Population structure of the purple sea urchin *Heliocidaris erythrogramma* along a latitudinal gradient in south-west Australia

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Sea urchins are key herbivores in many coastal ecosystems. The purple sea urchin, Heliocidaris erythrogramma*, is widely distributed across temperate Australia where it exhibits considerable plasticity in feeding behaviour and ecophysiology. In this study we examined* H. erythrogramma *populations on subtidal reefs along ~4° of latitude in south-west Australia. We used a multi-factorial survey design to assess variability in* H. erythrogramma *abundances between locations (>200 km part), sites (≥1 km apart) and habitat types (reef flats and slopes). We also examined spatial variability in urchin size, condition (measured by gonad index), and the relative abundances of two co-occurring subspecies. Urchin densities were generally low and did not vary between locations, but did vary between habitat types and amongst sites. Site-level variability in urchin size and condition was also pronounced. The southernmost population comprised smaller individuals and greater relative abundance of the* H. e. erythrogramma *subspecies, which is abundant on the east coast of Australia. We observed no indication of population-level responses to a recent extreme warming event that impacted the wider ecology of the region, but further investigation into the effects of both gradual warming and short-term climatic events on the ecology of* H. erythrogramma *and other key herbivores is required.*

INTRODUCTION

Herbivorous invertebrates are important components of benthic marine ecosystems, as they represent a critical trophic link between primary producers, such as kelps and seagrasses, and higher organisms, including predatory fish and mammals (Estes & Duggins, 1995; Pace *et al.*, 1999; Bruno & O'Connor, 2005). Some invertebrate herbivores have a disproportionately high influence on local patterns of community structure and biodiversity, thereby acting as ecosystem engineers (*sensu* Jones *et al.*, 1994). Overgrazing by sea urchins, in particular, can cause phase-shifts from biologically diverse and complex macroalgae-dominated habitats towards low diversity habitats characterized by urchin 'barrens' (Andrew, 1993; Estes & Duggins, 1995; Leinaas & Christie, 1996; Steneck *et al.*, 2002). Overgrazing by high densities of urchins can occur following sporadic intense recruitment events (e.g. Hart & Scheibling, 1988; Valentine & Edgar, 2010), or as a result of overexploitation of urchin predators, leading to elevated grazing pressure through trophic cascade effects (reviewed by Jackson *et al.*, 2001; Steneck *et al.*, 2002). In Tasmania, for example, urchin recruitment has increased in response to recent changes in ocean climate,

and concurrent overfishing of urchin predators has allowed the urchin population to expand unchecked (Ling, 2008; Ling *et al.*, 2009). Recent decimation of kelp forests, resulting in a loss of habitat complexity and diversity, has been attributed to elevated grazing pressure from sea urchins.

In contrast, many species of sea urchin are largely sedentary and, generally, do not actively graze benthic macrophytes. When the supply of unattached 'drift' algae is sufficient, these urchins remain sedentary and collect and feed on detrital material (e.g. Vanderklift & Kendrick, 2005). In wave-exposed habitats, for example, kelps and other large macroalgae are frequently dislodged from rocky reefs and transported up to many kilometres, before being consumed as detritus by sea urchins (Vanderklift & Kendrick, 2005; Vanderklift & Wernberg, 2008). By consuming algal detritus, sea urchins provide an important service in terms of energy flow, trophic linkages and nutrient cycling (Vanderklift & Wernberg, 2010). Some urchin species exhibit plasticity in their feeding strategy, by acting as detritivores when drift algae is plentiful and reverting to direct grazing when the supply of detritus is insufficient, because of either reduced drift algae supply or increased urchin density (Kenner, 1992; Livore & Connell, 2012a). Whether active grazers, drift feeders, or both, sea urchins are key benthic organisms and documenting population structure and condition is crucial for understanding wider ecosystem structure and functioning.

