

## Stronger positive association between an invasive crab and a native intertidal ecosystem engineer with increasing wave exposure

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### ARTICLE INFO

#### Keywords:

Crabs  
Ecosystem engineer  
Facilitation  
*Galeolaria caespitosa*  
Introduced species  
*Petrolisthes elongatus*  
Tasmania  
Wave exposure

### ABSTRACT

Ecosystem engineers are predicted to have stronger facilitative effects when environmental stress is higher. Here we examined whether facilitation of the invasive porcelain crab *Petrolisthes elongatus* by the ecosystem engineering serpulid tube worm *Galeolaria caespitosa* increased with wave exposure. *Petrolisthes* occurs beneath intertidal boulders which often have a high cover of *Galeolaria* on their underside. Surveys across nine sites demonstrated *Petrolisthes* abundance beneath boulders increased with wave exposure and *Galeolaria* cover, although only when the habitat matrix beneath boulders was rock or mixed rock and sand. Moreover, as wave exposure increased, the strength of relationship between *Petrolisthes* abundance and the surface area of *Galeolaria* also increased. Experimentally, the presence of *Galeolaria* on the underside of boulders increased *Petrolisthes* abundance by 50% compared to boulders lacking *Galeolaria*. Our findings suggest the facilitative role of *Galeolaria* is stronger at more wave-exposed sites, which appears to contribute to a higher abundance of invasive *Petrolisthes*.

### 1. Introduction

Ecosystem engineers create habitat and modify abiotic conditions, thus exerting much control over species composition (Jones et al., 1997; Hastings et al., 2007). Through their environmental modification, ecosystem engineers often facilitate species, and understanding when and where engineers have strong effects is important. For example, facilitation is predicted to be more important where abiotic stress is stronger because the engineer provides a greater relative reduction of harsh abiotic conditions (Bertness and Callaway, 1994; Bruno et al., 2003; Crain and Bertness, 2006; Brooker et al., 2008).

On intertidal boulder fields, marine invertebrates often take refuge from harsh abiotic conditions or predators beneath boulders (McGuinness and Underwood, 1986; McGuinness, 1987). The benefits of this abiotic habitat can be augmented by biotic habitat provided by ecosystem engineers such as polychaetes, sponges and bryozoans on the bottom of boulders (Sousa, 1979; McGuinness, 1987). Although a number of factors contribute to small-scale variation in mobile invertebrate assemblages beneath intertidal boulders (Sousa, 1979; Chapman, 2002, 2005; Liversage and Benkendorff, 2013), the addition of ecosystem engineers often increases the abundance and richness of associated species (McGuinness, 1988; Wright et al., 2016). Moreover,

because the importance of facilitation is context dependent, the net effect of intertidal ecosystem engineers on associated species may increase under harsher conditions. This can occur when the engineer reduces thermal and desiccation stress during emersion at low tide, and/or reduces boulder instability or provides a rugose structure for attachment in wave-exposed areas (Bertness et al., 1999; Altieri et al., 2010; Wright and Gribben, 2017).

A range of factors determine the spread and abundance of invasive species including characteristics of the receiving environment, disturbance, propagule pressure and traits of the invader (Lockwood et al., 2013). Environmental characteristics such as habitat availability (Lohrer et al., 2000; Byers, 2002) and biotic interactions including predation (DeRivera et al., 2005), competition, and facilitation (Cavieres et al., 2007) vary spatially across the invaded range. As occurs for native species, the facilitation of invasive species by native ecosystem engineers can change across abiotic gradients, with strong facilitation typically observed in environments with strong abiotic stress but weak facilitation in more benign environments (Bertness and Hacker, 1994; Tewksbury and Lloyd, 2001; Cavieres et al., 2007). However, the effect of an engineer on associated species under strong abiotic stress can be both positive and negative (Smith et al., 2018). Despite the recognition that facilitation is an important process

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determining the abundance of invasive species (Bulleri et al., 2008; Northfield et al., 2018), there are relatively few examples demonstrating its importance in determining invader abundance among sites in the invaded range (Altieri et al., 2010; Kollars et al., 2016).

