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The role of sediments in the distribution of *Uca pugilator* (Bosc) and *Uca pugnax* (Smith) (Crustacea, Brachyura) in a salt marsh of Cape Cod

EDUARDO JARAMILLO and KARIN LUNECKE

Instituto de Zoología and Instituto de Ecología y Evolución, Universidad Austral de Chile, Valdivia, Chile

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Abstract

The distribution of the fiddler crabs *Uca pugilator* (Bosc) and *Uca pugnax* (Smith) in relation to the quality of the sediments was analysed in the Great Sippewissett Marsh, Cape Cod (Massachusetts, USA). This study involved a survey of crab distribution along a transect of 150 m, together with laboratory and field experiments dealing with substrate burrowing preference.

U. pugilator was found along most of the transect with exception of stations with >15 % of mud. *U. pugnax* was restricted to sediments with high percentages of mud, organic matter and plant cover. Laboratory substratum preference experiments showed that *U. pugilator* dug in sandy and muddy sediments, but mostly in sand. *U. pugnax* made burrows almost exclusively in muddy sediments.

Field substratum preference experiments (reciprocal transplants of sediments) generally agreed with the laboratory results. *U. pugilator* dug in both kinds of substrate in the sandy area, but only in the sandy squares in the muddy area. *U. pugnax* made burrows only in the muddy squares, regardless of the area.

It is concluded that the quality of the sediments plays a more significant role in the distribution of *U. pugnax* than in *U. pugilator*. For *U. pugilator* factors other than quality of substratum may be involved in its present pattern of distribution.

Kurzfassung

Rolle des Sediments für die Verteilung von Uca pugilator (Bosc) und Uca pugnax (Smith) (Crustacea, Brachyura) in einer Salzwiese in Cape Cod, USA

Die Verteilung der Winkerkrabben *Uca pugilator* (Bosc) und *Uca pugnax* (Smith) in Relation zur Sedimentqualität wurde in der Great Sippewissett Marsh, Cape Cod (Massachusetts, USA) untersucht. Die vorliegende Arbeit enthält eine Aufnahme der Krabbenverteilung entlang einem Schnitt von 150 m Länge sowie Labor- und Feldexperimente zur Substratselektion.

U. pugilator wurde fast überall auf dem Transekt gefunden; eine Ausnahme machten Stationen mit >15 % Schlick. *U. pugnax* war nur auf Sedimenten mit hohen Anteilen an Schlick, organischem Material und Pflanzenbedeckung zu finden. Labor-Experimente zur Substratpräferenz zeigten, daß *U. pugilator* sowohl in sandigen wie in schlickigen Böden gräbt, jedoch meist in Sand. *U. pugnax* grub ihre Löcher fast ausschließlich in schlickigen Sedimenten.

Die Ergebnisse aus Feldexperimenten zur Substratpräferenz (Überkreuz-Transplantation von Sedimenten) stimmten i. a. mit den Laborresultaten überein. *U. pugilator* grub auf beiden Bodentypen im Sand-, aber nur auf den Sandstellen im Schlickgebiet. *U. pugnax* grub nur auf den angebotenen Schlickstellen, ohne Rücksicht auf den Bodentyp der Umgebung.

Die Qualität der Sedimente spielt also anscheinend für die Verteilung von *U. pugnax* eine größere Rolle als für die von *U. pugilator*. Bei dieser Art mögen andere Faktoren als die Sedimentqualität für das gefundene Verteilungsmuster verantwortlich sein.

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Resumen

El rol de los sedimentos en la distribución de Uca pugilator (Bosc) y Uca pugnax (Smith) (Crustacea, Brachyura) en una marisma de Cape Cod, USA

Se analizó la distribución de los cangrejos *Uca pugilator* (Bosc) y *Uca pugnax* (Smith) en relación a la calidad del sedimento en Great Sippewissett Marsh, Cape Cod (Massachusetts, USA). Este estudio incluyó un análisis de distribución en un transecto de 150 m, además de experimentos de selección de sustrato en laboratorio y en terreno.

U. pugilator fué colectada en la mayor parte del transecto, con excepción de estaciones con contenido de fango >15 %. *U. pugnax* estuvo restringida a sedimentos con alto porcentaje de fango, materia orgánica y cobertura de plantas. Los experimentos de laboratorio mostraron que *U. pugilator* excavó en sedimentos arenosos y fangosos, pero mayoritariamente en los arenosos. *U. pugnax* excavó casi exclusivamente en los sedimentos fangosos.

Los experimentos de terreno (transplantes recíprocos de sedimentos) mostraron una concordancia general con los de laboratorio. *U. pugilator* excavó en sedimentos arenosos y fangosos localizados en las áreas arenosas, pero sólo en los sedimentos arenosos de las áreas fangosas. *U. pugnax* excavó sólo en sedimentos fangosos, en una u otra área.