The benthic ecosystem off south-west Australia represents a global hotspot of biodiversity and endemism for marine

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macroalgae (Phillips, 2001; Kerswell, 2006) and also supports rich assemblages of sessile invertebrates (Hatcher, 1989) and demersal fish (Fox & Beckley, 2005; Langlois et al., 2012). Extensive subtidal limestone and granite reef habitats fringe the south-west Australian coastline, which support dense kelp beds in the shallows and rich assemblages of macroalgae and invertebrates in deeper water (Smale et al., 2010a, b). Mature reef assemblages exhibit high species richness and turnover (Kendrick et al., 1999; Wernberg & Goldberg, 2008), while biodiversity patterns shift predictably along a regional-scale temperature gradient (Wernberg et al., 2003; Smale et al., 2010b; Tuya et al., 2011), albeit with pronounced small-scale variability (Phillips et al., 1997; Tuya et al., 2009; Smale et al., 2010b).

Conspicuous mobile macro-invertebrates such as echinoderms and large molluscs are, however, fairly low in diversity and abundance in south-west Australian kelp forests compared with many other temperate and polar ecosystems, and exhibit highly patchy distributions (Vanderklift & Kendrick, 2004; Wernberg et al., 2008; Azzarello et al., 2013). The most abundant sea urchin in the region is the purple sea urchin Heliocidaris erythrogramma (Valenciennes, 1846), which is widely distributed across temperate Australia. Heliocidaris erythrogramma is primarily a drift-feeder, preferentially consuming detrital fragments of the kelp Ecklonia radiata (Vanderklift & Kendrick, 2005; Vanderklift & Wernberg, 2010). Previous removal experiments have shown that H. erythrogramma has minimal influence on the structure of proximal benthic assemblages (Valentine & Johnson, 2005; Vanderklift & Kendrick, 2005). However, other manipulative and observational studies have shown that at medium to high densities of H. erythrogramma, as often found within wave-sheltered locations, can restrict the development of macroalgal canopies and facilitate the persistence of urchin 'barrens' (Wright et al., 2005; Ling et al., 2010; Livore & Connell, 2012b). On exposed subtidal reefs off southern and western Australia, H. erythrogramma densities are generally assumed to be too low to exert control over macroalgae assemblage development (Connell & Irving, 2008).

In south-west Australia, only one previous study has examined abundance distribution patterns of H. erythrogramma at large spatial scales (Vanderklift & Kendrick, 2004), and very little is known about population size structure and condition along the latitudinal temperature gradient that defines the ecology of the region (Smale & Wernberg, 2009). Moreover, recent work by Binks et al. (2011) has identified two morphologically distinct subspecies of H. erythrogramma in south-west Australia, but their relative abundances and habitat preferences remain largely unknown. We examined population structure of H. erythrogramma along >500 km of coastline, encompassing a 1.5°C temperature gradient, to address these knowledge gaps.

MATERIALS AND METHODS

Study region

The purple sea urchin Heliocidaris erythrogramma was examined at three locations off south-west Australia; Hamelin Bay (34.2°S 115.0°E), Marmion Lagoon (31.8°S 115.7°E) and Jurien Bay (30.2S 115.0°E). Adjacent locations were situated >200 km apart (Figure 1) and the study encompassed
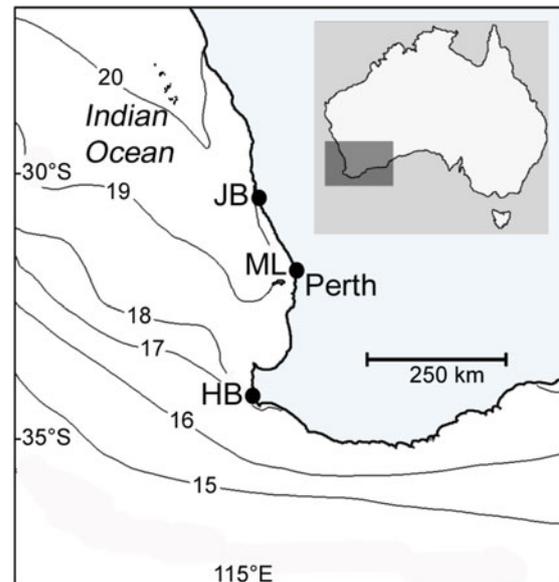

Fig. 1. Map of south-west Australia indicating the Jurien Bay (JB), Marmion Lagoon (ML) and Hamelin Bay (HB) study locations. The region is characterized by a well-defined oceanic temperature gradient, represented here by average winter isotherms (in °C, 2005–2007).