Introduced crabs have major impacts on invaded marine ecosystems (Griffen and Byers, 2009; Grosholz et al., 2011; Ruiz et al., 2011; Mancinelli et al., 2017). In the rocky intertidal, invasive crabs typically use boulders for shelter and larger boulders usually have more crabs beneath them (Lohrer et al., 2000; Lohrer and Whitlatch, 2002). In Tasmania, Australia, the New Zealand porcelain crab *Petrolisthes elongatus* (hereafter *Petrolisthes*) is abundant beneath boulders on rocky shores on the sheltered north coast and in channels and embayments of the south-east coast (Gregory et al., 2012; Gribben et al. 2013, 2015). Both abiotic and biotic habitat appear important for *Petrolisthes* abundance. They only occur beneath boulders and their abundance is positively correlated with the cover of boulders (Gribben et al., 2015). In addition, *Petrolisthes* recruitment to the underside of boulders is facilitated by the matrix of tubes formed by the native, ecosystem engineering serpulid *Galeolaria caespitosa* (Wright et al., 2016), which reduces temperature beneath boulders by up to 6 °C compared to boulders lacking *Galeolaria*, although long-term effects on adults *Petrolisthes* are not as strong (Wright and Gribben, 2017). Because *Petrolisthes* occurs across multiple sites, the strength of facilitation by *Galeolaria* may be influenced by large scale factors such as wave exposure as well by local-scale factors such as boulder size, the cover of *Galeolaria* on boulders and the underlying matrix beneath the boulders (see Jensen and Armstrong, 1991). Large-scale variation in environmental factors may set the context for the relative importance of facilitation, and examining the relationship between the facilitator and the facilitated species across an environmental gradient should identify when facilitation may be more important.

To explore the possible positive association of *Galeolaria* and *Petrolisthes* abundance across an environmental gradient we combined a large-scale observational study with a manipulative field experiment. First, we determined the influence of boulder surface area, cover of *Galeolaria* and underlying habitat matrix on the abundance of *Petrolisthes* beneath boulders at nine sites across a wave exposure gradient. We also examined whether the strength of the relationship between *Galeolaria* cover and *Petrolisthes* abundance changed with increasing wave exposure at sites. We hypothesised that as wave exposure increases, a greater cover of *Galeolaria* will become more important for *Petrolisthes*. Second, we experimentally manipulated the presence of *Galeolaria* on the underside of boulders at wave-exposed sites to determine whether *Galeolaria* facilitated the abundance of *Petrolisthes*.

## 2. Methods

### 2.1. Study system

The northern coast of Tasmania contains numerous intertidal rocky shores, mostly boulder fields, separated by sandy beaches. Although this coast is comparatively sheltered and mostly subject to wind-driven waves (Short, 2006) the boulder fields occur across a gradient of wave exposure reflecting differences in their orientation and fetch. The beaches and boulder fields have low vertical relief (Gribben et al. 2013, 2015) and the boulders vary in size with the surface area of their underside ranging between 100 and 2000 cm<sup>2</sup>.

The underside of boulders is usually covered by a matrix of *Galeolaria*, which is a small (~3 cm) tube worm that forms dense aggregations (Minchinton, 1997; Smith and Bolton, 2007). A diverse assemblage of mobile invertebrates dominated by *Petrolisthes*, native chitons, gastropods and crabs occurs beneath these boulders (Gribben et al., 2015; Wright and Gribben, 2017). The tube matrix can persist even after the *Galeolaria* that constructed them have died (personal observations). Boulders without *Galeolaria* are not common in the low and mid intertidal zones and typically only occur in the high zones.

*Petrolisthes* was introduced to Tasmania in the early 1900s, possibly on ballast rock or via the live oyster trade. They are filter-feeders (Greenwood, 1965) and feed by filtering suspended particles from the water using enlarged third maxillipeds bearing setae or by removing particulate matter from the substratum. In its native range in New Zealand, *Petrolisthes* also occurs beneath intertidal boulders but there is very limited similar biogenic habitat on the underside of these boulders (Gribben et al. unpublished data).

### 2.2. The relationship between *Galeolaria* and *Petrolisthes* across sites of different wave exposure

To determine the influence of *Galeolaria*, other habitat components, and wave exposure to large-scale patterns of *Petrolisthes* abundance, nine sites covering approximately 175 km of the northern coast of Tasmania were surveyed in winter, 2014. Sites were selected to provide a broad geographic range and to cover the range of wave exposure conditions on the north coast from relatively protected to moderately exposed. The sites from west to east were: Stanley North (40° 45' 6"S, 145° 17' 42"E), Stanley South (40° 45' 31"S, 145° 17' 58"E), Mersey Point (41° 9' 41"S, 146° 21' 23"E), Hawley Beach (41° 8' 15"S, 146° 32' 40"E), Badger Head (41° 6' 2"S, 146° 40' 21"E), Greens Beach (41° 4' 57"S, 146° 44' 36"E), Low Head river (41° 4' 41"S, 146° 48' 14"E), Low Head ocean (41° 3' 45"S, 146° 48' 6"E), and Bell Buoy (41° 02' 25"S, 146° 49' 58"E). *Petrolisthes* are absent from the very wave-exposed east and west coasts of Tasmania (Gregory et al., 2012) so we did not include sites from those regions in our surveys. All surveyed sites also contained large intertidal boulder fields. Sites were at least 5 km apart with the exception of Low Head ocean and Low Head river, which were approximately 2.5 km apart (by coast) and Stanley North and Stanley South, which were approximately 850 m apart, but separated by a sandy beach.

