Mestrado em Qualidade e Gestão do Ambiente

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Mecanismos de dispersão passiva de camarão-de-rio entre massas de água

Mechanisms of river shrimp passive dispersal between water bodies

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1.- Resumo

Mecanismos de dispersão passiva de camarão-de-rio entre massas de água

Neste trabalho investigou-se a dispersão passiva, externa, do camarão de rio (*Athyaephyra desmarestii*) através de aves aquáticas e analisaram-se os factores que influenciam este processo. Experiências demonstraram que em condições laboratoriais o camarão de rio pode sobreviver fora de água até 90,1 minutos. Já em condições de voo de ave simulado usando um carro o mesmo pode sobreviver ao transporte até 24 km de distância. Verificou-se que o camarão de rio tem capacidade para aderir a um vector de transporte (pato) sendo esta capacidade dependente da profundidade da água. Calculou-se também a probabilidade de sobrevivência ao transporte em função da distância percorrida. Com este estudo demonstrou-se que pode ocorrer dispersão passiva do camarão de rio através de aves aquáticas. Este processo pode ser fundamental para o fluxo genético entre as populações e para a colonização de novos locais.

Palavras-chave

Athyaephyra desmarestii, dispersão passiva, dissecação, aves aquáticas.

2.- Abstract

Mechanisms of river shrimp passive dispersal between water bodies

The purpose of this study was to investigate the possibility of passive external dispersal of river shrimp (*Athyaephyra desmarestii*) by waterfowl, and to analyze the factors influencing this process. Experiments focused on desiccation survival showed that river shrimp can survive out of water up to 90.1 minutes in laboratory conditions. Experiments with simulated bird flight conditions using a car indicated that river shrimp can survive 24 km transport distances. Our results show that the river shrimp's capacity to take a transport vector (a duck) is dependent upon water depth. We also found out that river shrimps can stay on the animal vector and we calculated the survival probabilities for each distance. This study demonstrated that waterfowl mediated passive dispersal (WMPD) of river shrimp can occur. WMPD may be fundamental for genetic flows between populations and for the colonization of new sites.

Keywords

Athyaephyra desmarestii, passive dispersal, desiccation, waterfowl.

3.- Introduction

Dispersal is the movement of organisms or propagules between spatially (or temporally) discrete localities or populations (Bilton et al., 2001). It is the major process influencing the dynamics and evolution of populations and species (Mayr, 1963 in Hulsmans et al., 2007). Dispersal defines the spatial limits for colonization of new sites (Cáceres and Soluk, 2002) and influences the probability of extinction (Vos et al., 2001). Therefore, it is important to know the patterns of dispersal to analyze the viability of fragmented populations (Jenkins et al. 2003), and also for the control of exotic species (Colautti et al., 2005). The many different mechanisms of dispersal can be generally classified into two modes: active and passive. The first mode entails self-generated movements of individual organisms, while the second mode entails movements achieved using an external agent. For freshwater invertebrates the relevance of passive dispersal is mostly associated to overland movement, because only some freshwater invertebrates like insects can cross the inhospitable terrestrial landscape. It is generally recognized that the main passive dispersal vectors of freshwater invertebrates are the water flow, the wind and animal vectors (Bilton et al., 2001). Nevertheless, human-mediated dispersal (intentional or not) is an important subgroup of passive dispersal mechanisms and is deeply connected to ecological invasions which are one of the most dangerous threats for biodiversity. Catford et al. (2009) divided the biological invasion processes into six different stages of which the first two correspond to passive dispersal process. These are called uptake and transport (first step) and release and introduction (second step) (Colautti and MacIsacc, 2004; Lockwood et al., 2005).

The passive transport process by animal vectors can occur in two different ways, the first is via external dispersal or ectozoochory (hitchhiking or phoresy). In this case the process takes place by the movement of resistant resting stages or of individuals that become attached to mobile animal vectors such as waterfowl or other aquatic vertebrates. The second way is internal dispersal or endozoochory, the process occur through transport of adults or resting stages in the guts of animal vectors followed by defecation of viable stages (Bilton, 2001).

Waterbirds have long been considered a major disperser of aquatic organisms, because of their abundance, widespread distribution across the world's wetlands, as well as their tendency to show long-distance movements (Figuerola and Green, 2002). Recent indirect evidence supporting the role of long-distance dispersal by waterbirds comes from studies of the genetic population structure of different aquatic animal species like cladocerans and bryozoans. Most of these studies have concluded that geographical distance is usually unrelated to the genetic distance between populations, and the genetic distribution of those species reflects the major waterfowl flyways (Hebert & Finston, 1996; Vanoverbeke & DeMeester, 1997; Taylor, et al., 1998; Freeland, et al., 2000). A few experiments helped to confirm this evidence and tested the potential for external transport of propagules by adhesion to the feathers, bills or legs of waterbirds. A number of anecdotal observations of organisms adhering to the plumage have also been reported (Maguire, 1959; Maguire, 1963; Swanson, 1984 in Figuerola and Green, 2002). One of the earliest studies was in fact performed by Darwin (1859), who removed the leg of a dead waterbird and placed it in a tank with pond snails. The snails crawled onto the bird paw and many stayed there when he removed it from the water and waved it around to simulate flight.