Se concluye que la calidad del sedimento tiene un rol más significativo en la distribución de *U. pugnax* que en la de *U. pugilator*. Otros factores, aparte de calidad del sedimento pueden estar involucrados en la distribución de *U. pugilator*.

Introduction

Fiddler crabs (*Uca* spp.) are common inhabitants on salt marshes along the east coast of North America (Barnwell and Thurman 1984; Crane 1975). Studies on their distribution and abundance have demonstrated that substratum characteristics and interspecific interactions have an important role in the observed patterns of distribution and abundance (Aspey 1971, 1978; Bertness 1985; Bertness and Miller 1984; Ringold 1979; Teal 1958).

Uca pugilator (Bosc) and *Uca pugnax* (Smith) are commonly found in the Great Sippewissett Marsh, northwest of Woods Hole, Cape Cod. *U. pugilator* typically inhabits sandy sediments, while *U. pugnax* predominates in the muddy substratum of the *Spartina* stand and edges of tidal creeks. Occasionally, both species occur together, e.g. in patches of sandy sediments located in the *Spartina-Salicornia* marsh.

This study was designed to answer two questions: (1) What is the abundance of *U. pugilator* and *U. pugnax* in relation to the quality of the substratum, and (2) to what extent can substratum characteristics explain the present distribution of these species in the Great Sippewissett Marsh? We analysed the species distribution along a transect covering different substrata and plant cover, and then undertook laboratory and field preference experiments during the summer of 1984.

Material and methods

Two sites within the Great Sippewissett Marsh were chosen for the field studies. To analyse the spatial distribution of fiddler crabs in relation to characteristics of the habitat, site 1 was surveyed along a transect of 150 m. The abundance of crabs was determined as number of animals collected during low tide in squares of 1 m^2. After counting the burrows in those squares, the burrows were dug up to a depth close to 30 cm. At each of those squares, samples of the surface 2 cm of substrate were collected for sedimentological analyses. For each sample, the percentages of mud (<63 µm), sand (63–1000 µm) and very coarse sand (1000–2000 µm) (after Wentworth scale; Folk 1980) were determined by wet sieving. The coarse fraction (very coarse sand) was present in low percentages (less than 6 %) at all those squares but one (20 %). Therefore, this fraction was eventually eliminated from consideration. The organic matter content of sediment samples was calculated as % weight loss of samples burned at 550 °C for 4 hours after drying for 48 hours at 65 °C. Plant cover percentage (mostly *Spartina alterniflora* Loisel and *Salicornia* spp.) was determined by counting the number of points (out of 100 equally spaced points in a square of 1 m^2) projected over the vegetation.

To study the substratum burrowing preference of *U. pugilator* and *U. pugnax*, groups of 10 crabs (> 4 mm length of cephalothorax; no cephalothorax length classes were established for this study) were placed in aquaria for 6 hours and given a choice of two different sediments. The aquaria measured 40 × 60 × 40 cm and were filled with a 5 cm deep layer of fresh sand (i.e. sediment used right after collection in the field) in one half and fresh muddy sediment in the other. The sand used came from the middle area of the surveyed transect in which the percentages of sand (63–1000 μm) varied between 95.7 and 99.3 %. The muddy sediment came from areas close to that transect with mud (< 63 μm) percentages close to 30 %. Aquaria filled with fresh sandy or muddy sediments only were used as controls. Six replicates of each sediment combination and three controls per species were run using new animals and sediments each time. At the end of the experiments, the number of burrows built by the crabs at each half of the aquaria was recorded. We also tested the substratum burrowing preference in the field. Reciprocal transplants of 0.3 m substratum squares were made at two salt marsh sites. The experimental squares were approximately 20 cm deep and covered areas which had been previously cleared of crabs. The two sites were located in areas of sandy sediments with established populations of *U.*

