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# Relationships between an invasive crab, habitat availability and intertidal community structure at biogeographic scales

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## ABSTRACT

At local scales, habitat availability influences interactions between native and invasive species. Habitat availability may also predict patterns in native communities and invasive species at biogeographic scales when both native and invasive species have specific habitat requirements. The New Zealand porcelain crab, *Petrolisthes elongatus*, has invaded intertidal rocky shores around Tasmania, Australia, where it is found in high densities (>1800 $m^2$) under rocks. A hierarchical sampling approach was used to investigate 1) the relationship between habitat availability (rock cover) and the biomass and abundance of *P. elongatus*, and 2) the relationship between *P. elongatus* biomass and native communities at local and regional scales. Invertebrate communities and habitat availability were sampled at multiple sites in the north and south regions of Tasmania. *P. elongatus* biomass and abundance were positively correlated with rock cover and patterns were consistent at the biogeographic scale (between regions). *P. elongatus* biomass was positively correlated with native species richness, biomass and abundance highlighting their co-dependence on rock cover. However, multivariate analyses indicated a different native community structure with increasing *P. elongatus* biomass. Flat, strongly adhering gastropods (chitons and limpets) were positively correlated with *P. elongatus* biomass, whereas mobile gastropods and crabs were negatively correlated with *P. elongatus* biomass. Despite local scale variation, there were clear consistent relationships between habitat-availability and the biomass of *P. elongatus*, and between native communities and the biomass of *P. elongatus* suggesting that the relationships between native and invasive species may be predictable at large spatial scales. Moreover, the strong relationships between *P. elongatus* biomass and changes in native community structure suggest a greater understanding of its impact is needed so that appropriate management plans can be developed.

## 1. Introduction

Invasive species are one of the major perturbations to native communities (Mack et al., 2000; Vitousek et al., 1996), and they have a range of direct and indirect effects on native biota (Gribben et al., 2013a; Levine et al., 2003; Wright and Gribben, 2008). Interestingly, the effects of direct interactions (e.g. competition and predation) between native and invasive species can be indirectly mediated by other processes. For example, the presence of suitable habitat available for an invader can mediate its abundance (Bohn et al., 2013) and thus its potential effects on native species. Invasive intertidal crabs often use small boulders for shelter which limits their impacts to areas with suitable boulder habitat (Lohrer et al., 2000; Lohrer and Whitlatch, 2002). Similarly, habitat characteristics (i.e. sediment grain size) influence the abundance and thus impact of an invasive infaunal bivalve (Byers, 2002). Thus, local scale variation in suitable habitat for the invader may indirectly contribute to the considerable local scale variation in community responses to invasive species (McKinnon et al., 2009; Neira et al., 2005). Nonetheless, the impacts of invasive species can be consistent across larger spatial scales (Grosholz and Ruiz, 1996) suggesting that when their effects are strong, or where invasive species and native communities share similar habitat requirements,

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consistent patterns in the response of native communities to invasive species may occur over large scales despite local scale variation.

Positive or negative relationships can occur between the abundance of invasive and native species depending on the availability of resources and local species diversity. Positive relationships may occur if there is an excess of resources and both invasive and native species respond positively to the resource (Stohlgren et al., 2008, 2003). Mechanistically, an excess of resources should weaken competitive interactions between invaders and the recipient community (Davis et al., 1998). Negative relationships may occur via competition if resources are limited although the outcome of competition could be in either direction: invasive species may be more abundant if they are better competitors than native species but less abundant if native species are better competitors and provide biotic resistance to suppress the invader(s) (Britton-Simmons, 2006; Byun et al., 2013; Dantonio and Mahall, 1991; Prieur-Richard et al., 2000; Stachowicz et al., 1999). Importantly, gradients of habitat-availability (Bishop et al., 2012; Bruno and Bertness, 2001; Dayton, 1972) can have direct positive influences on the density of invasive species (Lohrer et al., 2000; Warnock and Rasmussen, 2013), although little is known about how variation in habitat availability influences relationships between invaders and native communities.

The filter-feeding porcelain crab, *Petrolisthes elongatus*, was introduced into Tasmania, Australia, from New Zealand via the live oyster trade during the late 1800s. It is now widespread throughout its introduced range and is among the most abundant intertidal invertebrates in this region obtaining adult densities >1800 $m^{-2}$ (Gribben et al., 2013b). It occurs under rocks on intertidal rocky shores (Edgar, 2000; Gribben et al., 2013b). Thus, the amount of rock cover available as habitat is a potentially limiting resource for this species and increasing habitat availability may play a key role in mediating the relationships between *P. elongatus* and native communities at local and biogeographic scales. However, little is known about the relationships between *P. elongatus* and native communities.