~530 km of south-west Australian coastline (south-east Indian Ocean). At each location, six comparable study sites were selected >1 km apart from one another. All study sites were at 8–13 m depth, and were dominated by extensive limestone reef habitats that comprised both flat reef platforms (hereafter 'flats') and complex topographical features such as rocky ledges, lumps and overhangs (hereafter 'slopes').

All locations were moderately exposed to the considerable oceanic swell systems that influence the ecology and geomorphology of the region (Searle & Semeniuk, 1985; Smale et al., 2011). In 2010, the average wave height recorded at wave buoys offshore from the study locations was ~2 m, with maximum wave heights exceeding 6 m (Bosserelle et al., 2012). All study sites were partially protected by offshore islands and submerged reefs which—to some extent—dissipate wave energy (Smale et al., 2011). These locations encompass a temperature gradient of ~1.5°C and fall within a larger regional-scale oceanic temperature gradient that defines the west coast of Australia (see Smale & Wernberg, 2009, for detailed climatology of the region). This coastline is strongly influenced by the Leeuwin Current (LC), which originates in the Indo-Pacific and flows polewards along the coast of Western Australia, before deviating eastwards into the Great Australian Bight (Pearce, 1991; Smith et al., 1991). The LC transports tropical (and subtropical) dispersal stages and warm, nutrient-poor water polewards, which enhances north to south mixing of species and effectively raises winter water temperatures (Ayvazian & Hyndes, 1995; Caputi et al., 1996; Smale & Wernberg, 2009). The coastal waters off Western Australia are considered oligotrophic, although localized nutrient enrichment can occur (Pearce, 1991; Lourey et al., 2006).

Field surveys

At each of the six sites within each location, two distinct habitat types were surveyed; (1) reef 'flats', which were flat

or gently sloping sections of open reef platforms; and (2) reef 'slopes', which were steeply sloping to vertical rock faces that often included ledges and cracks (surveys were conducted at the base of the slopes). All *H. erythrogramma* individuals within a 5×1 m belt transect were counted using SCUBA (the same observer completed all transects), and five replicate transects were conducted within each habitat type at each site. Transects were positioned haphazardly and placed >5 m apart from one another. Surveys were completed in February 2013 (austral summer).

Sea urchin metrics

Specimens of *H. erythrogramma* were collected and returned to the laboratory for further analysis. Urchins were collected from reef slopes at four survey sites at Marmion Lagoon and Jurien Bay and from three sites at Hamelin Bay. At each site 10 urchins were collected, except for Marmion sites 1 (8 urchins) and 2 (9 urchins). Only adults were collected (test diameter ranged from 40 to 96 mm), and urchins were selected randomly to provide a representative sample of the adult population at each site. We obtained size–frequency data by measuring the test diameter of each urchin. The gonad index (a measure of urchin condition) was calculated as the percentage of an individual's total weight (blot dried) that was gonad (urchins were dissected, gonads were carefully extracted and then blot dried before weighing, as per Livore & Connell (2012a)). Research from the east coast of Australia has shown that the gonad index of *H. erythrogramma* remains relatively constant throughout the year, and the timing of collection here would likely have corresponded to the summer spawning period (Laegdsgaard *et al.*, 1991). Furthermore, we used the morphological characteristics described by Binks *et al.* (2011) to assign each urchin to one of the two distinct subspecies found in the region, *H. e. erythrogramma* and *H. e. armigera*. Specifically, urchins with a red dermis and wide, relatively blunt, violet/violet–green coloured spines were classified as *H. e. armigera*, while urchins with a white dermis and pointed green spines were classified as *H. e. erythrogramma* (Binks *et al.*, 2011).