For 10 boulders at each site, we measured its top and bottom surface area, percent cover of *Galeolaria*, the surface area of *Galeolaria*, and the abundance of *Petrolisthes*. We also categorized the habitat matrix underlying each boulder. Boulders were sampled within the broad zone where *Petrolisthes* was most abundant, between 0.7 and 1.2 m above MLLW. Sampling was done by walking approximately parallel to the water line and selecting every fifth boulder which met the following criteria: the boulder was a very rough cuboid in shape so that the upper surface area would approximate lower surface area; had a surface area on its upper face of at least 250 cm<sup>2</sup> to set a minimum rock size; was positioned relatively flat on the bedrock or cobbles to provide the appropriate crevice habitat for *Petrolisthes*; and was not positioned in a water filled depression or sitting up high on other boulders above the bedrock or cobble matrix, both of which appeared avoided by *Petrolisthes*.

The abundance of *Petrolisthes* beneath each boulder was determined using high speed video. High speed video was used because the slow-motion replay provided good resolution for counting the many fast-moving small *Petrolisthes* as boulders were turned over. It was also time-efficient allowing us to sample in the appropriate zone at sites as the tide came in. Recordings were done by two people. One person turned the boulder over so that the downwards facing side was turned up while ensuring the boulder was not blocking the view of the substrate from where it had been removed. As the boulder was turned over, the second person took a video that captured both the bottom surface of the boulder and the substrate where the boulder had been. *Petrolisthes* either remained attached to the bottom surface of the boulder as it was turned over or remained on the substrate beneath the boulder and thus our videos recorded all *Petrolisthes* for each boulder. Videos were usually less than 20 s in length but ran until all *Petrolisthes* beneath the boulder had moved, thus becoming obvious in the recording. Most *Petrolisthes* moved quickly away from the boulder or empty space and scurried beneath nearby boulders. Videos were taken with a Nikon Coolpix Aw110 camera set at 30 frames per second in 720p format. We

validated the use of high-speed video as a technique for sampling *Petrolisthes* in this system with a pilot study done at Bell Buoy. In this pilot study, 11 boulders were sampled using a hand-collection technique described in Gribben et al. (2013, 2015) and by high speed video recorded at the same time. For the hand-collection technique, the boulder was picked up and placed into a tray and all *Petrolisthes* on the bedrock, and small cobbles beneath the boulder or attached to the boulder in the tray were collected and counted. The *Galeolaria* matrix was inspected carefully for any small *Petrolisthes*. There was a very strong positive relationship between both techniques for *Petrolisthes* abundance ( $y = 0.92x + 5.2371, R^2 = 0.960, P < 0.001$ ).

Surface areas of the top and bottom sides of boulders and *Galeolaria* percentage cover on the bottom were measured using ImageJ. Surface area of bottom side ranged in size from 122.2 to 1134 cm<sup>2</sup> across all boulders from the nine sites. We calculated the surface area of *Galeolaria* by multiplying boulder underside surface area and *Galeolaria* percentage cover. The underlying habitat matrix beneath each sampled boulder was categorised as “rock” (either small cobbles on top of bedrock or bedrock itself), “sand” (sand or sediment) or “sand/rock” (a mix of small cobbles and sand or sediment). Only nine boulders were processed at Low Head ocean and Stanley North due to poor video quality for one boulder at each site.

The wave exposure at each site was calculated using the Baardseth Index (Baardseth, 1970). This index relates strongly to wave height and water velocity (Fowler-Walker et al., 2006) although it does not take swell direction or temporal variability into account. It was estimated by dividing each site into 40 sectors each with 9° of compass orientation. Each sector was scored as either a ‘1’ if it had an unobstructed fetch of  $\geq 7.5$  km (i. e. no land including islands present) or a ‘0’ when land or islands were present within 7.5 km. A total Baardseth score was computed by summing across all 40 sectors with a possible range of 0 (complete shelter) to 40 (complete exposure).

