

Landscape features correlate with spatial distribution of red-swamp crayfish *Procambarus clarkii* in a network of ponds

A. Treguier^(1,2), J.-M. Roussel⁽¹⁾, M.A. Schlaepfer⁽¹⁾, J.-M. Paillisson⁽²⁾

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ABSTRACT

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The red-swamp crayfish *Procambarus clarkii* has become the most cosmopolitan freshwater crayfish species in the world as a result of numerous intentional and accidental introductions. This species was introduced approximately 30 years ago into the Brière marshes (France) where it has spread rapidly since this date. The colonization of *P. clarkii* in the network of ponds surrounding the Brière marshes is poorly documented despite the high conservation value of such ecosystems. Here, we describe the spatial distribution of *P. clarkii* in a subset of this network of ponds. We also test whether the presence of *P. clarkii* is explained by three landscape metrics that measure the level of isolation of a pond with other waterbodies (marshes, streams or ponds). Sixty-nine ponds were sampled in spring 2010 using baited funnel traps. *P. clarkii* was detected in 20% of the sampled ponds. Moreover *P. clarkii* was most likely to be present in ponds in close proximity of marshes and a stream. These findings suggest that colonization of a pond depends primarily on the proximity to existing populations, despite the efficiency of overland dispersal of *P. clarkii*.

RÉSUMÉ

La distribution spatiale de l'écrevisse rouge de Louisiane *Procambarus clarkii* dans un réseau de mares est corrélée à des variables paysagères

Mots-clés :
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clarkii

L'écrevisse rouge de Louisiane *Procambarus clarkii* est devenue, du fait de nombreux événements d'introductions, l'espèce d'écrevisse la plus répandue dans le monde. Elle a été introduite, il y a presque 30 ans, au sein des marais de Brière (France) dans lesquels elle s'est rapidement répandue. La colonisation par *P. clarkii* du réseau de mares entourant les marais de Brière n'est pas décrite malgré la valeur patrimoniale de ce type d'écosystème. Dans cette étude, nous décrivons la distribution spatiale de *P. clarkii* dans un sous-ensemble de ce réseau de mares. Nous testons également si la présence de *P. clarkii* peut être expliquée par trois variables paysagères mesurant l'isolement des mares aux autres milieux aquatiques (marais, cours d'eau ou mares). Soixante-neuf mares ont été échantillonnées durant le printemps 2010 grâce à des nasses appâtées. *P. clarkii* a été détectée dans 20 % des mares échantillonnées. *P. clarkii* a plus de probabilité d'être présente

(1) UMR 985 ESE INRA/Agrocampus Ouest, 65 route de Saint-Brieuc, 35042 Rennes Cedex, France, anne.treguier@rennes.inra.fr

(2) UMR 6553 ECOBIO CNRS/Université de Rennes 1, Campus de Beaulieu, avenue du Général Leclerc, 35042 Rennes Cedex, France

dans les mares proches du marais et d'un cours d'eau. Ces résultats suggèrent que la colonisation des mares par cette espèce dépend de la proximité de milieux aquatiques déjà colonisés, malgré sa facilité à disperser par voie terrestre.

INTRODUCTION

Small waterbodies, such as ponds, are widely distributed landscape feature (Oertli *et al.*, 2009). Moreover, ponds are major contributors to freshwater biodiversity at regional scale. Indeed, they host more unique species and, in the case of the UK, more rare species (according the species rarity index) than other waterbodies. In the same way, species composition is more variable between ponds than between other kinds of aquatic habitats (Williams *et al.*, 2004; Davies *et al.*, 2008a, 2008b). In cases where ponds are found in networks of independent units, they may serve as stepping stones for aquatic species. This may facilitate the persistence of rare species by metapopulation dynamics (De Meester *et al.*, 2005; Cereghino *et al.*, 2008). Ponds are also easily managed because of their small size (Cereghino *et al.*, 2008; Jurado *et al.*, 2009). Thus, their management has to be integrated into strategies for conservation of freshwater biodiversity (Cereghino *et al.*, 2008; Davies *et al.*, 2008a). Despite these features, ponds are currently threatened by various anthropogenic impacts such as habitat modification, habitat loss, or introduction of non-native species (Oertli *et al.*, 2002; Cereghino *et al.*, 2008; Correia and Anastacio, 2008).