The passive dispersal via external dispersal or ectozoochory in freshwater environments is limited by the exposure to desiccation of organisms during the transport. As yet no study has addressed how desiccation affects the viability of different kinds of propagules (Figuerola and Green, 2002). Some aquatic organisms have adaptations which allow survival to desiccation. These may have a dormant stage with some sort of protection such as shells in the case of snails, protein capsules, or slime coats in the case of of resting eggs of Anostraca (fairy shrimps), Notostraca (tadpole shrimps) and Cladocerans (water fleas) (Lahr, 1997).

In this study we evaluate the possibility of the river shrimp (*Athyaephyra desmarestii*) to disperse by external passive transport (ectozoochory) mediated by waterfowl. The river shrimp *Athyaephyra desmarestii* is a phytophilous, eurythermal and euryhaline crustacean, who prefers slow flowing waters, rich in macrophytes and dissolved oxygen (Fidalgo & Gerhardt, 2002). The original distribution of the river shrimp was restricted to the Mediterranean area, being observed in North Africa and southern Europe (Tittizer et al., 2000). In recent years it has expanded its distribution, colonizing rivers of central Europe, reaching the Baltic, Northern and Black seas (Fidalgo & Gerhardt, 2002), mainly due to the boat transit (Tittizer, 1996), and slowly migrated northwards through canals connecting different river basins (Galhano, 1979). *A. desmarestii* has been found in many Portuguese freshwaters, including reservoirs, rice fields, coastal lagoons and temporary streams, although its distribution is still uncertain (Fidalgo and Gerhardt, 2002). With regard to food, this decapod is omnivorous, eating a wide variety of food items such as algae, mud and even fecal matter. It has an important role in freshwater ecosystems due to the recycling of organic matter (Fidalgo, 1990), and also because it constitutes an important food item for many species of fishes (García-Barthou & Moreno, 2000, 2000; García-Barthou, 2000, 2001). Some characteristics of the river shrimp seem to favor its passive external dispersal. Among these are the small size of this species, ca. 25 mm of total length and the high densities found, with values up to 1811 animals m^{-2} inside its micro-habitats (Fidalgo, 1990; Meurisse-Génin et al., 1985). These micro-habits include plants which constitute a food item for *Anatidae* and this may increase the probably of river shrimps to adhere to the duck's plumage and to be transported. The aim of this work is therefore to evaluate the possibility of passive external dispersal of *A. desmarestii* by waterfowl, and to analyze the factors influencing this process, namely: river shrimp's desiccation survival capabilities, its capacity to attach to waterfowl during their movements out of water and its survival rate during transport.

4.- Materials and methods

A set of experiments was performed to obtain a perspective on the probability of successful external transport (ectozoochory) of river shrimps by an animal vector. All the river shrimps used were collected at the Raia river near Mora, river Tejo basin, Portugal (38°57'N, 8°09'W) using a quadrangular dipnet (1mm mesh; 60 cm × 40 cm; 120 cm cable). These were kept for 2 days before the experiments in an aerated tank (57 × 43 × 39 cm) and feed with *Juncus* sp. leaves. Statistical analyses were carried out using PASW Statistics 18. Air temperature and relative humidity were measured during the experiments using a thermo-hygrometer and the water temperature was measured using a multiparameter probe (Multiline-WTW). Wind direction and velocity were taken from a nearby meteorological station.

4.1- Desiccation survival

We performed two laboratory experiments to check how long would river shrimp survive out of water, under controlled conditions and in the absence of wind. 120 river shrimp (TL= 23.25 mm ± 3.89 S.D.) were distributed by 12 groups of 10 individuals each. Each shrimp was individually placed into a plastic cup, and cups were kept at 19°C and a relative humidity of 33%. The experiment lasted 2 hours and every 10 minutes the number of live shrimp in one randomly selected group was checked. Shrimps were considered alive if we could detect movement after pouring water into the plastic cups. The experiment was repeated at 24°C and 44% relative humidity, using the same protocol (N=120; TL= 24.85 mm ± 4.49 S.D.). Probit analysis was used to calculate the probability of desiccation survival and LT_{50} and LT_{90} were calculated for both temperatures used.

4.2- Survival under simulated flight conditions (car)

After the previous experiments and to obtain results under more real conditions, we conducted another experiment to test the river shrimp's survival time out of water. This time the factor "wind" was present since we simulated bird flight using a car. One hundred river shrimps (TL= 23.88 mm ± 3.08 S.D.) were distributed by 20 groups of 5 individuals each and each group was placed into a plastic mesh bag with individual compartments (mesh 1mm×1mm; dimensions 9×9cm). The bags were suspended and immobilized 10 cm over a car using two tight strings. Since the mean flight speed for *Anas* spp. ranges from 60 to 78 km/h (Welham, 1994) and the real car's velocity is usually a bit lower than shown by the speedometer, the car was kept at a constant speed of 80km/h (real velocity – 75 km/h). The experiment lasted 30 minutes and at each 3 minutes period, without stopping the car, two bags were randomly taken from the lines and were placed into a bucket full of water. During the experiment, 1 additional group was kept in a water bucket as a control. The number of shrimps alive was registered for each time period and the length of each shrimp was measured. Probit analysis was used to calculate the probability of desiccation survival and LT_{50} and LT_{90} were calculated.