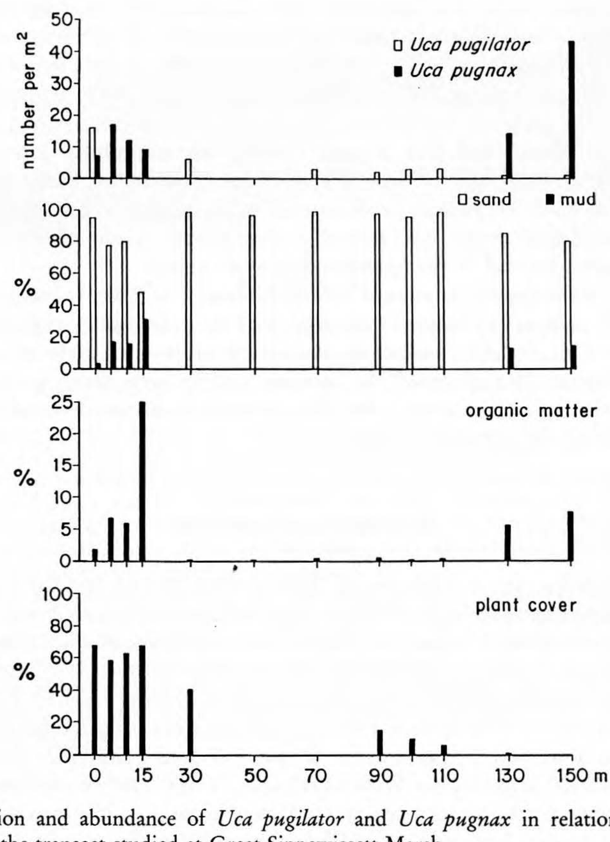

Fig. 1. Distribution and abundance of *Uca pugilator* and *Uca pugnax* in relation to the habitat characteristics of the transect studied at Great Sippewissett Marsh.

pugilator occurring near muddy substrata inhabited by *U. pugnax*. At site 1 the sandy and muddy areas were 15–20 meters apart, separated by a stand of *Spartina alterniflora* and a narrow (4 m wide) tidal creek, while at site 2 a belt of *S. alterniflora* (6 m wide) separated the two substrata. Muddy sediment squares were transplanted to the sandy areas and vice versa. As controls for handling effects, we removed and replaced in situ 0.3 m^2 sediment squares in each area. The manipulated sediments were carefully examined in order to remove the animals living in them and then examined again after two weeks.

Results

Distribution of crabs

Spatial distribution of *U. pugilator* and *U. pugnax* as well as the habitat characteristics of the transect are presented in Fig. 1. The number of specimens of *U. pugilator* varied between 1 and 16 per m^2; *U. pugnax* reached abundances up to 43 individuals per m^2. *Uca pugilator* was found along most of the transect with the exception of some stations located in the *Spartina* stand, where the percentage of mud was higher than 15 % (Fig. 1). *Uca pugnax* was absent at the sandy stations of the transect, and was instead restricted to both muddy ends of the transect, where the percentage of organic matter was highest (Fig. 1). These stations also had the highest plant cover or were located near zones with high percentages of *Spartina* cover.

Substratum burrowing preference

The mean number of burrows built by *U. pugilator* and *U. pugnax,* in the two combinations of sediments and control treatments offered in aquaria, is shown in Fig. 2. *Uca pugilator* clearly preferred the sandy substratum. On the other hand *Uca pugnax* preferred burrowing in the muddy sediment given the same choice. Clearly, *U. pugnax* showed very little tendency for burrowing in sand. Both species built a similar number of burrows in the muddy sediment.

The mean number of individuals of each species recorded in the field experimental squares after two weeks is shown in Fig. 3. *Uca pugilator* colonized the handling and muddy squares in the sandy area. This species was found in low numbers in the muddy area and then only in the sandy squares. *Uca pugnax* colonized only the muddy squares, regardless of where they were placed.

Discussion

The analyses of the spatial distribution, together with those of the substratum burrowing preference experiments, show the important role of the substratum quality in the distribution of *Uca pugilator* and *Uca pugnax* in Great Sippewissett Marsh.

The presence of *U. pugilator* in the sandy handling controls, as well as the presence of *U. pugnax* in the muddy handling controls, demonstrates that both species were able to reach and become established in the recently implanted squares located within those areas, where they naturally occurred before our manipulations.

The fact that *U. pugnax* only colonized the muddy squares regardless of where they were placed, agrees with the marked preference that this species showed in the laboratory experiments. It also suggests that *U. pugnax* was not deterred by the presence of *U. pugilator* in the sandy area. In fact, both species occurred together in some squares of the studied transect (see Fig. 1). The general restriction of *U. pugnax* to muddy substratum has been explained in part by the lack of mouth parts adapted for foraging in sandy sediments