Anthropogenic activities facilitate the transport of non-native species which can lead to invasion events (Davis, 2009; Usio *et al.*, 2009). For instance, the red-swamp crayfish *Procambarus clarkii* has been introduced around the world, and particularly in Europe, to replace native crayfish populations decimated by a plague, and because of its commercial success (Henttonen and Huner, 1999; Kerby *et al.*, 2005; Souty-Grosset *et al.*, 2006; Gherardi and Acquistapace, 2007). As a result, this species, which is native to north-eastern Mexico and south-central USA, is nowadays the most cosmopolitan freshwater crayfish species in the world (Gutiérrez-Yurrita *et al.*, 1999; Lindqvist and Huner, 1999; Gherardi, 2006). The success of *P. clarkii* invasion may be the result of its r-selected strategy, its ecological plasticity as well as its high dispersal ability (e.g. Gutiérrez-Yurrita *et al.*, 1999; Gherardi *et al.*, 2002; Alcorlo *et al.*, 2004; Souty-Grosset *et al.*, 2006). Indeed, movements of *P. clarkii* can exceed several kilometres per day in rice fields during wandering periods (Gherardi and Barbaresi, 2000).

The ecological effects of *P. clarkii* in aquatic ecosystems often are detrimental for native species (Rodríguez *et al.*, 2005; Ilhéu *et al.*, 2007; Correia and Anastacio, 2008). Indeed, *P. clarkii* is an omnivorous species that modifies food web dynamics in invaded ecosystems *via* predation and competition (Kerby *et al.*, 2005; Rodríguez *et al.*, 2005). For example, this species is probably the cause of the local extirpation of two gastropod species in Doñana Park in Spain (Montes *et al.*, 1993, in Alcorlo *et al.* (2004)) and of several amphibian species in Spain and Portugal (Rodríguez *et al.*, 2005; Cruz *et al.*, 2008). Moreover, *P. clarkii* is considered as an engineering species, which can significantly impoverish water quality *via* an increase of turbidity through its burrowing activity and its herbivorous diet (Angeler *et al.*, 2001; Rodríguez *et al.*, 2003; Anastácio *et al.*, 2005).

The Regional Nature Park of Brière contains the Brière marshes, one of the largest systems of wetlands (190 km²) in France. Local fish (e.g. pike and eel) and plant (e.g. reeds) species are of great socio-economic and cultural importance. *P. clarkii* was introduced into one sector of the Brière marshes in 1981 as a result of individuals escaping from a crayfish farm located in the vicinity of these marshes. It rapidly spread throughout the marshes (Arrignon *et al.*, 1999) and it is currently found in high abundance (3.4–21.5 individuals-trap⁻¹·24 h⁻¹; Paillisson *et al.*, 2010). Moreover, some of the ponds adjacent to these marshes have also been colonized by *P. clarkii*. But no study on the spatial distribution of this non-native species has been conducted to date on the network of ponds. Thus, to conserve the current biodiversity

and functioning of these small waterbodies, which may strongly contribute to regional freshwater biodiversity, the distribution of *P. clarkii* should be mapped as Kerby *et al.* (2005) and Kopp *et al.* (2010) recommended. Indeed, invasion specialists highlighted that dispersal is very important for the success of an invasive species (Davis, 2009). In this context, the aims of this study were: 1) to quantify the presence of *P. clarkii* in a network of ponds in the vicinity of Brière marshes and 2) to investigate if landscape metrics can explain *P. clarkii* spatial distribution in this network of ponds.

MATERIALS AND METHODS

> STUDY AREA

This study focuses on the Regional Nature Park of Brière, Northwest France (47° 23' N 02° 12' W). This park of 490 km² includes the Brière marshes, which are surrounded by a network of numerous ponds in agricultural landscapes (Figure 1). This park is intersected by streams and canals, which were built for navigation and to control the hydrology of the marshes. These aquatic habitats (ponds, streams and marshes) are occasionally connected by ditches during periods of heavy rain.