4.3- Passive transport

4.3.1- Experiments with dead ducks

To evaluate the probability of river shrimp's adhesion to duck's plumage and transport, a freshly dead 3.75 kg domestic duck was used to simulate the passive transport process. 98 shrimps (TL= 25.85 mm ± 4.22 S.D.) were placed into each of 3 different containers (density per box= 400 individuals/m^2) (57 × 43 cm) with three different water depths (5 cm, 10 cm and 20 cm). A similar plastic box without shrimps (water depth = 15 cm) was placed 5 meters apart and was used as receiving tank for each replicated duck movement. The duck was kept in the natural position, tied by a nylon thread around the wings and neck, and was maintained in each plastic box with shrimps for 1 minute and 30 seconds. Then, using the nylon thread, the duck was transported to the plastic box without shrimps and was shaken, three times in the water. The receiving tank was verified, the number of shrimps transported was counted and their size was measured. The duck was then placed again into a box with shrimps and the process was repeated 200 times for each of the three different depths. Data was organized into a contingency table and a Chi-square test was applied to verify if there were differences on the proportions of shrimps transported at three different depths.

4.3.2- Experiments with live ducks

To try to obtain the actual probability for a river shrimp to adhere to duck's plumage and being transported, we performed one experiment using live ducks. This experiment was conducted at Monte dos Três Bicos (Brotas, Alentejo; Portugal). 15 domestic ducks were trained to pass inside a 6 m long corridor limited by a plastic mesh. This corridor had two small pools (57 × 43 cm), 5 meters apart from each other, filled with water to a 10 cm depth in the first pool and 15 cm in the second. 98 river shrimps (21.12 mm ± 2.96 S.D.) were placed in the first pool, thus at a density of 400 individuals/m^2. The domestic ducks passed in the corridor from the first pool with shrimps to the second without shrimps. After passing the second pool ("arrival pool") the number of transported shrimps was counted and they were measured. The experiment was repeated under the same conditions but adding 300 g of *Ranunculus aquatilis* in the first pool, i.e. the one containing the shrimps (21.32 mm ± 2.98 S.D.). This change served to provide a substrate along the water column, which could allow the river shrimps to have more duck's plumage area to adhere. Another possibility would be the transport of animals attached to plant parts.

To try to increase the time spent by the ducks in the first pool, the area was increased to the double (57 × 86 cm). The number of river shrimps, 98 individuals (21.46 mm ± 2.96 S.D.), was the same, so the density decreased to half (200 individuals/m^2) and the experiment was conducted with the same protocol. This was repeated with 50 g of straw of *Avena sativa* in the depression that containing the river shrimps, which was a less attractive source of food for ducks than *Ranunculus aquatilis*. The remaining conditions were kept unchanged.

4.3.3- Probability of transport and survival during simulated bird flight conditions

We conducted an experiment to verify the capacity of river shrimps to stay on the animal vector and to survive the transport process. In this experiment, a freshly dead 3.750 kg domestic duck was soaked with water before the experiment and suspended over a pickup car, just as a live duck during flight. 60 river shrimps (24.02 mm ±2.79 S.D.) were randomly distributed in 3 groups of 20 individuals and each group was placed all around the duck, under and between feathers. The car was then driven at a speedometer velocity of 80km/h (real velocity – 75 km/h). After a period of time, the duck was inspected to verify the number of river shrimps that remained on the duck and how many of these were alive. This protocol was repeated for each of the three groups and each of these corresponded to one different period of time (5, 10 or 15 minutes). These periods were chosen in agreement with the information obtained regarding survival during the previous experiment "survival under simulated flight conditions". A probit analysis was applied to the data and the LT_{50} and LT_{90} was obtained. A contingency table was built and a chi-square test was applied to verify if the survival of the transported shrimps was influenced by flight duration.

5.- Results

5.1.- Desiccation survival

The mortality of river shrimps increases logistically with time during air exposure (see, figure 1 e 2) and was faster at 24 °C, as expected. At 19°C the mortality was null after 10 minutes, and the largest survival period (100 minutes) was registered for one river shrimp with 30.63 mm length. At an air temperature of 24°C and relative humidity of 44%, as referred, the mortality increases fast, reaching 10% at 10 minutes and 100% at 70 minutes.

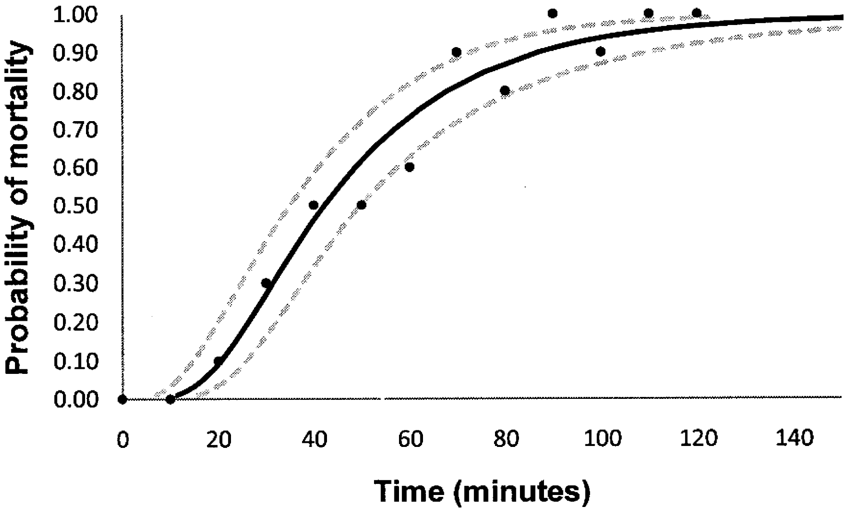

Fig. 1 Probability of river shrimps mortality as a function of time at an air temperature of 19°C, and 33% relative humidity. The black points are the observed proportions of dead river shrimps; the black line was obtained by probit analysis, with the respective 95% confidence intervals (dotted line).