### 2.3. The effects of *Galeolaria* on *Petrolisthes* abundance

To determine whether *Galeolaria* on the underside of rocks influenced the abundance of *Petrolisthes* at high wave exposure sites, we set up experiments in boulder fields at Bell Buoy and Beechford (41° 1' 24"S, 146° 50' 41"E) in March/April which is outside the peak recruitment time for *Petrolisthes* (Wright et al., 2016). These two sites are situated 8 km apart and experience similar, high levels of wave exposure (Baardseth Index of 15 and 14 respectively). At both sites, we selected 20 boulders with a high cover of *Galeolaria* (> 80%) on one side, and a low (< 5%) cover of *Galeolaria* on the other side. Boulders were a mix of those with the *Galeolaria* side face up and face down at the time of the experiment. No other sessile species occurred on these boulders. We removed all mobile species, including *Petrolisthes*, from both the boulder and the substratum before boulders were put in place. Ten of these boulders were placed with the *Galeolaria* side face down (which we called *Galeolaria* present) and 10 with the *Galeolaria* face up (which we called *Galeolaria* absent). Boulders were selected and allocated to treatments haphazardly. All boulders were placed into position between the 0.8–1.0 m MLLW mark roughly parallel to the shore. Each experimental boulder was placed into a space made vacant by moving another boulder of a similar size and we alternated placing *Galeolaria* present and *Galeolaria* absent boulders along the row. We marked the top of each boulder with a small amount of green marine paint to help identify them. Before putting the boulders in place, we took a photo of the underside of each boulder, with a ruler for reference, from which we calculated its bottom surface area using ImageJ. Surface area of the underside did not differ significantly between sites or treatments (2-Factor ANOVA on log<sub>10</sub> transformed data: Site:  $F_{1, 36} = 0.184, P = 0.670$ ; Treatment:  $F_{1, 36} = 3.284, P = 0.078$ ; Site x Treatment:  $F_{1, 36} = 0.034, P = 0.954$ , Bell Buoy: *Galeolaria* present,  $538.5 \pm 60.8$  cm<sup>2</sup>, *Galeolaria* absent,  $416.3 \pm 35.0$  cm<sup>2</sup>; Beechford: *Galeolaria* present,  $601.3 \pm 97.8$  cm<sup>2</sup>; *Galeolaria* absent,

$461.9 \pm 65.4$  cm<sup>2</sup>, mean  $\pm$  SE). After 10 days, we returned and determined the abundance of *Petrolisthes* under each boulder using the hand-collection technique (Gribben et al. 2013, 2015). Given it was outside the main recruitment time all crabs would have moved in from adjacent rocks. Although there was moderate swell, no boulders flipped over or moved during the 10 days of the experiment.

### 2.4. Statistical analyses

To examine the quantitative relationship between boulder bottom surface area, cover of *Galeolaria*, habitat matrix, wave exposure (all fixed effects) and *Petrolisthes* under boulders we ran a generalized linear model (GLM) in SAS (proc glimmix) with a lognormal (x+1) transformation used for *Petrolisthes* abundance. We examined all possible interactions, removing them one at a time if they were non-significant (based on *P*-values), before re-running the model. GLM assumptions were checked using diagnostic plots. Including both boulder surface area and the cover of *Galeolaria* allowed us to independently assess the relationship between *Galeolaria* and *Petrolisthes* abundance after taking into account boulder surface area, along with the habitat matrix and wave exposure. Relationships between the percentage cover of *Galeolaria* on the underside of boulders and *Petrolisthes* abundance (log x + 1) were examined separately for each of the three underlying habitat matrices (pooled across the nine surveyed sites) with linear regression. We hypothesized that the area of *Galeolaria* coverage might be more important for *Petrolisthes* abundance as wave-exposure increased. Thus, to explore this hypothesis we ran linear regressions between the surface area of *Galeolaria* and *Petrolisthes* abundance per boulder within each site and compared the *R*<sup>2</sup> values of the nine site-level relationships against the Baardseth index for each site. We used the surface area of *Galeolaria* in these analyses as it combines boulder surface area and the percentage cover of *Galeolaria* to examine their net effect on *Petrolisthes* abundance at sites of different wave exposure.