> SELECTION OF SAMPLED PONDS

To study the distribution of *P. clarkii* within the network of ponds, a sampling window of 10.5 km × 6.5 km was chosen in the southwest part of the park (Figure 1). This sampling window included 241 ponds (according to an ArcGIS database of all ponds within the park). A subset of 69 ponds (presumed to be permanent) was selected based on ease of access, landlord's permission, and in such a way as to cover the sampling area. The selected ponds ranged from 40 to 3100 m² in surface area (median of 321 m²) and were located up to 6 km away from the marshes.

Sampling was carried out from 22nd to 31st March, 2010. Three kinds of funnel traps were set along the shoreline of the pond to detect the presence of *P. clarkii*. The first kind of trap (large) was a collapsible cylindrical funnel trap (60 cm/30 cm/30 cm) of nylon wire (9 mm mesh). The second one (intermediate) was a semi-cylindrical funnel trap (50 cm/29 cm/21 cm) of galvanized steel wire (5.5 mm mesh). The third one (small) was a collapsible cylindrical funnel trap (55 cm/17 cm/17 cm) of polyamide wire (5 mm mesh). This latter kind of trap had one entrance whereas the other had two entrances. Each funnel trap was baited with dog food and set for 48 h.

Ponds were classified according to their surface into six classes: 40–50, 50–170, 171–400, 401–700, 701–1100 and 1101–3100 m². The number of funnel traps was standardized to these classes of surface: 3, 5, 6, 7, 8 and 9 respectively. Each pond was sampled with a set of funnel traps. Each set was composed of a maximum of one big funnel trap, six intermediate funnel traps and five small funnel traps. A total of 436 traps were deployed in the 69 sampled ponds.

> LANDSCAPE METRICS

In this study, we chose to focus on landscape metrics and not on habitat variables for two reasons. First, the spatial distribution of *P. clarkii* is poorly explained by habitat variables (Cruz and Rebelo, 2007). Secondly, as *P. clarkii* is an engineering species, it is difficult to know if the value of a habitat variable (as the covering of vegetation or turbidity) is the cause of colonization by *P. clarkii* or the consequences of its impacts on the habitat.

Information on the presence of *P. clarkii* was analysed according to landscape metrics that measure the level of isolation between a sampled pond and the other waterbodies: (1) the