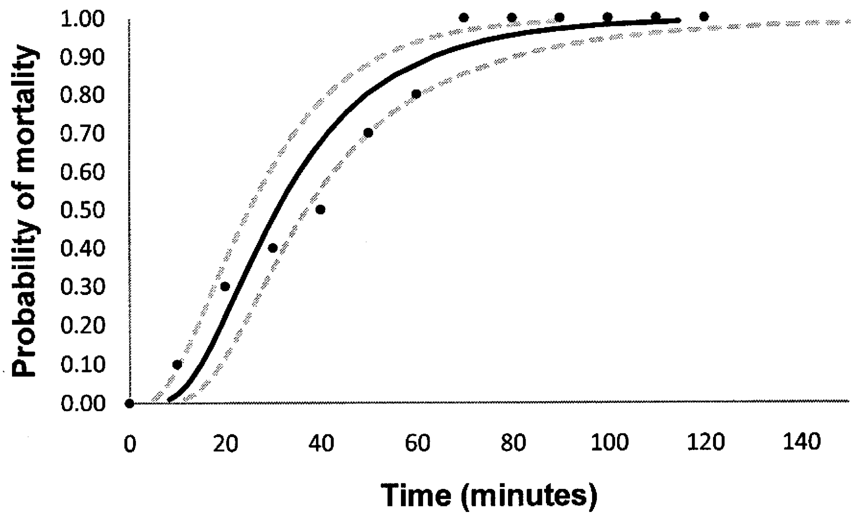

Fig. 2 Probability of river shrimps mortality as a function of time at 24°C air temperature and 44% relative humidity. The black dots are the observed proportions of dead river shrimps, the black line was obtained by probit analysis and the 95% confidence intervals are presented.

The probit analysis indicated a LT_{50} of 42.3 and 30.9 minutes respectively for 19°C and 24°C air temperature (table 1). The LT_{90} for 19°C air temperature was 90.1 minutes and 63.7 minutes for 24°C. For an increase of 5 degrees the LT_{50} decreases 11.4 minutes but the LT_{90} decreases 26.4 minutes.

Table 1 Estimated time (in minutes) to 90% (LT_{90}) and 50% (LT_{50}) mortality of River shrimps at different air temperatures with standard errors (SE) and 95% confidence intervals (CI).

Temperature (°C)	LT_{50} (min.)	95% CI	LT_{90} (min.)	95% CI	SE
19	42.3	35.0-49.9	90.1	75.1-114.3	0.825
24	30.9	25.0-37.1	63.7	52.6-80.8	0.774

5.2.- Survival under simulated flight conditions (car)

The mortality of the river shrimps exposed to the air during simulated flight conditions increases faster with time than observed in the previous experiment (Fig. 3). The mortality at 3 minutes was zero, at 6 minutes it was 10% and it was 50% at 15 minutes. After 18 minutes or longer periods, all the shrimps died. All the river shrimps of the control group, kept in a bucket, survived. The probit analysis indicated a LT_{50} of 11.6 minutes and 18.5 minutes for the LT_{90} (table 2). These values are much lower when compared with the values obtained in previous experiments with laboratory conditions.

The meteorological conditions during the experiment may be observed in table 6. The average air temperature was 27°C; average relative humidity was 34% and average wind speed was 2.5 m/s.

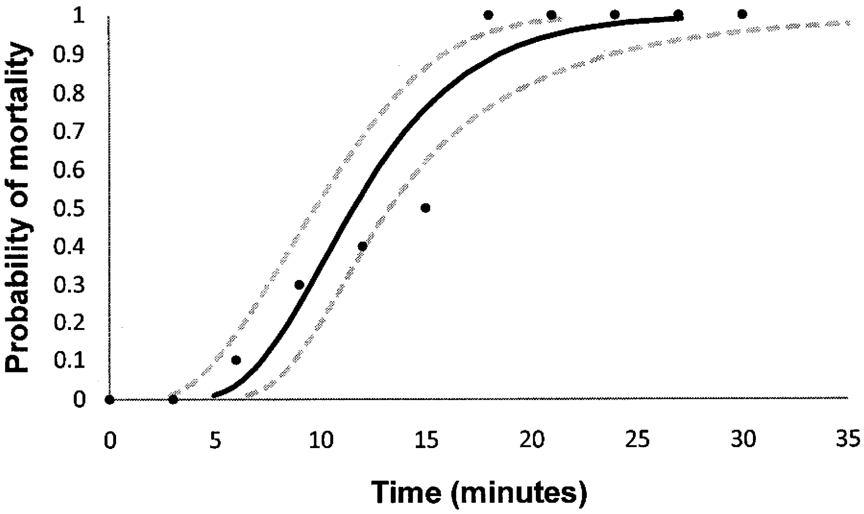

Fig. 3 Probability of river shrimps mortality as a function of time, under simulated flight conditions. The black dots are the observed proportions of dead river shrimps, the black line was obtained by probit analysis, and the 95% confidence intervals are represented as dotted lines.