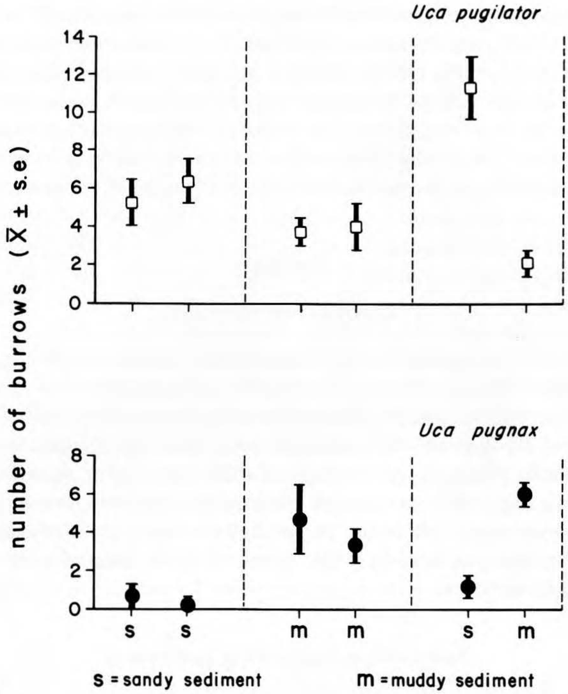

Fig. 2. Number of burrows built by *Uca pugilator* and *Uca pugnax* in relation to the sediment combinations and control treatments offered in the laboratory. Each value is the mean of six replicates in the two-choice experiments and three in the controls.

(MILLER 1961; ROBERTSON and NEWELL 1982). On the other hand, root mat density has also been involved in the causal explanation of the distribution of *U. pugnax* (BERTNESS and MILLER 1984; RINGOLD 1979).

Uca pugilator colonized both types of the experimental squares (handling and muddy squares) in the sandy areas, supporting the laboratory results which demonstrated that this species is able to burrow in both types of sediments. However, the fact that this species showed a higher density in the muddy squares (cf. a and b, Fig. 3) was not expected from the results of the laboratory experiments. The facultative ability of *U. pugilator* for inhabiting a variety of substrata has also been reported by ROBERTSON and NEWELL (1982) on Sapelo Island, Georgia.

Uca pugilator was found in low density in the muddy areas, and then only in the sandy squares. This fact suggests that it may have suffered some kind of deterrence by *U. pugnax* that kept it from becoming established there. This suggestion is supported by evidence reported in other studies. TEAL (1958) found that the presence of other species of *Uca* was reduced by 50 % or more, while ASPEY (1971, 1978) mentions that the agonistic display exhibited by *U. pugnax* is a factor contributing to the reduced number of burrows built by *Uca pugilator* when occurring together with *Uca pugnax*. Thus, factors other than quality of substratum and feeding-related anatomy (MILLER 1961) may be involved in the absence of *U. pubilator* from the muddy areas dominated by *U. pugnax*, whose distribution in turn seems to be mainly determined by the quality of the sediments as mentioned earlier.

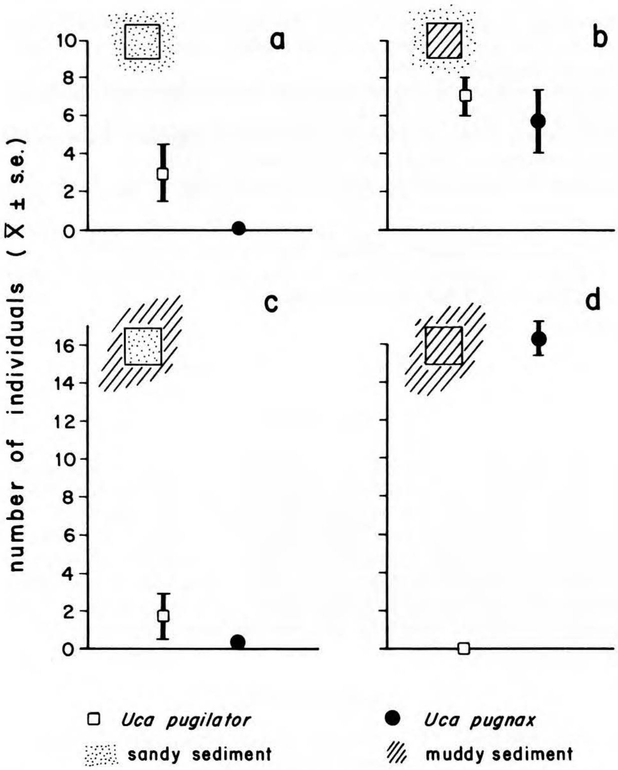

Fig. 3. Number of specimens of *Uca pugilator* and *Uca pugnax* collected in the field experimental squares after two weeks. a and d were the handling controls, b and c, the transplant experiments. Each value is the mean of three observations, one in site 1 and two in site 2.

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Authors' addresses: Dr. EDUARDO JARAMILLO, Instituto de Zoología, Universidad Austral de Chile, Casilla 567, Valdivia, Chile.
KARIN LUNECKE, Instituto de Ecología y Evolución, Universidad Austral de Chile, Casilla 567, Valdivia, Chile.