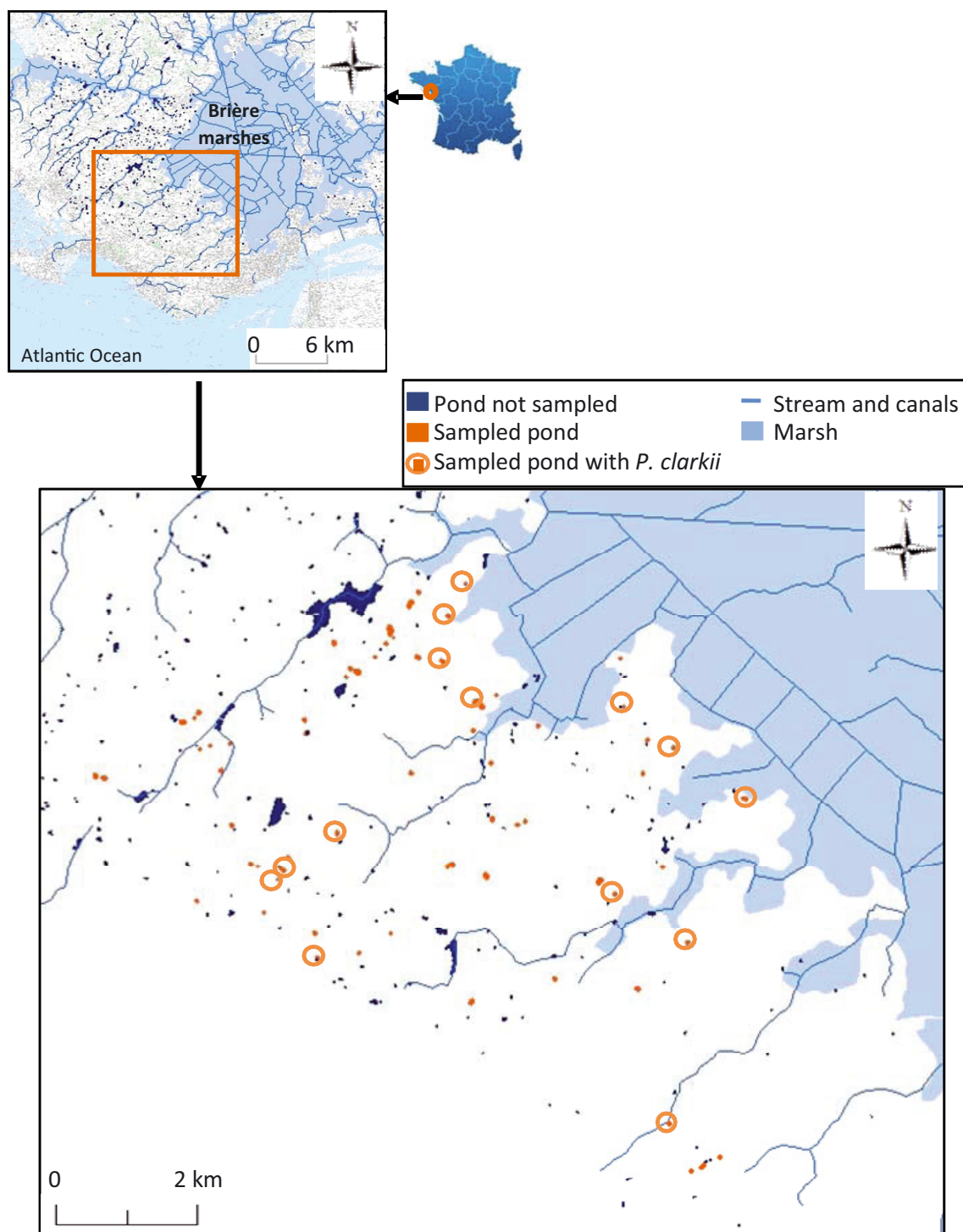


Figure 1
Top left: The core area of the Regional Nature Park of Briere in the Department of Loire-Atlantique, France, central marshes surrounded by many ponds and intersected by streams and canals. Bottom: Southwest portion of the park, including the 69 sampled ponds.

Figure 1
En haut à gauche : le cœur du Parc naturel régional de Briere en Loire-Atlantique en France, des marais centraux entourés de nombreuses mares et parcourus par des cours d'eau et des canaux. En bas : la partie ouest du parc, comprenant les 69 mares échantillonnées.

shortest linear distance between the sampled pond and Brière marshes (*DM*, expressed in m); (2) the shortest linear distance between the sampled pond and the nearest stream (*DS*, in m); (3) the shortest distance between a pond and the closest pond (*PP*, in m); and (4) the density of ponds (*PD*), which is the number of ponds (sampled or not) within three radii around the sampled pond: 200 m, 500 m and 1 km. We calculated the two first linear distances using ArcGIS (version 9.2, extension NEAR), and the third linear distance with the ruler of ArcGIS (version 9.2).

In another study carried out from 3rd to 14 April 2010, we measured water temperature in 30 ponds (13 with *P. clarkii* and 17 without).

> DATA ANALYSIS

We first tested if the efficiency of capture differed between types of funnel traps with a Wilcoxon paired test. Then, we used a Spearman correlation matrix to test whether landscape metrics were correlated with one another. To test for an association between presence of *P. clarkii* in ponds and landscape metrics, we conducted logistic regressions (generalized linear model). A binomial error with a logit link was implemented. Finally, we performed a principal component analysis (PCA) to illustrate the relationships between the presence and the absence of *P. clarkii* in ponds and the landscape metrics. We conducted all analyses using R (version 2.6.0) and considered tests significant when $p \leq 0.05$.