Table 2 Estimated time (in minutes) to 90% (LT90) and 50% (LT50) mortality of River shrimps in simulated flight conditions (car) with standard errors (SE) and 95% confidence intervals (CI).

LT_{50} (min.)	95% CI	LT_{90} (min.)	95% CI	SE
11.6	9.8-13.3	18.5	15.9-23.9	1.136

5.3.- Passive transport

5.3.1- Experiments with dead ducks

A contingency table (table 3) analyzed the proportions of river shrimps transported for each depth. A chi-square test of independence showed that the proportion of river shrimps transported is dependent upon water depth (X^2=30.670; df= 4; p ≤0.001).

The results of this experiment show that, the probability of transport of one river shrimp is largest at a 10 cm depth, with values of 0.035 at 5 cm and 0.11 at 10 cm. At a 20 cm water depth the probability decreases to 0.01. At 10 cm water depth the probability of transport of 2 individuals at each time was 0.02 which is in fact larger than the probability of transport of one individual at a depth of 20 cm (Fig. 4). The biggest river shrimp transported had 34.15 mm of total length (TL) (ovigerous female) and the smallest had 15.88 mm. The average air temperature varies between 28°C and 18.5 °C; the average water temperature varied between 21-17°C and the average relative humidity varied between 44-26 %. The meteorological conditions during the experiment may be observed in table 6.

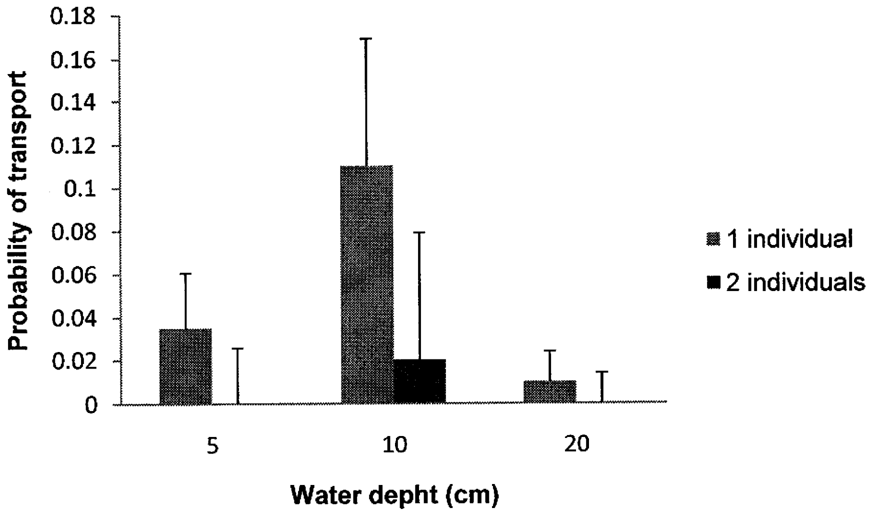

Fig. 4 Number of individuals transported at different water depths (n = 600). The error bars are the 95% confidence intervals.

Table 3 Number and percentage of river shrimps transported at different water depths (n=600).

Number of individuals transported	Water depth (cm)			Total
	5	10	20	
0	193	174	198	565
1	7	22	2	31
2	0	4	0	4
Total	200	200	200	600

5.3.2- Experiments with live ducks

The first run of this experiment involved the transit of 720 ducks between pools, but there was no transport of river shrimps. The depressions had no substrate and therefore the ducks passed rapidly by the corridor. The mean time spent by each duck in the starting pool was 1.29 seconds (± 0.15 S.D.). After the experiment the number of river shrimps in the starting pool, was counted and all the 98 river shrimps were recovered, although 6 were crushed by duck's paws.

During the second run, which involved the presence of an aquatic plant (*Ranunculus aquatilis*) in the starting pool, the ducks passed by the corridor 720 times, too. During this trial we observed that ducks fed heavily on the aquatic plant, presumably eating both the plant and the shrimps. At the end of the experiment only 10 shrimps were recovered from the starting pool, 2 of which were dead.

The third run involved a donor pool with the double of the area, 4 ducks, no substrate and a total of 160 duck transit occasions by the corridor. Again, no shrimps were transported from the first to the second pool. The forth run, involved the same number of ducks, the same donor pool's area, and the same number of duck transit occasions (although with straw added to the starting pool) resulted in no shrimp transport among pools. Ducks showed no interest to feed on straw. In the "start" pool, 93 river shrimps were recovered, 6 of which were dead. The mean time spent by ducks in the starting pool was 2.23 seconds (± 0.19 S.D.). The air temperature oscillated between 19.5 °C and 25°C; water temperature varied between 21-24.5°C and the relative humidity varied between 44.5 -65% (Table 6).

