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What regulates crab predation on mangrove propagules?

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ABSTRACT

Crabs play a major role in some ecosystems. To increase our knowledge about the factors that influence crab predation on propagules in mangrove forests, we performed experiments in Gazi Bay, Kenya in July 2009. We tested whether: (1) crab density influences propagule predation rate; (2) crab size influences food competition and predation rate; (3) crabs depredate at different rates according to propagule and canopy cover species; (4) vegetation density is correlated with crab density; (5) food preferences of herbivorous crabs are determined by size, shape and nutritional value. We found that (1) propagule predation rate was positively correlated to crab density. (2) Crab competitive abilities were unrelated to their size. (3) *Avicennia marina* propagules were consumed more quickly than *Ceriops tagal* except under *C. tagal* canopies. (4) Crab density was negatively correlated with the density of *A. marina* trees and pneumatophores. (5) Crabs prefer small items with a lower C:N ratio.

Vegetation density influences crab density, and crab density affects propagule availability and hence vegetation recruitment rate. Consequently, the mutual relationships between vegetation and crab populations could be important for forest restoration success and management.

1. Introduction

The mangrove ecosystem is unique; as a forested vegetation it is remarkably well adapted to high salt concentrations, hypoxic to anoxic soils, and is influenced by tidal action in most of its ecological settings (Krauss et al., 2008). The mangrove ecosystem structure is affected by various abiotic (e.g. temperature, salinity, nutrient, tidal amplitude, topography) and biotic factors (e.g. inter- and intra-specific competition, interactions with fauna, anthropogenic pressure) (Lee, 1999).

Impacts of mangrove fauna are predominantly due to crab activity, as they are the most abundant macrofauna taxon in mangroves (Macnae, 1968; Cannicci et al., 2009). Some authors refer to crabs as keystone species in mangrove ecosystem (Macnae, 1968; Schories et al., 2003; Kristensen, 2007; Amarasinghe et al., 2009; Cannicci et al., 2009; Lindquist et al., 2009). Crabs can affect forest structure through at least two activities: burrowing (Macnae, 1968; Cannicci et al., 2009) and herbivory (Schories et al., 2003).

Some herbivorous crab families are known to depredate on propagules. This predation can affect mangrove regeneration in natural and restored stands (Dahdouh-Guebas et al., 1998), and they can also regulate competitive interactions between tree species in high density reforested stands (Bosire et al., 2005). Most decapods are opportunistic feeders and exploit a wide range of food sources (Cannicci et al., 2007). Sesarmid crabs are predominantly herbivorous (Dahdouh-Guebas et al., 1999), but do not exclusively feed on leaf litter (Bouillon et al., 2002a,b; Thongtham and Kristensen, 2005). While some arboreal climbing species actively forage on tree leaves (Cannicci et al., 1996), the majority of herbivorous sesarmid crabs rely on mangrove litter made up of leaves and seasonal propagules (Nicholson, 2009). Arboreal herbivorous climbing species can affect propagules before dispersal by increasing premature propagule abscission rate (Farnsworth and Ellison, 1997). Other decapods may damage propagules after abscission (Smith, 1987; Wilson, 1989; Robertson et al., 1990).

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Most mangrove species are viviparous and produce fruit, propagules or seeds that can disperse through water (Macnae, 1968; Tomlinson, 1986; Tomlinson and Cox, 2000). However, these adaptations do not prevent predation and crabs may access to propagules of species other than the locally dominant ones (Dahdouh-Guebas et al., 1998; Bosire et al., 2005).

Crab predation on propagules could be affected by many factors such as predation pressure on crabs, inter- and intra-specific competition, reproductive period, and season (Erickson et al., 2004). The most influential factors of predation rate are the amount (Beever et al., 1979) and size (Emmerson and McGwynne, 1992; Nordhaus et al., 2006) of predators, food availability (Smith, 1987) and vegetation cover (Osborne and Smith, 1990; Farnsworth and Ellison, 1991; Clarke and Kerrigan, 2002). The nutritional value (Smith, 1987; Farnsworth and Ellison, 1991; McKee, 1995; Clarke and Kerrigan, 2002; Ditzel Faraco and da Cunha Lana, 2004; Nordhaus et al., 2011), nature (leaf or propagule) (Salgado Kent and McGuinness, 2008), size (Salgado Kent and McGuinness, 2008; Camilleri, 1989) and shape of the food can also lead to different feeding preferences and rates.

This study focuses on the predation behaviour of two herbivorous crab species: *Neosarmatium africanum* Ragionieri, Fratini and Schubart (formerly *Neosarmatium meinerti* De Man) and *Neosarmatium smithii* H. Milne Edwards. We examined their feeding habits and the factors that could influence their predation behaviour. Specific objectives of the study were to evaluate: (1) whether predation rate increases with crab density (*cf.* Dahdouh-Guebas et al., 1998); (2) whether larger crabs are dominant food competitors and thus depredate more propagules; (3) whether propagules from two species are depredated at the same rate and if the rate of crab predation on propagules are affected by the propagule species, dominant canopy trees, and crab species; (4) whether higher tree densities lead to higher crab densities and a higher predation rate on propagules; (5) whether species, size, nature (leaf or propagule), colour or C:N ratio of the food items influence crab preferences.

