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The distribution of the European shore crab, *Carcinus maenas*, with respect to mangrove forests in southeastern Australia

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ABSTRACT

There is growing interest in associations between non-native species and native foundation species. Along the southeast coast of Australia, the European shore crab, *Carcinus maenas*, overlaps with the distribution of the grey mangrove, that provides refuge to many native invertebrates from predators and physiological stress. We tested the hypothesis that *C. maenas* would be more abundant under the canopy of mangrove forests than in adjacent unvegetated intertidal habitat. Trapping surveys within three estuaries found greater abundances of *C. maenas* in mangrove forests than in adjacent unvegetated habitat and, within mangrove forests, under the canopy than in the pneumatophores zone. Average temperatures under the mangrove canopy were up to 2 °C lower than in unshaded habitats and maximum temperatures up to 5.7 °C less. The results of tethering studies did not support the hypothesis that predatory mortality of *C. maenas* was reduced in mangroves. To the contrary, survivorship of tethered crabs was much lower under the mangrove canopy than in adjacent unvegetated habitat. Habitat choice experiments, however, indicated that crabs chose shaded and protected over unshaded and exposed habitat. Hence, along this coastline where summertime maximum air temperatures may approach the known LD_{50} of *C. maenas* (40 min at 40 °C), mangroves may help to facilitate persistence in intertidal habitats. Our study adds to a growing number indicating that foundation species may not only facilitate native species, but non-native species too. Additional studies are now needed to confirm the mechanism of the association between *C. maenas* and mangroves in eastern Australia.

1. Introduction

The introduction of non-native species to novel environments is recognized as a major driver of ecological change (Simberloff, 2005; Vitousek et al., 1996). Non-native species are now found in every ecosystem, and have impacts ranging from negligible to transformative (Simberloff, 2005; Vitousek et al., 1996). Given the potential for some non-native species to cause significant ecological and economic costs, understanding the ecological factors that regulate them has become a key concern of applied ecologists. For species that are known to have established in a novel environment, a first step in this process requires gathering information on their distribution and abundance, and then on the abiotic and biotic controls of these.

There is growing interest in how the distribution of non-native species follows distributions of foundation species (sensu Dayton, 1972). Foundation species produce changes in environmental conditions that may be positive, negative or neutral to individual species, but on the whole tend to enhance biodiversity and species abundances (Bruno et al., 2003; Dayton, 1972; Jones et al., 2004). Just as foundation species may make the environment more suitable for many native species, they might also have high associated abundances of non-native species (e.g. Bulleri and Benedetti-Cecchi, 2008; Byers et al., 2012; Thompson and Schiel, 2012).

The European shore crab, *Carcinus maenas* (Linnaeus, 1758), is a global invader that has spread from northwest Europe and North Africa (Broekhuysen, 1936; Crothers, 1967; Naylor, 1962) to the Atlantic and Pacific coasts of North America, the Patagonian coast of South America, Japan, South Africa and southern Australia (Carlton and Cohen, 2003; Hidalgo et al., 2005; Thresher et al., 2003). The crab is an omnivore and is found on hard and soft substrata in the upper littoral and sub-littoral zone, down to 60 m, in protected marine and estuarine habitats (Crothers, 1968; Grozholz and Ruiz, 1996; Thresher et al., 2003). In environments where the crab is vulnerable to high densities of predators, or to physiological stress, for example during periods of emersion at intertidal sites, it frequently is associated with foundation species such as marsh, algae and seagrass (e.g. Bertness and Coverdale, 2013; Dijkstra et al., 2012; Ellis et al., 2012; Watt and Scrosati, 2013). Along the east coast of Australia, mangroves are one of the most abundant foundation species in the intertidal environment and support dense and diverse native communities of epiphytic algae, terrestrial and aquatic invertebrates, fish and mammals (Morrisey et al., 2010). In southern New South Wales and the east coast of Victoria, the distribution of the temperate grey mangrove, *Avicennia marina*, overlaps with that of *C. maenas* and

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it may provide an important habitat refuge for the crab in the intertidal habitat zone.

Previous large scale-surveys in southeastern Australia indicate that higher densities of *C. maenas* exist in mangroves than in saltmarsh, seagrass, oyster beds or in unvegetated sediment near the mouth of the estuary (Garside et al., 2014). However, it is unclear whether at smaller scales mangroves also support greater abundances of the non-native crab than adjacent unvegetated intertidal habitat. The prop roots and peg roots (pneumatophores) of mangroves form a structurally complex habitat that greatly enhances the availability of hard substrata for molluscs to attach to (Nagelkerken et al., 2008) and can reduce the foraging efficiency of benthic predators such as toadfish (Tetraodontidae spp.) and bream (*Acanthopagrus australis*), which feed in mangrove forests at high tide (Primavera, 1997; Smith and Hindell, 2005; Warren, 1990). Furthermore, the mangrove canopy helps to maintain a shaded and humid environment which might be particularly important in enabling *C. maenas* which tolerates temperatures from <0 to 35 °C (Eriksson and Edlund, 1977; Hidalgo et al., 2005) to withstand air temperatures that can exceed 44 °C during the southeastern Australian summer.

In this study, we investigate the distribution of *C. maenas* in intertidal waters of southeastern Australia with respect to *A. marina* mangroves. Specifically, we assess whether: (1) within invaded southeast Australian estuaries, the European shore crab (*C. maenas*) is more abundant within mangrove forests than in adjacent unvegetated habitat; (2) in mangrove forests *C. maenas* experiences reduced rates of mortality; (3) temperatures on the surface of sediments are cooler in mangrove forests than in unvegetated areas; and (4) when offered a choice between shaded and unshaded environments, *C. maenas* choose shaded habitat.

