	60.50
5	20.50	10.50	8.05	15.87	.47	52.00	45.00	66.00
5	17.90	10.50	8.05	15.87	.50	64.20	57.70	131.50
5	24.20	10.50	8.05	15.87	.51	68.40	61.40	162.00
5	14.80	11.50	8.05	15.87	.57	70.60	64.60	199.00
5	11.50	11.50	8.05	15.87	.53	68.20	60.60	168.50
5	15.50	11.50	8.05	15.87	.48	54.40	49.40	77.00
5	11.30	11.50	8.05	15.87	.45	58.00	51.60	88.50
5	11.40	11.50	8.05	15.87	.39	58.90	52.40	79.50

5	19.40	11.70	8.05	15.87	.53	66.00	58.60	153.00
5	15.70	11.70	8.05	15.87	.54	63.00	56.60	134.50
5	1.90	11.70	8.05	15.87	.44	68.00	60.90	139.50
5	17.40	11.70	8.05	15.87	.49	65.60	57.70	137.00
5	19.90	11.70	8.05	15.87	.50	62.00	56.00	119.00
5	8.10	11.70	8.05	15.87	.43	63.00	56.80	107.00
5	13.60	11.70	8.05	15.87	.55	62.60	56.40	134.50
5	13.50	12.40	7.71	10.46	.48	49.30	44.05	57.50
5	11.30	12.40	7.71	10.46	.46	49.60	44.10	56.00
5	.0	12.40	7.71	10.46	.46	50.40	44.85	58.50
5	5.50	12.40	7.71	10.46	.50	57.60	50.60	95.50
5	7.00	12.40	7.71	10.46	.50	62.29	55.80	120.00
5	13.40	11.70	7.71	10.46	.44	56.70	49.80	81.00
5	7.50	11.70	7.71	10.46	.47	60.70	54.06	106.00
5	.0	11.70	7.71	10.46	.47	57.30	50.10	89.00
5	14.50	11.70	7.71	10.46	.46	61.20	54.25	104.50
5	16.70	11.70	7.71	10.46	.50	59.70	52.70	105.50
5	9.90	11.70	7.71	10.46	.55	78.40	69.30	264.50
5	15.30	11.70	7.71	10.46	.48	61.10	54.12	110.50
5	15.30	11.70	7.71	10.46	.45	53.80	48.20	70.50
5	16.40	11.70	7.71	10.46	.45	63.05	57.60	112.00
5	21.50	11.70	7.71	10.46	.44	60.05	53.60	94.50
5	22.70	11.80	7.71	10.46	.52	72.14	62.79	194.50
5	15.40	11.80	7.71	10.46	.44	72.05	64.40	164.50
5	17.20	11.80	7.71	10.46	.41	59.00	52.60	83.50
5	13.90	11.80	7.71	10.46	.57	64.23	56.99	150.50
5	22.00	11.80	7.71	10.46	.45	54.20	49.20	71.50
5	.70	11.80	7.71	10.46	.51	59.10	54.10	104.50
5	24.60	11.80	7.71	10.46	.48	64.40	58.60	129.50
5	21.00	11.80	7.71	10.46	.53	68.15	61.30	166.50
5	7.60	11.80	7.71	10.46	.45	64.90	58.75	124.00
5	.40	11.80	7.71	10.46	.49	62.20	54.30	119.00
10	7.10	14.20	7.70	12.10	.55	81.66	73.35	299.50
10	4.60	14.20	7.70	12.10	.47	66.05	58.68	136.00
10	10.60	14.20	7.70	12.10	.43	62.37	58.04	104.50
10	11.40	14.20	7.70	12.10	.54	64.82	57.17	147.50
10	1.40	14.20	7.70	12.10	.45	60.34	53.57	98.50
10	14.20	14.20	7.70	12.10	.53	60.61	53.92	118.00
10	11.30	14.20	7.70	12.10	.52	57.79	52.83	100.50
10	8.70	14.20	7.70	12.10	.47	71.47	64.63	170.00
10	.0	14.20	7.70	12.10	.41	61.23	53.58	95.00
10	11.00	14.20	7.70	12.10	.52	61.66	54.89	122.50
10	5.00	14.20	7.70	12.10	.56	69.28	64.31	186.00
10	12.40	14.20	7.70	12.10	.53	68.30	60.98	168.50
10	10.70	14.20	7.70	12.10	.56	56.95	51.46	103.50
10	11.10	14.20	7.70	12.10	.46	54.16	47.38	72.50
10	23.80	14.20	7.70	12.10	.50	51.05	46.26	67.00
10	20.30	14.20	7.70	12.10	.41	66.84	59.42	122.50
10	16.70	14.20	7.70	12.10	.49	68.22	60.04	156.50
10	9.60	14.20	7.70	12.10	.45	50.82	44.98	58.50
10	12.80	14.20	7.70	12.10	.45	63.60	57.20	117.00
10	22.20	14.20	7.70	12.10	.49	54.51	49.24	79.00
10	19.60	13.20	7.98	13.57	.27	53.49	58.96	41.00
10	12.40	13.20	7.98	13.57	.63	50.56	56.06	82.00
10	8.60	13.20	7.98	13.57	.70	46.57	51.61	70.50
10	1.10	13.20	7.98	13.57	.67	48.08	50.82	74.50
10	12.60	13.20	7.98	13.57	.69	56.69	62.73	125.00
10	13.00	13.20	7.98	13.57	.72	57.19	62.72	135.00
10	11.40	13.20	7.98	13.57	.66	44.57	50.11	58.50
10	18.80	13.20	7.98	13.57	.52	65.15	57.27	143.00
10	15.70	7.60	7.48	12.54	.52	61.00	57.30	119.00
10	24.50	7.60	7.48	12.54	.52	56.80	50.40	95.50
10	14.70	7.60	7.48	12.54	.47	63.50	56.80	120.50
10	21.90	7.60	7.48	12.54	.51	56.35	50.65	91.50
10	21.70	7.60	7.48	12.54	.44	60.90	52.45	100.00
10	20.50	7.60	7.48	12.54	.56	55.70	50.75	96.00
10	16.80	7.60	7.48	12.54	.41	48.10	43.30	46.00