Statistical analysis

Variability in the abundance of *H. erythrogramma* was examined with permutational analysis of variance (hereafter 'permutational ANOVA'; see Anderson, 2001) using the PERMANOVA add-on to PRIMER 6.0 (Clarke & Warwick, 2001). A three-factor model including location (fixed factor), site (random factor, nested within location) and habitat type (reef flat vs slope, fixed factor) was used to partition variability in urchin abundance. As *H. erythrogramma* density may be influenced by wave action (Ling *et al.*, 2010; Livore & Connell, 2012a), sites within each location were ranked by wave exposure. Estimates of effective fetch were generated by measuring the distance from each study site to an obstruction that offered protection from wave action (i.e. an island, skerrie or submerged reef <5 m in depth, or the mainland). Distances (to a maximum of 20 km) were calculated for every $15°$ of the compass rosette, generating 24 measurements per site, then averaged to allow ranking of sites within each location (see Ruuskanen *et al.*, 1999 for a similar approach). Relative wave exposure was then included in the model as a covariate. Permutations were based on a similarity matrix generated from Euclidian distances of untransformed abundance data (4999 permutations under a reduced model). As a significant interaction between habitat type and site was detected, further permutational ANOVAs were conducted on abundance data from each habitat type separately. Here, a two-factor model using location (fixed factor) and site (random factor, nested within location) was employed and permutations were based on two separate similarity matrices generated for both reef 'flats' and reef 'slopes'.

For the urchin metrics, test diameters were used to generate size–frequency histograms for each location. Differences in urchin gonad index between sites and locations were visualized by plotting mean values for each site ($\pm$ SE). Spatial patterns in the abundance of each subspecies were visualized by plotting relative abundances for each site. A two-factor permutational ANOVA (with 'Location' as a fixed factor and 'Site' as a random, nested factor) was used to examine spatial variability in urchin size, gonad index and subspecies relative abundance (based on Euclidian distances and 4999 permutations under a reduced model).

RESULTS

Abundance patterns of *Heliocidaris erythrogramma* on subtidal rocky reefs off south-west Australia exhibited high spatial variability, and ranged from 0 to 8 inds 5m^{-2}. Urchin densities were higher on reef slopes than reef flats, and were highly
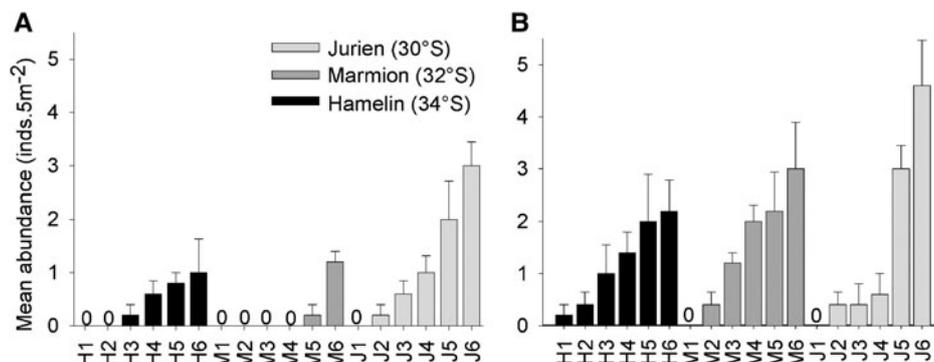

Fig. 2. Mean abundance ($\pm$ SE) of *Heliocidaris erthyrogramma* at each of six sites within the three study locations in temperate Western Australia. Abundances are means of five replicate transects (5 m^{-2}) for both habitat types, reef flats (A) and reef slopes (B).

Table 1. Results of permutational ANOVA to test for differences in the abundance of *Heliocidaris erythrogramma* between locations ('Lo', fixed factor), sites ('Si', random factor, nested within location) and habitat type ('Ha', reef flat vs slope, fixed factor). Relative wave exposure ('Exp') was included in the model as a covariable (CO). Permutations were based on a similarity matrix generated from Euclidian distances of untransformed abundance data (4999 permutations under a reduced model). Significant factors (at $P < 0.05$) are indicated with an asterisk (*). Percentage contributions of each term to total variability (i.e. estimates of components of variation, 'CV') are also shown.