In this study, we used a hierarchical sampling approach to investigate the relationships between variation in the amount of the main habitat resource for invertebrates on intertidal shores (rocks for shelter; hereafter referred to as rock cover), invasive *P. elongatus* and native communities in the invasive range of *P. elongatus* (Tasmania). Hierarchical sampling approaches are a powerful tool for assessing the influence of different ecological processes at different spatial scales (Anderson et al., 2005; Estrada-Villegas et al., 2011; Lande, 1996; Lloyd et al., 2012), but they have seldom been used to explore the relationships between invasive species and native communities at multiple spatial scales (Gribben et al., 2013b). Specifically, we determined 1) the relationship between habitat availability (rock cover) and the biomass and abundance of *P. elongatus*, and 2) the relationship between *P. elongatus* biomass and native communities at multiple spatial scales.

## 2. Methods

### 2.1. Species, study sites and sampling

Throughout its invasive range in Tasmania, *P. elongatus* reaches high densities between the spring mid- and low-tide marks on low energy rocky shores, where they shelter beneath boulders and in interstitial spaces among cobbles (Gribben et al., 2013b). *P. elongatus* is larger and often found in higher abundance in Tasmania compared to its native range (New Zealand) (Gribben et al., 2013b). In New Zealand, *P. elongatus* often co-occurs with the chitons *Acanthochiton zelandica, Ishnochiton maorianus*, and *Sypharochiton pelliserpentis*, and the crabs *Cyclograpsus lavauxi*, *Halicarcinus cookii*, *Halicarcinus varius*, and *Heterozius rotundiforms* (Phillips N. unpub. data). In Tasmania, *P. elongatus* occurs with a similar suite of intertidal organisms including the chitons *S. pelliserpentis* and *Chiton glaucus* and the grapsid crabs *Paragrapsus quadridentatus* and *P. laevis* (Gregory et al., 2012).

We quantified habitat availability (i.e. rock cover in quadrats), *P. elongatus* and native communities in two regions separated by >350 km of coast (northern and southern Tasmania) and at six sites within each region separated by an average of ~30 km (Fig. 1; Table 1). Our sites encompassed the broad latitudinal distribution of *P. elongatus* in Tasmania, and all sites were located on semi to fully exposed rocky shores characterized by low wave energy and low vertical relief cobble and rocky substrata with numerous interstitial spaces (Gregory et al., 2012). *P. elongatus* is largely absent from the high wave energy east and west coasts of Tasmania. We found no low wave energy sites in the regions we sampled that did not have *P. elongatus*. Sampling was conducted from 4th to 25th March 2013.

Sampling was done in 0.5 × 0.5 m quadrats ($n = 12$/site) haphazardly placed in the spring low-to mid-tide zones. Briefly, quadrats were positioned and all loose rocks removed and placed into a large tray. We only removed rocks that one person could lift readily and that were not firmly embedded into the underlying matrix (*P. elongatus* do not occur under rocks that are buried in the sediment). All mobile invertebrates beneath the rocks within each quadrat were collected and preserved in 70% ethanol (see Gribben et al., 2013b for full methods). A photograph was taken of the underside of all rocks in the quadrat to quantify the surface area of rock and identify sessile invertebrates on rocks (e.g. Serpulid worms and mussels) which were not collected. Because the tube forming Serpulid *Galeolaria caespitosa* (hereafter, we refer to *Galeolaria* as Serpulids) represented 95% of all sessile species it was the only sessile species we quantified (pers. obs). Samples were transported to the University of Technology, Sydney (UTS) where all organisms were identified and counted. We did not count newly recruited megalopae of *P. elongatus* although they were observed in several samples. Once all species were identified and counted, the total dry biomass of *P. elongatus* and total dry biomass of native species were determined by placing them in a drying oven at 60 °C for 48 h and then weighing each component. Rock cover (i.e. rock surface area) and the percent cover of Serpulids on rocks were determined using the video impage software ImageJ.

#### 2.1.1. Relationships between habitat availability and P. elongatus invasion at multiple spatial scales

We used 2-factor nested Analysis of Variation (nested ANOVA) to determine variation in the spatial distribution of habitat availability (i.e. rock cover) in response to the factors region (fixed, two levels: north and south) and site (random, nested with region). Variation in the spatial distribution of *P. elongatus* abundance and biomass in response to the factors region (fixed, two levels: north and south), site (random, nested with region) and total rock cover (random, covariate) was determined using 2-factor nested Analysis of Covariance (nested ANCOVA). Total rock cover and not rock size was used because the biomass and abundance of *P. elongatus* appears more correlated to the availability of surfaces to hide under, not rock size *per se*. Both *P. elongatus* biomass and abundance were log-transformed to meet the assumption of homogeneity of variances. We conducted additional regression analyses to further explore the relationship between rock cover and *P. elongatus* biomass and abundance. For all analyses, the assumptions of ANOVA were explored using plots of the residuals. Interactions between covariates and factors were examined in all ANCOVAs and non-significant interaction terms ($P > 0.25$) were removed from the