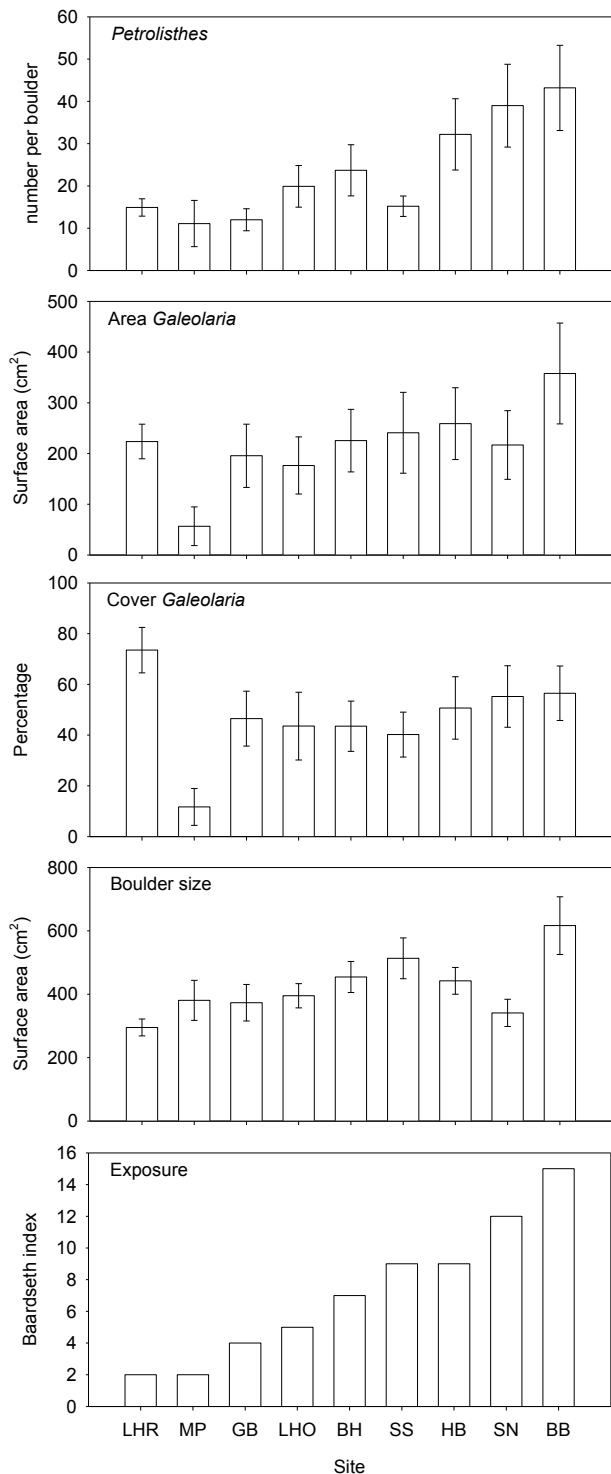
A Generalized Linear Mixed Effects Model in SAS (proc glimmix) with a negative binomial distribution was used to determine whether *Petrolisthes* abundance beneath boulders differed among *Galeolaria* treatment (present or absent), site (Bell Buoy and Beechford), and the interaction of treatment and site all as fixed effects. We also included boulder bottom surface area as a continuous covariate in our model.

## 3. Results

### 3.1. The relationship between *Galeolaria* and *Petrolisthes* across sites of different wave exposure

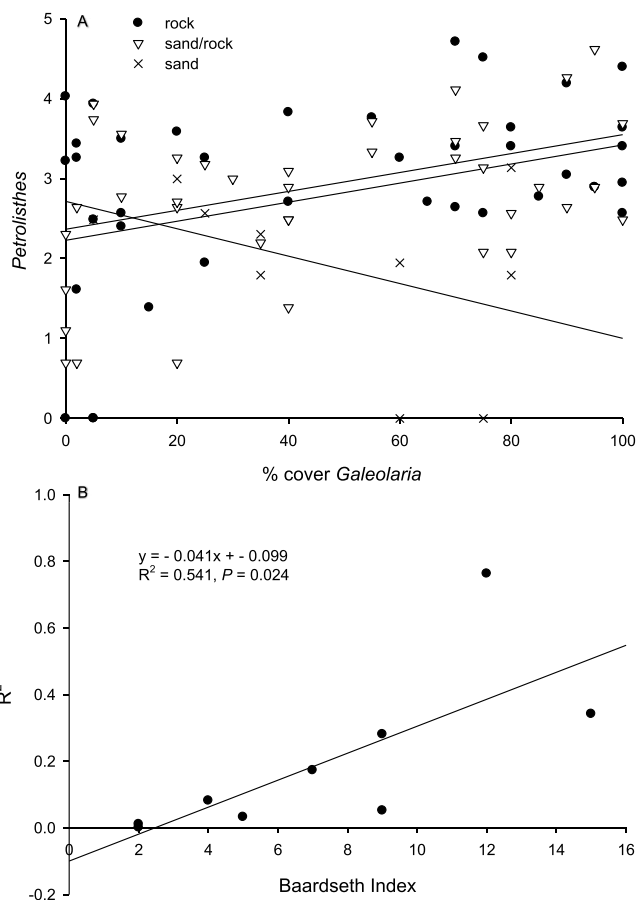
All metrics varied sizably among sites (Fig. 1). The gradient in wave exposure based on the Baardseth index ranged from 2 at Low Head river and Mersey Point to 15 at Bell Buoy while boulder surface area, the percentage cover and surface area of *Galeolaria*, and *Petrolisthes* abundance also varied among sites (one-factor ANOVAs across sites: all  $P < 0.018$ ). Notably, boulder size and *Petrolisthes* abundance per boulder generally increased with site wave exposure (Fig. 1).