Source	df	MS	F	P	CV
Exp (CO)	1	19.62	2.10	0.153	4.4
Lo	2	4.68	0.47	0.678	0.0
Ha	1	28.00	14.17	0.004*	17.0
Si (Lo)	15	10.02	11.83	0.001*	29.1
Lo × Ha	2	2.82	1.43	0.287	5.3
Si (Lo) × Ha	15	1.97	2.33	0.006*	15.0
Res	144	0.85			29.1

Table 2. Results of permutational ANOVA to test for differences in the abundance of *Heliocidaris erythrogramma* between locations ('lo', fixed factor) and sites ('si', random factor, nested within location) within each habitat type separately. Permutations were based on a similarity matrix generated from Euclidian distances of untransformed abundance data (4999 permutations under a reduced model). Significant factors (at $P < 0.05$) are indicated with an asterisk (*). Percentage contributions of each term to total variability (i.e. estimates of components of variation, 'CV') are also shown.

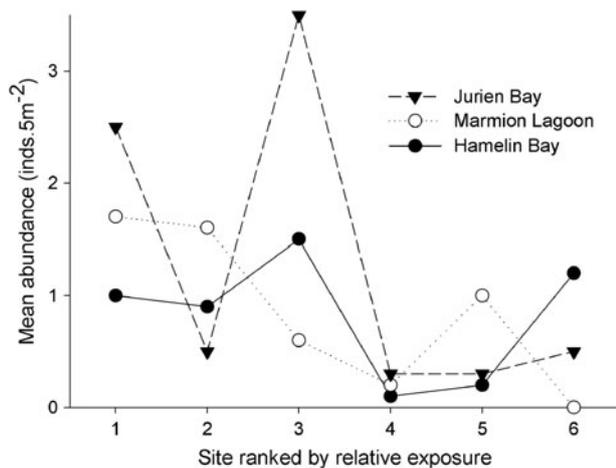| Source	df	MS	F	P	CV
Reef flats					
Lo	2	6.70	2.29	0.119	20.7
Si (Lo)	15	2.92	6.92	0.001*	41.3
Res	89	0.42			38.0
Reef slopes					
Lo	2	0.81	0.08	0.923	0.0
Si (Lo)	15	9.08	7.14	0.001*	52.5
Res	89	1.27			47.5

Fig. 3. Mean abundance of *Heliocidaris erthyrogramma* at each of six sites within the three study locations in temperate Western Australia. Sites within each location are ranked by their relative exposure to wave action. Abundances are means of 10 replicate transects (5 m⁻²) per site (reef flats and slopes pooled).

variable between sites but not locations (Figure 2; Table 1). As permutational ANOVA detected a highly significant Site × Habitat interaction (Table 1), variability patterns for each habitat type were examined separately. This showed that the relative magnitude of site-level variability was greater for reef slopes compared with reef flats (Figure 2; Table 2). For both the 'global' permutational ANOVA (Table 1) and the within-habitat permutational ANOVA (Table 2), variability between sites was the major contributor to total variability, as shown by the estimates of components of variation. Within each location, urchin abundances were highly variable along the wave exposure gradient and did not alter predictably between sites (Figure 3). This was shown statistically in the global model, as relative wave exposure was not a significant covariable (Table 1).

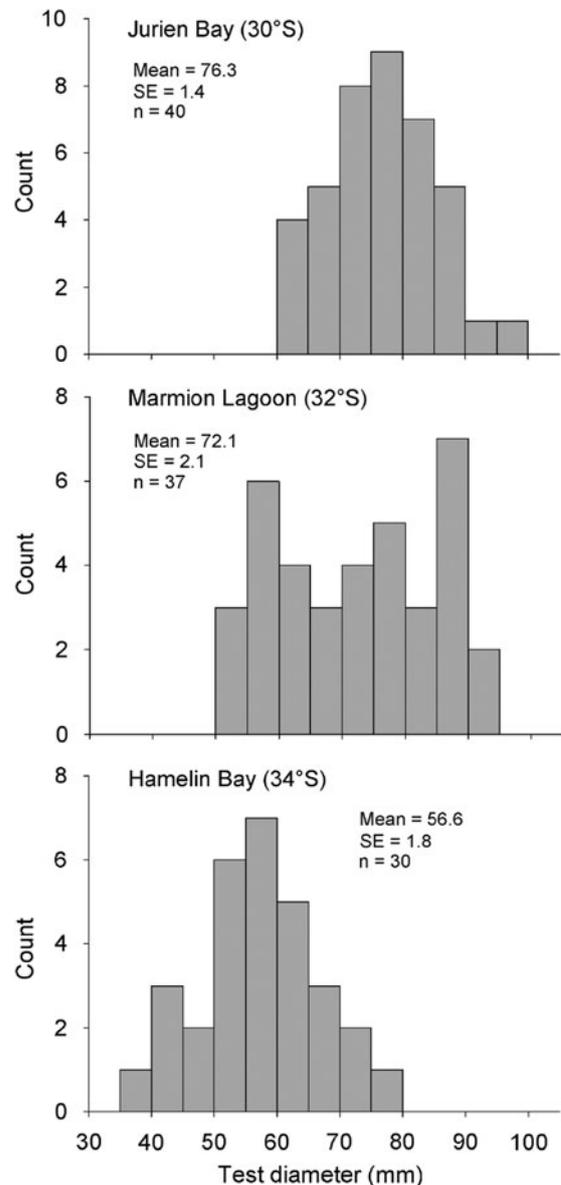Size–frequency histograms based on test diameter suggested that urchins at the southernmost location,