5.3.3- Probability of transport and survival during simulated bird flight conditions

The percentage of river shrimps transported, i.e. not falling off the duck, was 95% for 5 minutes, 100% for 10 minutes and for 15 minutes it decreased to 35%. The percentage of shrimps which remained on the duck and were alive was 80% for 5 minutes. At 78 km/h, which is the mean flight speed of ducks, this would allow the transport of shrimps to a distance of approximately 7 km. For a 10 minutes flight (13 km) the percentage was 65% and for the 15 minutes period (20 km), it was 30% (figure 5).

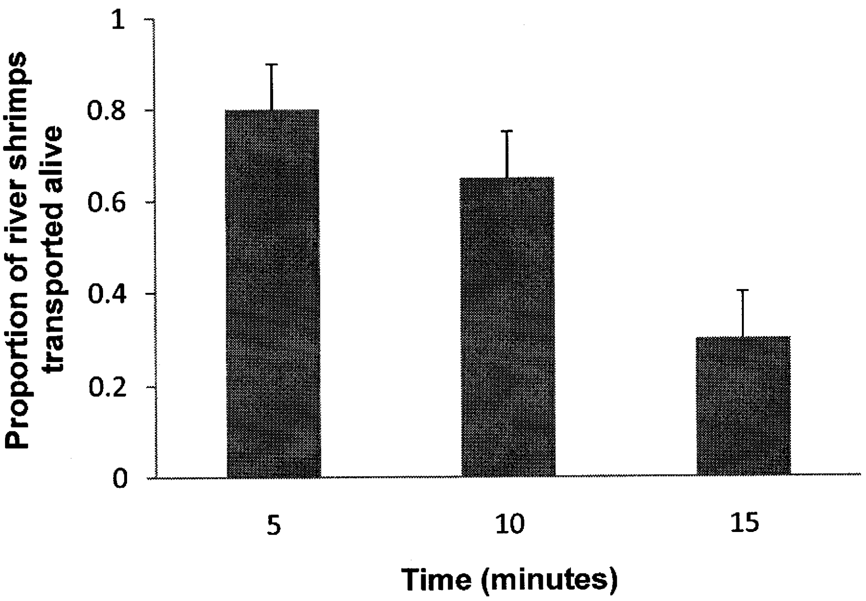

Fig. 5 Percentage of river shrimps transported alive as a function of time (n=60). The error bars are the 95% confidence intervals.

The Chi-square on the contingency table (table 4) indicates that the proportion of shrimps transported alive varies with time (X^2=10.834; df= 2; P = 0.004). The probit analysis indicated that the LT_{50} was at 11.2 minutes, i.e. 50% river shrimps are expected to die until that time. The LT_{90} value was 32.4 minutes (table 5). The average temperature was 25.5°C, the average relative humidity was 43% and the average wind speed was 3.7 m/s (Table 6).

Table 4 Number of river shrimps transported alive at different periods of time (n=60).

Survival	Time (minutes)			Total
	5	10	15	
No	4	7	14	25
Yes	16	13	6	35
Total	20	20	20	60

Table 5 Estimated time (in minutes) to 50% (LT_{50}) mortality of River shrimps in simulated bird flight conditions. Standard errors (SE) and 95% confidence intervals (CI) are presented.

LT_{50} (min.)	95% CI	LT_{90} (min.)	95% CI	SE
11.2	8.3-18.8	32.4	19.1-322.6	0.913

Table 6 Meteorological variables (Experiment: Car - Survival under simulated flight conditions (car); Dead duck - Experiments with dead ducks; Live Ducks - Experiments with live ducks; Duck car - Probability of transport and survival during simulated bird flight conditions) (T°C – temperature in Celsius degrees; RH% - relative humidity in percentage). Air temperature and relative humidity were measured using a thermo-hygrometer and the wind direction and velocity were taken from a nearby meteorological station (Geophysical Center, University of Évora).

Experiment	Date	hours	Mean air T°C	Interval air T°C	Mean water T°C	Interval water T°C	Mean RH%	Interval RH%	Mean wind velocity	Interval wind velocity	Wind direction
Car	13 April	21-21h30	27	26-28	-	-	34	33-35	2.5	2.2-2.8	West
Dead duck	27 April	15-20	28	28	21	19-23	35	35	-	-	-
	28 April	15-20	26	25-27	20.5	19-22	41	38-44	-	-	-
	05 May	14-19	18	18	18	18	26	26	-	-	-
	07 May	14-19	18.5	18-19	17	16-18	44	40-48	-	-	-
Ducks alive	04 June	7-10	19.5	17-22	21.5	20-23	61	54-68	-	-	-
	08 June	14-17	22.5	22-23	23	22-24	44.5	40-49	-	-	-
	29 June	7h30-8h30	21	19-23	21	20-22	65	62-68	-	-	-
	29 June	9h30-10h30	25	24-26	24.5	24-25	58	57-59	-	-	-
Duck car	16 July	20-21	25.5	24-27	-	-	43	38-48	3.7	2.9-4.4	West