2. Methods

2.1. Spatial sampling

To test whether *C. maenas* is more abundant (1) inside than outside of mangrove habitat patches and (2) under the mangrove canopy, where there is shading, than in the pneumatophore zone where there is structure but not shading, we conducted sampling within three estuaries on the south coast of New South Wales (NSW) Australia: Merimbula Lake (36.89°S, 149.92°E), Bermagui River (36.42°S, 150.06°E) and Wagonga Inlet (36.21°S, 150.13°E). Each of these estuaries is known to contain small populations of *C. maenas*, which is widely distributed, though not yet abundant, on the NSW coast (Garside et al., 2014), and has patchy mangrove forest along its shoreline. Within each estuary, we randomly selected three study sites, each of which contained adjacent habitat patches (each at least 100 m in along-shore width) with mangrove and without (hereafter unvegetated). Within the mangrove habitat patch of each site, we set replicate traps ($n = 4$–7) at each of three elevations: under the mangrove canopy; in the pneumatophore zone; and 30 m seaward of the canopy. To control for effects of tidal elevation, traps were set at corresponding elevations in the adjacent unvegetated habitat. Traps were separated by at least 15 m.

Within each estuary, trapping was done on each of two consecutive days in spring of 2011, using 62 × 42 × 20 cm traps, constructed of 1.3 cm square plastic netting with two horizontal entrances at the apex of two inward facing 45° panels of netting at either end. These traps have been previously used for surveillance of *C. maenas* in Australian ports (Hewitt and Martin, 2001; Thresher et al., 2003). Traps were baited with a single 8–15 cm pilchard (*Sardinops neopilchardus*), deployed on a day time low tide and left to fish for 22–24 h (as per Garside et al., 2014). At the end of this period we enumerated the number of *C. maenas* per trap. Traps were then redeployed at different positions within each elevation of each habitat, and re-sampled after another 22–24 h.

PERMANOVA (Anderson et al., 2008) assessed differences in crab abundance among tidal elevations and habitats in each estuary. Separate analyses were conducted for each estuary because the abundance of *C. maenas* differed markedly among these. The analyses had the factors: Site (3 levels, random); Height on the shore (3 levels, fixed: high [a tidal elevation equivalent to that under the mangrove canopy], medium [a tidal elevation equivalent to that just seaward of the canopy, within the pneumatophore zone], low [30 m seaward of high]); and Habitat (2 levels, fixed: mangrove, unvegetated). There was no significant difference in crab catches between sampling dates ($p > 0.05$), so these were pooled to give 8–14 replicate traps per tidal elevation and habitat at each site. The analyses used unrestricted permutation of Euclidean distances calculated from raw data and were based on 999 permutations. Where significant treatment effects were seen (at $\alpha = 0.05$), the analyses were followed by pair-wise post-hoc tests to assess sources of difference.

2.2. Survivorship experiment

To assess whether *C. maenas* experiences greater survivorship under the canopy of the mangrove forest than in adjacent unvegetated habitat, a tethering experiment was performed at the three sites in Merimbula Lake (36.89°S, 149.92°E) in December 2012. At each site, nine tethered crabs were deployed at each of the high and low elevations of the mangrove forest and the adjacent unvegetated habitat. The elevations were as described for the trapping study, such that in the mangrove patch, the high elevation was under the mangrove canopy, and the low elevation, below the pneumatophore zone, in unvegetated sediment. Tethered crabs were at least 15 m apart and in the intertidal zone.

The tethered crabs, collected by trap from intertidal habitats within Fisheries Creek, Twofold Bay, NSW, were 15–36 mm in carapace width, had a male to female ratio of 6:5 and were undamaged at the time of deployment. Individual crabs were randomly assigned to habitats and tidal elevations. They were tethered using 35 cm long pieces of nylon uncoated 14 kg test wire, one end of which was anchored to the sediment using a 15 cm long steel pin, and the other secured to the crab using a 3.2 mm diameter zinc-plated washer, glued (using Selleys® Tarzan's grip® shock-proof super glue) to the middle of the crab's carapace. Although the tethers restricted movement of crabs, they did not impede burial. Further, in a pilot study we found that in the absence of predation, the crabs remained attached to their tethers. We assessed the status of each tethered crab 4 and 11 days after deployment. Crabs were noted as alive and undamaged, alive and damaged (e.g. missing chelae), dead and undamaged, or dead and damaged, or missing. These data were used to calculate the proportion of crabs surviving at each elevation of each habitat and site.

We assessed the influence of habitat on the proportionate survival of *C. maenas* using a separate PERMANOVA for each of the two temporally non-independent sampling dates. The PERMANOVAs, which used sites as replicate blocks ($n = 3$), had two factors, Height on the shore (2 levels: high, low) and Habitat (2 levels: mangrove, unvegetated) and used square-root transformed data. Statistical procedures were otherwise as described for the spatial survey.

2.3. Temperature data collection

To assess whether there are differences in the average or maximum temperature among the four habitat strata in which crabs were tethered, we deployed miniature Thermochron® iButton temperature loggers (Thermodata Pty. Ltd., Brisbane). At each of the three sites in Merimbula Lake where crabs were tethered, three waterproofed iButtons were randomly deployed on the sediment surface of each habitat strata, at least 15 m apart. The iButtons were programmed to take readings hourly throughout the tidal cycle for four consecutive days in December 2012 (i.e. summer). Three-way PERMANOVAs with the factors habitat (2 levels: mangrove, unvegetated), height on the