Fig. 4. Size–frequency histograms (5 mm size classes) for each of the three study locations in temperate Western Australia (sites pooled). Mean test diameter ($\pm$SE) and total *n* are shown for each location.
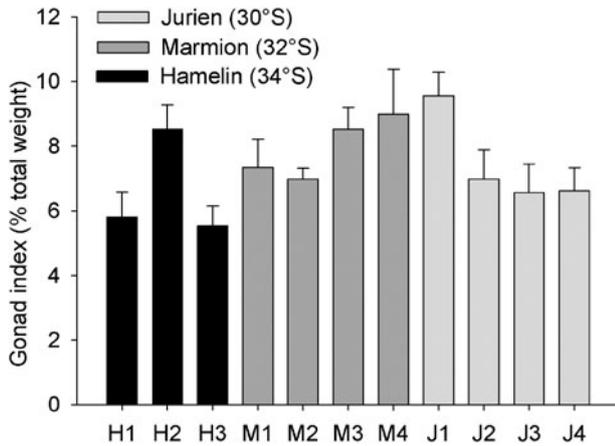
Fig. 5. Mean gonad index ($\pm$ SE) of *Heliocidaris erthyrogramma* at each site within the three study locations in temperate Western Australia. Urchins were collected from three sites at Hamelin Bay and four sites at Marmion Lagoon and Jurien Bay. At each site 10 urchins were analysed, with the exception of M1 (8 urchins) and M2 (9 urchins).

Hamelin Bay, were smaller than at the other locations (Figure 4). This was confirmed by permutational ANOVA, which detected significant variability between both sites ($F_{8,96} = 5.54$, $P = 0.001$) and locations ($F_{2,96} = 7.66$, $P = 0.017$, pairwise tests; JB = ML > HB). Interestingly, size–frequencies were normally distributed at Jurien Bay and Hamelin Bay (Shapiro–Wilk's tests, JB; W = 0.98, $P = 0.781$, HB; W = 0.98, $P = 0.865$) but not at Marmion Lagoon (W = 0.93, $P = 0.023$). The gonad index for each individual ranged from 1.94 to 16.51%; no clear pattern in mean gonad index between locations was observed (Figure 5). Gonad index varied significantly between sites ($F_{8,96} = 2.64$, $P = 0.013$) but not locations ($F_{2,96} = 0.84$, $P = 0.469$). Finally, the abundance of each subspecies did vary between locations, as *H. e. erythrogramma* was much more abundant at Hamelin Bay compared with the other locations (Figure 6). This observation was supported by permutational ANOVA ($F_{2,96} = 21.39$, $P = 0.002$, pairwise tests; HB > ML = JB), which also detected significant variability at the site level ($F_{8,96} = 2.04$, $P = 0.05$). On average, *H. e. erythrogramma* was smaller than *H. e. armigera* (mean test diameter 56.0 $\pm$ 1.6 versus 72.7 $\pm$ 1.3, $n = 22$ and 85, respectively) but had similar gonad index values (*H. e. erythrogramma* = 7.6 $\pm$ 0.3, *H. e. armigera* = 6.4 $\pm$ 0.5).
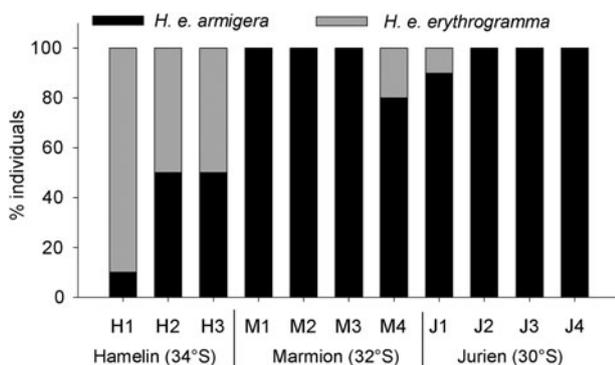