6- Discussion

In this study, we verified that *A. desmarestii* has the potential to be dispersed by ducks at short distances. Our experiments showed that *A. desmarestii* can survive desiccation during transport. The probability of survival is high for distances close 15 km and the limit survival distance is near 24 km. As expected, results show that the survival time was shorter, in the experiments with moving vectors, because the dehydration is faster. The results obtained by the indoor experiment i.e. without wind, cannot be directly extrapolated for natural conditions because there is air movement during bird flight. Nevertheless, with other animal vectors, such as otters (*Lutra lutra*) the air movement may be ignored and therefore survival time is expected to be larger although the travelled distances are usually shorter. From our results, and using the mean flight speed a duck, we extrapolate that the river shrimp have a 10% survival to 117 km and 82 km transport respectively at 19ºC and 24ºC. Segerstråle (1954) did the same type of extrapolation and established that the amphipod *Gammarus lacustris* can survive air exposure for up to 2 h (room temperature) and potentially survive transport by waterfowl for 140 km. This species appear to have more capacity to survive desiccation during transport when compared to river shrimp. Just as for river shrimp the values obtained in this type of experiments are distant from the real limit distances for waterfowl mediated passive transport. We believe that the values referred for *Gammarus lacustris* by this author are an overestimation.

The desiccation resistance in crustaceans is a limiting factor for their distribution and is inversely related with gill area. A reduction in gill area, which reduces desiccation, is related to the acquisition of terrestrial habits whereas an increase in gill area may be promoted in reduced salinities as a means of facilitating ion uptake (Moore and Taylor, 1984). Other authors conducted experiments on desiccation survival of crustaceans (Table 7) and the survival time ranged from 2 to 708 hours, with different temperature and relative humidity conditions. For *Uca* spp. species there is a tendency for a larger desiccation survival time with terrestrial species, followed by semi-terrestrial species and finally by aquatic species, as showed by Rabalais and Cameron (1985). Within aquatic crustacean species, of the genus *Gammarus*, the marine ones have a major gill area and have a lower desiccation survival capacity (Bulnheim, 1979). Freshwater crustaceans have a few adaptations to desiccation in the more primitive and small species, such as e.g. encysted embryos (cysts) in *Artemia franciscana* (Clegg, 2005). The desiccation survival experiments conducted in these groups are focused in these dormant stages. Their capacity to face desiccation and high temperatures are notable, sometimes facing temperatures near 100°C and long periods without water (Clegg, 2005).

In the experiment "Probability of transport and survival during simulated bird flight conditions" we evaluated two important factors to the success of the passive transport of river shrimp by waterfowl. The first factor is the desiccation survival capacity. We think that the survival was larger than what we found during the previous experiment using mesh bags because the air friction of feathers is bigger and therefore desiccation is slower. In this experiment the value of LT_{50} (11.2 minutes) obtained by the probit analysis is very similar to the value obtained for the experiments using nets (LT_{50}=11.6 minutes). This result doesn't match the previous hypothesis. The LT_{90} value for this experiment was 32.4 minutes, yet the confidence interval was very large and more observations just below the 100% mortality time were needed for best results. When this value is compared with the one in the previous experiment using mesh bags (LT_{90}= 18.5 minutes) the survival time is much bigger, almost the double. So river shrimp should have a 10 % probability of surviving 42 km of passive transport by waterfowl although we suspect that the real value of LT_{90} is lower.

The second factor for the success of the passive transport is the capacity to stay attached to waterfowl's plumage during flight. The results indicate that the capacity to stay attached to waterfowl during flight is connected with shrimp survival, since for the largest period of time (15 minutes), only one of the 6 river shrimps found in the duck was dead. During flight, after a short time the water in the feathers or in the river shrimp evaporates, and the adhesion process by surface tension of water ceases to have an effect. Only the live river shrimps have the capacity to cling on the duck's plumage.

We found the potential limits for passive dispersal with viable or alive river shrimps, but still we needed the probability of attachment to the vector. This is one essential parameter for passive dispersal. In this work two experiments were conducted to study this process. In the first experiment using a dead duck, this process was confirmed to occur with river shrimp and it depended on water depth. Segerstråle (1954) performed similar experiments with the amphipod *Gammarus lacustris* which has a mean length around 25 mm i.e. very similar to the river shrimp's (*Athyaephyra desmarestii*) mean length. Nevertheless, the density used by Segerstråle (1954) was approximately 30 individuals/m^2, which was lower than the one we used in this study. Segerstråle (1954) observed that *Gammarus lacustris* attached to a duck in 3 /10 cases. The potential of this species to attach to waterfowl seems larger than what we found for river shrimp, because the probability of attachment found by Segerstråle (1954) was larger (0.30) for a lower density than the one used in this study with river shrimp. During our experiment we verified that larger individuals such as big ovigerous females can also be transported. In fact, for the size intervals used (adults and immature adults), size does not seem to have an impact on the probability of transport.

Within its home range in Portugal it is during the summer (August - September) that this epilimnic river shrimp's density reaches highest values (Fidalgo, 1990; Meurisse-Génin et al., 1985). Ovigerous females and planktonic juveniles also occur in this period, and while the former have a major capacity to colonize new locals due to the offspring they are carrying, the later could be the easiest ones to get attached to waterfowl's plumage. We expect that the probability for attachment and passive transport by ducks is highest during the summer. However, the density of the vector is also of great importance. In Portugal the highest density of waterfowl is normally observed during the autumn and the winter, and the *Anatidae* family is the most representative group (Moreira, 1999). In spite of this, the lowest river shrimp's density is observed during the winter (Fidalgo, 1990; Meurisse-Génin et al., 1985). This fact can be unfavorable for the passive transport of river shrimp but one the most common and abundant species of duck, the mallard (*Anas platyrhynchos*), has highest densities during the summer (Moreira, 1999) and may be one of the most important vectors for river shrimp transport. Still, air temperatures are highest and relative humidity is lowest in this period of year, so the mortality during transport should be high.