RESULTS

We captured 32 individuals of *P. clarkii* in 14 of 69 sampled ponds (*i.e.* 20.2%, Figure 1) and in 30 of the 436 deployed funnel traps (*i.e.* 6.9%). The number of crayfish caught per colonized pond ranged from 1 to 12 individuals. Water temperature was on average 14.2 °C (min: 7.5 °C; max: 20.1 °C).

The large funnel trap failed to capture a single *P. clarkii* individual. There were, however, no differences in the efficiency of capture between the two other kind of traps in our studied ponds ($N = 11$, $V = 45$, $p = 0.31$). This efficiency was measured by the mean number of individuals for each kind of trap. The sum of intermediate and small traps per pond was proportional to pond surface. We therefore pooled the data from both traps for the remained of our analyses.

> CORRELATION BETWEEN LANDSCAPE METRICS

The three pond density indexes were significantly positively correlated with one another ($0.49 \leq \rho \leq 0.72$, and $3.33e^{-12} \leq \rho \leq 1.800e^{-5}$). For the rest of this study, we chose the pond density index which used a radius of 500 m because it generated a wide range of values and yet captured local variation in pond density.

Moreover, pond density and the distance of the closest pond were significantly negatively correlated ($\rho = -0.58$, $p = 4.59e^{-7}$). Thus, ponds with a weak pond density were isolated from other ponds. However, the distance to the marshes and the distance to a stream were not significantly correlated with these two pond metrics, nor with one another (Spearman correlation tests, $-0.15 \leq \rho \leq 0.20$, and $0.10 \leq \rho \leq 0.68$). Nevertheless, ponds close to the marshes tended to be isolated from other ponds (Figure 1).

> LANDSCAPE METRICS AND *P. CLARKII* PRESENCE ON PONDS

We constructed two GLMs with the four landscape metrics. We did not include a model with *DS* (distance to stream), *DM* (distance to marshes), *PD* (pond density) and *PP* (proximity

Table 1

Results of the generalized linear model (binomial error family) testing the link between the probability of presence of *P. clarkii* and the three landscape metrics ($n = 69$ ponds: 14 with *P. clarkii* and 55 without *P. clarkii*). *DM*: distance to the marsh; *DS*: distance to a stream; *PD*: pond density (see Materials and methods section for details). Significant values are in bold.

Tableau 1

Résultats du modèle linéaire généralisé (famille d'erreur binomiale) testant la relation entre la probabilité de présence *P. clarkii* et les trois variables paysagères ($n = 69$ mares : 14 avec *P. clarkii* et 55 sans *P. clarkii*). *DM* : distance au marais ; *DS* : distance à un cours d'eau ; *PD* : densité de mares (voir les détails dans la partie Matériel et méthodes). Les valeurs significatives sont en gras.

	Estimate	Std. error	z value	Pr (> z)
Intercept	-2.316e+00	2.329e+00	-0.994	0.32017
DM	1.541e-03	1.300e-03	1.186	0.23574
DS	8.814e-03	4.685e-03	1.881	0.05995
PD	2.166e-01	5.574e-01	0.389	0.69762
DM:DS	-6.092e-06	2.379e-06	-2.561	0.01045
DM:PD	-5.176e-04	3.963e-04	-1.306	0.19152
DS:PD	-2.007e-03	1.189e-03	-1.688	0.09149
DM:DS:PD	1.400e-06	5.341e-07	2.622	0.00875

to pond) because the last two factors were strongly correlated. The first GLM included *DS*, *DM* and *PD* whereas the second included *DS*, *DM* and *PP*. The first model explained almost 40% of the variation of the data (GLM; null deviance: 69.606, residual deviance: 41.930; AIC: 57.93) whereas the model including proximity of ponds explained only 25% of the variation of the data (GLM; null deviance: 69.606, residual deviance: 52.355; AIC = 68.355). The first model was therefore selected for further analysis of its components. The 3-way interaction between distance to the marshes, distance to a stream and pond density in model 1 was highly significant (Table 1).