10	25.00	7.60	7.48	12.54	.44	58.40	51.90	88.50
10	24.60	7.60	7.48	12.54	.57	45.50	41.30	54.00
10	25.00	7.60	7.48	12.54	.50	57.00	50.85	93.00
10	15.30	9.70	7.48	12.54	.48	60.90	53.50	109.50
10	23.20	9.70	7.48	12.54	.52	48.70	43.90	60.50
10	22.10	9.70	7.48	12.54	.47	52.00	45.00	66.00
10	14.50	9.70	7.48	12.54	.50	64.20	57.70	131.50
10	16.30	9.70	7.48	12.54	.51	68.40	61.40	162.00
10	14.70	9.70	7.48	12.54	.57	70.60	64.60	199.00
10	22.80	9.70	7.48	12.54	.53	68.20	60.60	168.50
10	17.50	9.70	8.05	15.87	.48	54.40	49.40	77.00
10	19.00	9.70	8.05	15.87	.45	58.00	51.60	88.50
10	19.60	9.70	8.05	15.87	.39	58.90	52.40	79.50
10	12.10	11.50	8.05	15.87	.53	66.00	58.60	153.00
10	11.10	11.50	8.05	15.87	.54	63.00	56.60	134.50
10	13.50	11.50	8.05	15.87	.44	68.00	60.90	139.50
10	13.70	11.50	8.05	15.87	.49	65.60	57.70	137.00
10	14.30	11.50	8.05	15.87	.50	62.00	56.00	119.00
10	17.10	11.50	8.05	15.87	.43	63.00	56.80	107.00
10	11.60	11.50	8.05	15.87	.55	62.60	56.40	134.50
10	14.50	11.70	7.71	10.46	.48	49.30	44.05	57.50
10	10.60	11.70	7.71	10.46	.46	49.60	44.10	56.00
10	.80	11.70	7.71	10.46	.46	50.40	44.85	58.50
10	17.50	11.70	7.71	10.46	.50	57.60	50.60	95.50
10	14.30	11.70	7.71	10.46	.50	62.29	55.80	120.00
10	19.20	11.70	7.71	10.46	.44	56.70	49.80	81.00
10	12.70	11.70	7.71	10.46	.47	60.70	54.06	106.00
10	.90	11.70	7.71	10.46	.47	57.30	50.10	89.00
10	10.20	11.70	7.71	10.46	.46	61.20	54.25	104.50
10	24.10	11.70	7.71	10.46	.50	59.70	52.70	105.50
10	8.10	17.70	7.71	10.46	.55	78.40	69.30	264.50
10	10.90	17.70	7.71	10.46	.48	61.10	54.12	110.50
10	17.00	17.70	7.71	10.46	.45	53.80	48.20	70.50
10	17.00	17.70	7.71	10.46	.45	63.05	57.60	112.00
10	21.10	17.70	7.71	10.46	.44	60.05	53.60	94.50
10	14.70	17.70	7.71	10.46	.52	72.14	62.79	194.50
10	5.50	17.70	7.71	10.46	.44	72.05	64.40	164.50
10	22.40	17.70	7.71	10.46	.41	59.00	52.60	83.50
10	10.30	17.70	7.71	10.46	.57	64.23	56.99	150.50
10	15.30	17.70	7.71	10.46	.45	54.20	49.20	71.50
10	.0	18.90	7.71	10.46	.51	59.10	54.10	104.50
10	8.40	18.90	7.71	10.46	.48	64.40	58.60	129.50
10	8.40	18.90	7.71	10.46	.53	68.15	61.30	166.50
10	.10	18.90	7.71	10.46	.45	64.90	58.75	124.00
10	.0	18.90	7.71	10.46	.49	62.20	54.30	119.00

Table E. Test of the homogeneity of the regression slopes by testing the interaction of the factor with each covariate. Results from the dispersal experiment in the water.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1996.024[a]	14	142.573	3.952	.000
Intercept	1215.723	1	1215.723	33.697	.000
density * temperature	19.901	2	9.950	.276	.759
density * oxygen	45.458	2	22.729	.630	.534
density * fulton	33.976	2	16.988	.471	.625
density * length	32.161	2	16.081	.446	.641
density	50.284	2	25.142	.697	.499
temperature	722.993	1	722.993	20.040	.000
oxygen	48.377	1	48.377	1.341	.248
fulton	140.005	1	140.005	3.881	.050
length	28.274	1	28.274	.784	.377
Error	8117.542	225	36.078		
Total	52453.394	240			
Corrected Total	10113.566	239			

Table F. Test of the homogeneity of the regression slopes by testing the interaction of the factor with each covariate. Results from the dispersal experiment out of water.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	915.890[a]	11	83.263	17.853	.000
Intercept	.926	1	.926	.199	.656
density	.610	2	.305	.065	.937
length	72.103	1	72.103	15.460	.000
Relative humidity	632.325	1	632.325	135.584	.000
density * length	4.218	2	2.109	.452	.637
density * Relative humidity	5.077	2	2.538	.544	.581
Fulton	9.578	1	9.578	2.054	.153
density * Fulton	5.605	2	2.803	.601	.549
density	1063.326	228	4.664		
length	4011.560	240			
Error	1979.216	239			
Total	915.890[a]	11	83.263	17.853	.000
Corrected Total	.926	1	.926	.199	.656