We performed a mesocosmos experiment to evaluate the capacity of river shrimp (*Athyaephyra desmarestii*) to attach to live ducks. No transport was observed in any of the four different situations used in this experiment. Our conclusion is that the probability of transport was below 1/750 in the case when we used a density of 400 ind./m^2 and much below 1/160 for the experiments using half of that density and the double of the pool area. In fact the probability for the second case should be lower than for the first because the density was halved but we used only 160 replicates. Comparing these results with the ones obtained in the experiment with the dead duck, we believe that the probability of attachment was lower because the ducks spent a much lower period of time in the pools. If the probability of transport is directly related with duck detention time, since in the previous experiment the probability was 0.11 for 1 minute and 30 seconds, for a detention time of 1.29 seconds the probability should be 0.0016. For the run with the double of the area and a detention time of 2.23 seconds, the probability would be 0.0027. Nevertheless, in this case the river shrimp density was halved, so the expected probability is lower than the estimated value. Another factor than may have contributed to the absence of transport was the stress caused by the ducks on river shrimps by movement and by predation. In fact we observed several crushed and dead river shrimps. The predatory behavior may have dual results, on one hand the predation invalidates the passive transport because surviving the transit by the alimentary canal is in principle excluded. On the other hand like Segerstråle (1954) referred for *Gammarus lacustis*, this behavior is favorable for the attachment of river shrimp to ducks because in the wild the more probable situation for attachment occurs when waterfowl are feeding in shallow waters on aquatic plants or small invertebrates.

This study presents evidence that short distance passive dispersal of river shrimp (*Athyaephyra desmarestii*) can occur. The possibility of transport of ovigerous females potentiates the establishment of viable populations in new water bodies, because on average females carry 374 eggs (Fidalgo, 1990; Meurisse-Génin et al., 1985). The capability for dispersal can be very important in the home range of this species. It may allow it to confront the drought events that will be more frequent in a climate change scenario. Dispersal may in fact be a critical predictor of a species ability to escape threats posed by global atmospheric change (Hogg et al., 1998; Hogg and Williams, 1996). It may allow the genetic flow through the river barriers made by Man (Olden et al., 2001). Thus, passive transport becomes important to overcome these barriers, to disperse overland, to colonize other water bodies or to colonize and recolonize streams after drought events. Regarding the expansion of river shrimp through the central Europe as exotic species, the passive dispersal by waterfowl may be of small importance for Long Distance Dispersal when compared with transport by boat ballast water between ports, just as referred for the Cladocera *Cercopagis pengoi* expansion in Lake Ontario (Makarewicz et al., 2001). Despite the lower probability and lower transport distance of waterfowl mediated passive dispersal (WMPD) of river shrimp, this process may contribute for a spread across river basins, therefore accelerating the speed of the invasion front.

This work demonstrates that WMPD is possible for river shrimp and opens a new window of future research. Other field studies may be carried in the future to detect the transport of this crustacean in bird's plumage of wild birds. Finally, studies on planktonic/juvenile phase of river shrimp should be performed since these may have a large potential to be transported.

Table 7 Desiccation survival time of some crustaceans.

Species	**Habitat**	**Relative Humidity (%)**	**Temperature (°C)**	**Survival time (hours)**	**Reference**
Orconectes eupunctus	Freshwater	89.9	24.1	20.3 (range 6.0–45.0)	Larson et al. , 2009
Orconectes neglectus chaenodactylus	Freshwater	89.9	24.1	123.3 (range 24.0–309.0)	
Procambarus clarkii	Freshwater	44	24	Until 8	Anastácio et al., 2010
		53	16	Until 16.5	
Ligia exotica	Semi-terrestrial	85.2	27.2	15.5	Tsai et al., 1998
Ligia taiwanensis	Semi-terrestrial	85.2	27.2	7.1	
Talorchestia quoyana	Semi-terrestrial	100	15	Over 24	Marsden, 1991
		75	15	Until 4	
Transorchestia chiliensis	Semi-terrestrial	100	15	Over 24	
		75	15	Until 2	
Gammarus locusta	Marine coastal	100	15	40.8 *	Bulnheim, 1979
Gammarus oceanieus	Marine coastal	100	15	96 *	
Gammarus salinus	Brackish waters	100	15	84 *	
Gammarus zaddachi	Brackish waters	100	15	134.4 *	
Gammarus duebeni	Freshwaters/ brackish waters	100	15	708 *	
Uca subcylindrica	Terrestrial	10	22	41	Rabalais and Cameron, 1985
Uca longisignalis	Semi-terrestrial	10	22	32	
Uca rapax	Semi-terrestrial	10	22	40	
Uca panacea	Semi-terrestrial	10	22	27	

*Lt_{50} values

7.-References

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