The first two axes of the PCA explained 75% of the variation of the data, 42% on the axis 1 and 33% on the axis 2 (Figure 2). The distance to the marshes and the distance to a stream highly contributed to the axis 1 (relative contributions of 61.65% and 45.42%, respectively) whereas the second axis was most strongly correlated with the density of ponds (relative contribution of 71.58%). Ponds without *P. clarkii* were located on the whole factorial plan. In other words, these ponds could not be uniquely characterized using these three landscape metrics. By contrast, most ponds with *P. clarkii* were located in the lower left part of the factorial plan, indicating that the number of ponds in their neighbourhood was low and that they were relatively close both to the marshes and a stream. In addition, three ponds with *P. clarkii* (bottom right in Figure 2) were relatively distant to the marshes and a stream.

DISCUSSION

The primary finding of this study was that landscape metrics partially explained the distribution of *P. clarkii* in this network of ponds. Indeed, *P. clarkii* was most likely to be present in ponds isolated from other ponds and close to both the marshes and a stream. However, contrary to the overall trends of our model, *P. clarkii* was present in some ponds located more than 1 km from both the marshes and the nearest stream. Moreover, ponds without *P. clarkii* did not share any unifying combination of analysed landscape metrics.

> LANDSCAPE METRICS AND *P. CLARKII* DISTRIBUTION

Some landscape metrics interacted to explain *P. clarkii* distribution. We show that ponds both near to the marshes, near to a stream and isolated from other ponds were likely to be colonized by *P. clarkii*. We suspected that the proximity to both the marshes and streams

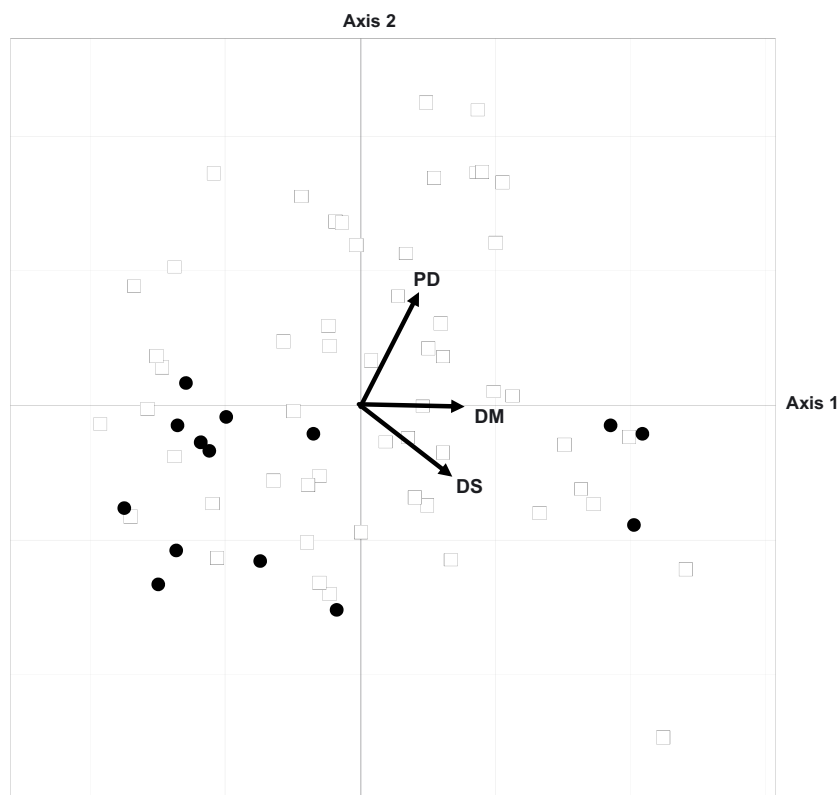


Figure 2

Principal component analysis (PCA) on landscape metrics values in ponds sampled in the vicinity of the Brière marshes. Axes 1 and 2 accounted for 42% and 33% of the total variation, respectively. Empty squares correspond to ponds without *P. clarkii* and full circles indicate ponds with *P. clarkii*. DM: distance to the marshes, DS: distance to a stream and PD: pond density (see Materials and methods section for details).