2. Materials and methods

2.1. Study area and organisms

Fieldwork was conducted in the mangrove forest of Gazi Bay on the southern coast of Kenya, situated 50 km south of Mombasa (4° 25′ S and 39° 30′ E). This mangrove forest is dominated by *Avicennia marina* (Forssk.) Vierh., *Rhizophora mucronata* Lamk. and *Ceriops tagal* (Perr.) C.B.Robinson and has a total area of 6 km^2 (Neukeurmans et al., 2008). Data was collected from the end of June to the beginning of August 2009, during the drier period of the rainy season. We have chosen that period because it is characterized by a high abundance of mature propagules of *A. marina* and *C. tagal*. We observed crabs at low tide when they were out of their burrows and more active. According to Micheli et al. (1991), crab activity depends mainly on the light–dark cycle. Their activity declines dramatically during the night. They are more active around sunset and sunrise or during the day, but in the latter case they stay in protected, shaded biotopes to avoid the risks of predation by birds (Micheli et al., 1991) and desiccation (Fusi et al., unpublished results). The study site was an area of 1 km^2 with a *R. mucronata* stand at lower tidal elevations, a *C. tagal* stand at the higher tidal elevations and a *A. marina* stand located in between them (Table 1). We have chosen this site since it is inhabited by the two largest herbivorous sesarmids: *N. smithii* and *N. africanum*. These species are distributed in association to vegetation species, inundation level, and soil characteristics (Table 1). *N. africanum* is found in the zone with *A. marina* and *C. tagal* cover, and *N. smithii* is found in the adjacent zone with *R. mucronata* cover (Table 1). Both crab species are assumed to usually encounter propagules of *A. marina* and *C. tagal*. We tested crabs of which the burrows were less than five metres away from *A. marina* or *C. tagal* trees. Propagules can fall on the ground and self-planted in soil or can fall in water and be transported by current (Dahdouh-Guebas et al., 1998; Bosire et al., 2005) becoming easily accessible to crabs from another area at low tide (personal observation). The randomization in our experiments was usually made by arbitrary selection of coordinates with a GPS or with the aid of a hand-drawn map where trees, roots, and burrows were represented. In some cases, we threw a stone and used the drop place as the left-hand bottom corner of our plot. We distributed our replicas through space but also through time in order to avoid crabs to become used to the experiment. Nonetheless, some replicas of some experiments were carried out simultaneously, to save time.

Table 1
Forest structure, crab zonation, soil characteristics and inundation level. Adapted from Matthijs et al. (1999) and Dahdouh-Guebas et al. (2002).

	← Land		Creek →	References
Dominant cover species	*C. tagal*	*A. marina*	*R. mucronata*	
Dominant crab species	*N. africanum*	*N. africanum*	*N. smithii*	
Soil variables				
Eh (mV)	−204	−182	−288	Matthijs et al. (1999)
NaCl (g/100 g)	4.4	5.3	3.4	
pH	6.44	6.41	6.84	
Substate	Sandy	Sandy	Dark grey muddy	
Hydrology				
'Height above datum'-range (m)	2.10–2.60	2.60–3.10	1.50–2.00	Dahdouh-Guebas et al. (2002)

2.2. Impact of crab density on predation

In order to observe how predation varies with crab density, we placed five *A. marina* or *C. tagal* propagules in a 2 m^2 plot. The 17 or 20 different crab density zones were chosen one by one after 20 min of observation. The experiment was repeated in 20 randomly chosen plots for each density ranges of 1–3 crabs/m^2, 4–6 crabs/m^2 and 7–15 crabs/m^2. This was carried out over approximately 14 days, distributed over a 6 week period. We noted how many propagules were depredated under *A. marina* stand 10 min after the propagules were placed in position, and under *R. mucronata* stand after 15 min. We established these exposure times based on the mean time for crabs to depredate the mean quantity of propagules under a mean crab density. The observer was at least ten metres away from the plots and was assumed to be out of sight of the crabs. We assumed that propagules had been depredated when they were inside a crab burrow.

2.3. Importance of crab size in food competition

To investigate intra-specific competition for food amongst *N. africanum*, and to establish the variation of the predation rate between different crab sizes, we randomly chose and observed pairs of crabs in an *A. marina* zone. We retained pairs which exited their burrows in front of each other, and which were moving in the same direction, in order to avoid displaying favouritism towards one individual from a studied pair. The minimum carapace width difference between the individuals of each pair was at least 1.5 cm. Before the experiment, we determined an approximate size of each crab, and after the experiment we caught the crabs and took