The GLM model demonstrated that *Petrolisthes* abundance beneath boulders was strongly influenced by wave exposure ( $F_{1, 82} = 13.809, P < 0.001$ ) with a significant interaction between *Galeolaria* percentage cover and the habitat matrix beneath boulders ( $F_{2, 82} = 3.622, P = 0.031$ ). The latter reflected significant positive relationships between *Galeolaria* cover and *Petrolisthes* abundance for both rock ( $y = 0.012x + 2.365; R^2 = 0.164, P = 0.011$ ), sand/rock ( $y = 0.012x + 2.227; R^2 = 0.179, P = 0.007$ ) habitat, but not for sand habitat ( $y = -0.017x + 2.715; R^2 = 0.176, P = 0.227$ , Fig. 2a). The habitat matrix at sites with high *Petrolisthes* abundance tended to be all rock (Bell Buoy and Hawley) or sand/rock (Stanley North) and across all sites, boulders with a rock ( $28.0 \pm 3.53$ , mean  $\pm$  SE,  $N = 39$ ) and a rock/sand matrix ( $23.26 \pm 2.95$ , mean  $\pm$  SE,  $N = 39$ ) had significantly more *Petrolisthes* than boulders with a sand matrix



**Fig. 1.** Mean ( $\pm$  SE) *Petrolisthes* per boulder, surface area of *Galeolaria* on the underside of boulders, percentage cover of *Galeolaria* on the underside of boulders and boulder size and wave exposure at nine sites (ranked low to high exposure from left to right on the x-axis) in northern Tasmania. Site abbreviations: SN (Stanley North), SS (Stanley South), MP (Mersey Point), HB (Hawley Beach), BH (Badger Head), GB (Greens Beach), LHR (Low Head river), LHO (Low Head ocean), BB (Bell Buoy).

( $8.90 \pm 2.32$ , mean  $\pm$  SE,  $N = 10$ , one-factor ANOVA:  $F_{2, 85} = 3.84$ ,  $P = 0.025$ , Tukey's  $\alpha < 0.05$ ). There was no significant effect of boulder surface area ( $F_{1, 82} = 2.581$ ,  $P = 0.112$ ) in this model.



**Fig. 2.** a) Relationships between the percentage cover of *Galeolaria* on the underside of boulders and *Petrolisthes* abundance (log  $x + 1$ ) separately for each underlying habitat matrix (pooled across the nine surveyed sites). b) The relationship between the Beardseth index and the  $R^2$  value for the regression between the surface area of *Galeolaria* on the underside of boulders and *Petrolisthes* abundance at each of the nine sites.

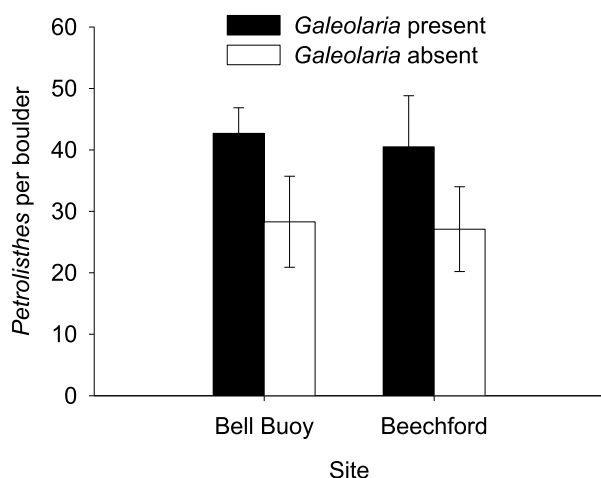
As wave exposure at sites increased, the strength of the relationship between the surface area of *Galeolaria* and *Petrolisthes* abundance at those sites also increased (Fig. 2b). At sites with Beardseth values of 5 or less, the surface area of *Galeolaria* explained < 10% of the variation in *Petrolisthes* abundance but this increased to up to 76% at sites with higher Beardseth values.