Figure 2

L'analyse en composantes principales (ACP) des variables paysagères des mares échantillonnées dans le voisinage des marais de Brière. Les axes 1 et 2 représentent respectivement 42 % et 33 % de la variance totale. Les carrés vides correspondent aux mares sans *P. clarkii* et les cercles pleins représentent les mares avec *P. clarkii*. DM : distance aux marais, DS : distance d'un cours d'eau et PD : densité de mares (voir la partie Matériels et méthodes pour les détails).

is biologically important. Indeed, these two habitats contain high densities of *P. clarkii* (3.4–21.5 individuals·trap⁻¹·24 h⁻¹ in marshes (Paillisson *et al.*, 2010)) and most likely represent source population from which individuals disperse (Penn, 1943). As a result, ponds in close proximity to both marshes and a stream are more likely to be colonized by *P. clarkii* because they are near two potential sources of individuals. By contrast, the correlation between the presence of *P. clarkii* and pond isolation may be an artefact of this particular landscape where clusters of ponds happened to occur far from the marshes and streams. Thus, the main result of this model is consistent with a prior study (Cruz and Rebelo, 2007) that showed that the overland distance between a pond and an established population play a role on the presence of *P. clarkii*.

Other hypotheses can be mentioned to explain why *P. clarkii* is present in some ponds both distant to the marsh and to a stream and why the absence of *P. clarkii* cannot be generalized with the studied landscape metrics. Firstly, the sampling did not indicate if a pond currently not colonized has never been colonized by *P. clarkii* individuals. Similarly, sampled ponds represent only a subset of all ponds of the network. Thus, we may not detect the presence of *P. clarkii* in ponds being used merely as transitory stepping stones. Moreover, dispersal

by humans cannot be excluded. Secondly, colonization of ponds by *P. clarkii* can be influenced by other landscape characteristics than those used in this study. For example, we did not measure the distribution of ditches in the landscape, nor the humidity of habitats in the terrestrial matrix, two factors that may influence the probability of successful overland dispersal (Gherardi *et al.*, 2002).

> A WEAK COLONIZATION OF PONDS BY *P. CLARKII*

Only 20% of the sampled ponds were colonized by *P. clarkii*. This proportion is low given the fact that *P. clarkii* has invaded all sectors of Brière marshes and that ponds are close to these marshes in the study window. Several studies found larger colonization rates of waterbodies by *P. clarkii*: 22 to 51% in temporary ponds, 54% in permanent ponds, 32 to 84% in streams (Kerby *et al.*, 2005; Cruz and Rebelo, 2007; Kopp *et al.*, 2010) and a more rapid colonization process (Cruz and Rebelo, 2007). The low capture rate found in the present study can be explained with three non-mutually exclusive scenarios. Firstly, these previous studies were not carried out in the same context. In this study, sampled ponds were more distant to aquatic sources (often more than 1 km). Thus, the *P. clarkii* colonization of the network of ponds is probably limited by the necessity of a larger overland dispersal to colonize ponds. Secondly, it is possible that a large fraction of these ponds are unsuitable habitats for *P. clarkii*. This scenario, however, is more unlikely since this species is known for its high ecological plasticity (Gutiérrez-Yurrita *et al.*, 1999; Souty-Grosset *et al.*, 2006) and, as a result, habitat characteristics would have a moderate influence on *P. clarkii* distribution (Cruz and Rebelo, 2007). Thirdly, minimum water temperatures may have been too low to induce *P. clarkii* activity and consequently it cannot be excluded that a few ponds were incorrectly classified free of *P. clarkii*.

Finally, the limited spatial distribution of *P. clarkii* in this network of ponds suggests that the ability of this crayfish species to disperse overland is limited. Thus, this hindrance to the possible colonization of a large number of ponds may permit to develop strategies to limit the expansion of *P. clarkii* in all freshwater ecosystems of the Regional Nature Park of Brière and to protect local aquatic biodiversity. We now have to follow the evolution of *P. clarkii* spatial distribution in all ponds and streams within a sampling window to detect potential *P. clarkii* sources of dispersal and to better understand *P. clarkii* dispersal processes between waterbodies.

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