Fig. 6. The relative abundances of the two different subspecies of *Heliocidaris erythrogramma* found in temperate Western Australia, based on colour variation and spine morphology (see Methods). At each site 10 urchins were analysed, with the exception of M1 (8 urchins) and M2 (9 urchins).

DISCUSSION

Despite being one of the most abundant mobile macroinvertebrates on wave exposed subtidal reefs in south-west Australia (Vanderklift & Kendrick, 2004), *Heliocidaris erythrogramma* abundances were relatively low, at $\sim$0–2 inds m^{-2}. Our abundance values were similar to those recorded by Vanderklift and Kendrick (2004) at corresponding locations, suggesting that there has been negligible change in location-specific abundances over the last $\sim$12 y. *Heliocidaris erythrogramma* exhibits a highly patchy distribution pattern and can be found in much greater densities at other locations within the bounds of the study region (Vanderklift & Kendrick, 2004; Azzarello *et al.*, 2013). *Heliocidaris erythrogramma* inhabited both reef flats and reef slope habitats, but was more abundant on reef slopes. In general, reef slopes had greater topographic complexity and heterogeneity, which may be favourable for sea urchin recruitment (Tomas *et al.*, 2004), predator avoidance (Tuya *et al.*, 2004; Hereu *et al.*, 2005; Clemente *et al.*, 2013) and retention of detrital algal fragments (Krumhansl & Scheibling, 2012). Although Vanderklift & Kendrick (2004) found no difference in *H. erythrogramma* abundances between reef flats and slopes, this finding was largely due to anomalously high densities on reef flats close to Fremantle Port, which were not surveyed in the current study.

The greatest source of spatial variability in *H. erythrogramma* abundance was at the scale of kilometres, between sites. In other regions of Australia, urchin densities are often higher at sheltered locations (Ling *et al.*, 2010; Livore & Connell, 2012a), but we did not record greater abundances at our least exposed sites. However, our locations were all moderately to very exposed to intense wave action, as the south-west Australian coastline offers little protection from substantial oceanic swells (Bosserelle *et al.*, 2012). In contrast, the coastal geomorphology of South Australia or Tasmania, for example, offers greater protection and the greater variability in wave exposure between locations. As such, the range of wave exposure captured by the current study was relatively limited. Previous surveys within the study area have indicated that sites with anomalously high abundances of *H. erythrogramma* are generally more sheltered (Vanderklift & Kendrick, 2004; Azzarello *et al.*, 2013), but this pattern is highly variable. Other factors that may promote between-site variability include localised oceanographic processes that influence larval dispersal and recruitment (Hereu *et al.*, 2004), physical habitat structure, such as the complexity, composition and integrity of the limestone reef itself (Azzarello *et al.*, 2013), and variability in predation pressure (Hereu *et al.*, 2005). Further work is needed to determine the relative importance of these factors in promoting small to medium scale variability in urchin abundance, size and condition.

The *H. erythrogramma* population at Hamelin Bay, our cooler southerly study location, was in some ways distinct from those at the other locations. Urchins at Hamelin Bay were smaller and the relative abundance of the *H. e. erythrogramma* subspecies was higher. There were no discernible differences in habitat structure, food availability or local stressors (i.e. pollution, nutrients) between Hamelin Bay and the other locations and, with average temperatures of $\sim$19.5°C (Smale & Wernberg, 2009), conditions at Hamelin Bay should be favourable (Byrne *et al.*, 2011). The reduced average urchin size at Hamelin Bay was, in part, related to

a higher relative abundance of the *H. e. erythrogramma* sub-species, which was generally smaller than *H. e. armigera*. As the distributions and ecologies of the two sympatric subspecies in south-west Australia are almost entirely unknown (Binks *et al.*, 2011), it is not possible to speculate as to why *H. e. erythrogramma* was considerably more abundant at our southernmost location. It is interesting to note that, despite differences in test diameter, gonad index values for the subspecies were similar.