### 3.2. The effects of *Galeolaria* on *Petrolisthes* abundance

At both experimental sites, the presence of *Galeolaria* increased the average abundance of *Petrolisthes* beneath boulders by approximately 50% although this was marginally non-significant ( $F_{1, 38} = 3.886$ ,  $P = 0.056$ , Fig. 3). *Petrolisthes* abundance did not differ between the two sites ( $F_{1, 38} = 0.177$ ,  $P = 0.676$ ). Both boulder surface area and the *Galeolaria* treatment x site interaction were strongly non-significant (*Galeolaria* treatment x site interaction:  $F_{1, 36} = 0.610$ ,  $P = 0.440$ ; bottom surface area:  $F_{1, 36} = 0.021$ ,  $P = 0.885$ ) and were removed from the model.

## 4. Discussion

Our experiment showed mechanistically that *Galeolaria* presence *per se* can boost *Petrolisthes* abundance by 50% however; our surveys indicated this facilitation was likely to be context-dependent. Both the underlying habitat matrix and wave exposure influenced the strength of the relationship between *Galeolaria* and *Petrolisthes*. In particular, as



**Fig. 3.** Experimental results depicting the abundance of *Petrolisthes* (mean  $\pm$  SE) beneath boulders with *Galeolaria* present vs. absent on the underside of boulders at Bell Buoy and Beechford. Boulders were matched in size and surface area of boulder was not a significant factor in analyses (see text for more details).

wave energy at sites increased, the strength of the relationship between the surface area of *Galeolaria* and *Petrolisthes* abundance beneath boulders also increased suggesting facilitation is stronger where wave energy is higher.

In our experiment, the facilitation of *Petrolisthes* by *Galeolaria* was consistent at both Bell Buoy and Beechford: the two sites are only ~8 km apart and both are reasonably wave-exposed. However, there was large variation among replicate boulders within treatments. Similarly, most of the variation in invertebrate assemblages in boulder-fields in New South Wales occurred among individual boulders or sites separated by 20 m (Chapman, 2005). Although we standardised boulder placement as much as possible, those in slight water-filled depressions or that were positioned slightly above the bedrock or cobble matrix typically had fewer *Petrolisthes* beneath them (personal observations), indicating the position of the boulder within the boulder-field was important. Nonetheless, our experiment adds to the growing number of studies, including for *Petrolisthes* recruitment (Wright et al., 2016), showing that native marine ecosystem engineers can facilitate invasive species (Bertness et al., 1999; Ruesink, 2007; Bulleri and Benedetti-Cecchi, 2008; Altieri et al., 2010; Kollars et al., 2016). The near-absence of a similar biogenic habitat associated with the underside of boulders in the native range of *Petrolisthes* in New Zealand (Gribben et al. unpublished data), reinforces the importance of *Galeolaria* in contributing to the higher abundance of *Petrolisthes* in the new range. Similarly, biogenic habitat provided by the native oyster *Crassostrea virginica* appears crucial to the high abundance of invasive *Petrolisthes armatus* in southeastern USA (Hollebone and Hay, 2007; Kinney et al., 2018).

The *Galeolaria* tube matrix may be providing benefit to *Petrolisthes* via several different mechanisms. These include reducing abiotic stress from desiccation and temperature; reducing direct removal by waves by providing better attachment; reducing the movement of boulders in waves and thus possible crush injuries by making the boulders more rugose; providing a refuge from predation or; by promoting the retention of waterborne food particles (Sousa, 1980; Bertness et al., 1999; Altieri et al., 2010; Wright et al., 2014). The stronger positive relationship between *Galeolaria* and *Petrolisthes* at higher wave energy sites suggests that reducing the crab's removal by waves or reducing boulder movement may be important. A larger area of the *Galeolaria* matrix, with more small crevices and interstices, may allow for greater

attachment for *Petrolisthes* when strong waves wash around the boulders. Indeed, many *Petrolisthes* would hang onto the *Galeolaria* matrix on the bottom of boulders when they were turned over during our counts of their abundance but they rarely stayed attached to the bottom of bare boulders.

Despite appearing to provide a benefit to *Petrolisthes* as wave energy increases on the relatively protected north coast of Tasmania, *Galeolaria* appears not to provide enough of a benefit to *Petrolisthes* on much higher wave energy coasts. The north coast of Tasmania faces Bass Strait, and is largely protected from swell by the Australian mainland (Short, 2006). Our highest energy site was 15 on the Baarsdeth index, which scales up to 40. In contrast, the east and particularly, the west coasts of Tasmania are much more exposed with wave energy approximately 2–3 times greater than the north coast (Hughes and Heap, 2010). *Petrolisthes* is absent from exposed sites on the west and north-east coasts (Gregory et al., 2012) despite *Galeolaria* being present and the greater wave exposure on those coasts may dislodge *Petrolisthes* or remove the boulders they use as habitat.

The finding of increasing *Petrolisthes* abundance with increasing *Galeolaria* cover when wave exposure was relatively high on the north coast is consistent with facilitation being more important as abiotic conditions increase in severity. This has been demonstrated in numerous studies of terrestrial plants (reviewed in Brooker et al., 2008) which often highlight the shift from competition between neighbouring species in benign environments to facilitation in harsh environments (Callaway and Walker, 1997). *Galeolaria* and *Petrolisthes* both consume microalgae (Greenwood, 1965; Smith and Bolton, 2007) and may compete at low wave energy sites especially if delivery of waterborne food particles is limiting. Our study also highlights the important role of variable abiotic conditions in influencing invasive species abundance across a landscape and in particular, that in harsher environments, invasive species may rely more strongly on facilitation provided by ecosystem engineers (Cavieres et al., 2007).

Sand beneath boulders was a poor habitat for *Petrolisthes* with higher densities and a positive association between *Galeolaria* cover and *Petrolisthes* abundance occurring when there was an underlying matrix of rock or rock/sand. Similarly, boulders positioned on sand or silt are avoided by native *Petrolisthes cinctipes* in western North America, although *P. eriomerus* is less affected by the underlying habitat matrix (Jensen and Armstrong, 1991). If the sand beneath boulders becomes suspended into the water column it may impact the feeding of *Petrolisthes*, which is negatively affected by high sediment concentrations which possibly clogs their setal sieves (Steger and Gardner, 2007). Sand beneath the boulders is also likely to result in boulders sitting flat or pressed firmly into the underlying substratum, resulting in little space for *Petrolisthes*. The site that was the largest outlier in terms of the relationship between *Galeolaria* surface area and *Petrolisthes* abundance was Stanley South, which had a Baardseth index of 9 but a relatively low *Petrolisthes* abundance. The habitat matrix beneath the boulders at this site consisted largely of firm sand with only two boulders having an underlying matrix of rock.

Other unmeasured factors that differ among sites may also contribute to large-scale patterns in *Petrolisthes* abundance. For example, sites with high wave exposure and high *Petrolisthes* abundance may also have higher food and larval supply. The spread of invasive *P. armatus* in the southeastern USA appears to be related to high propagule pressure with densities  $> 1000 \text{ m}^{-2}$  recorded on oyster reefs during periods of high recruitment (Hollebone and Hay, 2007). Although both *Galeolaria* and *Petrolisthes* might be responding positively to site-level factors such as wave energy, our experiment demonstrated that *Galeolaria* also have a facilitative effect on *Petrolisthes*. Additionally, there may be lower predation on *Petrolisthes* at sites with high wave exposure. Non-native *Petrolisthes* are often an easy food source for some native predators (Hollebone and Hay, 2008; Pintor and Byers, 2015). In Tasmania, seastars, shore birds and fish have been observed consuming *Petrolisthes*, and numerous studies indicate lower predation pressure on

intertidal invertebrates as wave exposure increases (Menge and Branch, 2001). Higher predation may explain the low *Petrolisthes* abundance at Low Head river despite its relatively high surface area of *Galeolaria*.

Our study provides evidence that *Galeolaria* facilitates *Petrolisthes* abundance but highlights that the strength of that relationship is likely to be context dependent. Because biological invasions occur across landscapes, the abiotic environment is likely to influence invasive species abundance at sites both directly and indirectly via mediating biotic interactions. We have highlighted how variation in the abiotic environment (wave-exposure and the underlying habitat matrix) influences the facilitation of an invasive species by a native ecosystem engineer. Increasing our understanding of the importance of different factors across invaded landscapes may increase our ability to predict sites that are more likely to have a high abundance of invader and thus be more strongly impacted.

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