In early 2011, west coast of Australia experienced its highest-magnitude oceanic warming event on record, as coastal sea temperatures soared to 2–4°C above average and record sea surface temperatures were observed (Rose *et al.*, 2012; Feng *et al.*, 2013; Wernberg *et al.*, 2013). The warming event, driven by anomalously intense La Niña conditions, persisted for >10 wk and affected >2000 km of coastline (Feng *et al.*, 2013; Wernberg *et al.*, 2013). The warming event had wide ranging impacts on temperate and tropical ecosystems, resulting in high levels of coral bleaching and mortality (Moore *et al.*, 2012; Smale & Wernberg, 2012), widespread mortality and consequent range contractions of habitat-forming macroalgae (Smale & Wernberg, 2013; Wernberg *et al.*, 2013), changes in demersal fish assemblages (Wernberg *et al.*, 2013), and a suite of unusual ecological phenomena (Pearce *et al.*, 2011).

The impact of the extreme warming event on mobile invertebrates, however, is poorly understood. Our warmest study location, Jurien Bay (∼30°S), is situated within a broader temperate–tropical transition zone and was particularly impacted by the warming event. In contrast, the cooler locations further south were considerably less impacted (Wernberg *et al.*, 2013; authors', unpublished data). At Jurien Bay, where temperatures peaked at 28.3°C and were in excess of 26°C for 3 week (Pearce *et al.*, 2011; Wernberg *et al.*, 2013), we did not observe declines in urchin abundance, size or condition, relative to the cooler locations. Moreover, *H. erythrogramma* abundances at Jurien Bay were not appreciably lower than those recorded by Vanderklift and Kendrick (2004) some 12 yr previously. This is somewhat counter-intuitive as experimental work on *H. erythrogramma* on the east coast of Australia has shown that temperatures >26°C retard larval development and exceed thermal tolerances of adults (Byrne *et al.*, 2009, 2011). This research has also indicated that *H. erythrogramma* has the potential to acclimatise and even adapt to increased temperature, as 'warmer' populations exhibit greater thermal tolerance (Byrne *et al.*, 2011). Therefore, it could be that the *H. erythrogramma* population at Jurien Bay, which persists close to its equator-ward range edge, were not directly impacted by the event because of enhanced thermal tolerance through phenotypic or genotypic adaptation. Moreover, it would appear that the *H. erythrogramma* population at Jurien Bay was not adversely impacted by indirect impacts of the warming event, specifically a decline in the quantity and quality of detrital food supply. Following the marine heat wave, the percent cover of the common kelp *Ecklonia radiata* decreased by >30% and other large fucoids were completely eliminated by the event as physiological thresholds were exceeded (Smale & Wernberg, 2013; Wernberg *et al.*, 2013). In the 2 yr since the event, there have been no signs of recovery (Wernberg, unpublished data). It may be that population persistence is not limited by detrital food supply, and a >30% reduction in local kelp abundance was buffered by

redundancy in detritus production, or perhaps the urchins switched feeding behaviour and/or diet preference. It is also possible that the effects of the decline in local kelp abundance will take time to materialize at higher trophic levels, following reduced recruitment and fitness, for example.

There is some evidence to suggest that invertebrate herbivores at warmer, lower latitude locations were impacted by the warming event (Pearce *et al.*, 2011) and multi-species surveys along a broader latitudinal/temperature gradient will provide insights into the response of invertebrate assemblages to the warming event. Even so, it is evident that both discrete warming events (Wernberg *et al.*, 2013) and gradual warming trends (Wernberg *et al.*, 2011) will influence the ecology of the region and understanding population-level responses of key herbivores such as *H. erythrogramma* is of critical importance.

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