Research article to *Marine Ecology Progress Series* – accepted 04/02/2017

Regional-scale variability in the response of benthic macroinvertebrate assemblages to a marine heatwave

Dan A, Smale[1,2*], Thomas Wernberg[2] and Mathew A. Vanderklift[3]

[1]Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth, PL1 2PB, United Kingdom

[2]UWA Oceans Institute and School of Plant Biology, University of Western Australia, 35 Stirling Highway, Crawley 6009 WA, Australia

[3] CSIRO Oceans & Atmosphere, Floreat, Western Australia 6014, Australia

Running head: extreme warming event and temperate reef fauna

ABSTRACT: Extreme climatic events are predicted to increase in severity as a consequence of anthropogenic climate change. In marine ecosystems, the importance of marine heatwaves (MHWs) – discrete periods of anomalously high sea temperatures - is gaining recognition. In 2011, the highest-magnitude MHW ever recorded impacted the west coast of Australia (southeast Indian Ocean). The MHW was associated with widespread mortality of habitat-forming species, including corals and kelps, and structural changes in assemblages of macroalgae and fish. However, the responses of benthic macroinvertebrate assemblages have not yet been fully documented. Here, we resurveyed 2 subtidal habitat types (reef 'flats' and 'slopes') at 4 locations (spanning >800 km of coastline and >6° of latitude) during the period 1999-2015 to examine the impacts of the 2011 MHW on herbivorous macroinvertebrates (i.e. sea urchins, gastropod molluscs). Responses to the MHW varied with latitude; at our warmest study location abundances were severely depleted whereas no effects were detected at the coolest location. Across the entire study region subtle but significant shifts in assemblage structure were observed due to decreased abundances of more southerly-distributed species (i.e. 'cool' affinity) and increased abundances of several more northerly-distributed species (i.e. 'warm' affinity). The 2011 MHW has had profound effects on the marine biota off the west coast of Australia, across multiple trophic levels and taxonomic groups. Here, as in many other regions, contemporary warming events are superimposed onto gradual warming trends, increasing the likelihood of abrupt changes in ecosystem structure and functioning.

KEY WORDS: Benthic herbivores; Extreme climatic events; Leeuwin Current**;** Mobile macro-invertebrates; Southeast Indian Ocean; Southwest Australia; Species distributions; Temperature variability

INTRODUCTION

Climatic variability, including the frequency and magnitude of extreme climatic events, is predicted to increase as a direct consequence of anthropogenic climate change (Meehl & Tebaldi 2004, Rahmstorf & Coumou 2011, IPCC 2012). Natural climate variability is now superimposed onto decadal warming trends in most regions, increasing the likelihood of discrete climatic events becoming ‘extreme’ or ‘anomalous' (Hansen et al. 2012, Trenberth 2012). Such events, which include heatwaves, droughts, storms and floods, can affect both terrestrial and marine ecosystems and cause high mortality (Garrabou et al. 2009, Marba & Duarte 2010) deleterious impacts on populations (Van De Pol et al. 2010, Smale & Wernberg 2013) and a reconfiguration of communities (Thibault & Brown 2008, Wernberg et al. 2013, Wernberg et al. 2016).

Marine heatwaves (MHWs) are broadly defined as discrete prolonged periods when sea temperatures are anomalously high relative to long-term records (Hobday et al. 2016). MHWs, which can be caused by a range of oceanographic and atmospheric processes, are gaining recognition as widespread and potent drivers of change in marine ecosystems (Wernberg et al. 2013, Hobday et al. 2016). Indeed, the number of days of anomalously high seawater temperatures has significantly increased along 30% of the world’s coastlines in the last 30 years (Lima & Wethey 2012), while several ‘high profile’ warming events have had far-reaching ecological impacts (Hobday et al. 2016). For example, the European meteorological heatwaves of 2003 and 2006 elevated seawater temperatures in the Mediterranean Sea, which in turn caused widespread mortality, shifts in species’ distributions and declines in local marine biodiversity (Garrabou et al. 2009, Lejeusne et al. 2009, Marba & Duarte 2010). More recently, the El Niño-driven warming event of 2015-2016 has devastated coral reefs at a global scale (Normile 2016). It is clear that prolonged periods of extremely high seawater temperatures affect processes across all biological scales, from genes (Bergmann et al. 2010) to organisms (Diaz-Almela et al. 2007) to ecosystems (Wernberg et al. 2016).

In the austral summer of 2010/2011, the southeast Indian Ocean experienced an extreme warming event, during which seawater temperatures were the highest on record (~30 years for satellite-derived SSTs and ~140 years for reconstructed SSTs, see Wernberg et al. 2013). During the MHW, warming anomalies of 2-4°C persisted for around two months across >2000 km of temperate and subtropical coastline (Feng et al. 2013, Pearce & Feng 2013, Wernberg et al. 2013). At the MHW's peak in late February/March 2011, warming anomalies of up to 5°C were observed at multiple coastal locations (Rose et al. 2012, Feng et al. 2013, Pearce & Feng 2013). The MHW was associated with unusually strong La Niña conditions, which increased the flow of the region's main ocean current (the Leeuwin Current, 'LC') and the transfer of tropical warm water polewards, and was superimposed onto a decadal scale warming trend in the southeast Indian Ocean (Pearce & Feng 2007).

The MHW had wide-ranging consequences for marine ecosystems along the western coastline of Australia, which is a global hotspot of marine diversity and endemism (Tittensor et al. 2010, Bennett et al. 2015a). Unprecedented rates of coral bleaching and mortality were recorded across >1000 km of tropical and subtropical coastline (Moore et al. 2012, Depczynski et al. 2013), including at high latitude locations that are historically resistant to bleaching events (Smale & Wernberg 2012). Significant declines in the abundance and geographical extent of habitat-forming macroalgae were observed (Smale & Wernberg 2013, Wernberg et al. 2013, Wernberg et al. 2016), as were changes in fish abundances and species composition (Wernberg et al. 2013, Bennett et al. 2015b, Wernberg et al. 2016) and mass mortalities of commercially-important finfish and shellfish (Pearce et al. 2011, Caputi et al. 2016). 'Warm-temperate' locations situated within the tropical-temperate transition zone were profoundly impacted, as they suffered widespread loss of cool-water adapted habitat-forming species (kelps and large fucoids), which were unable to cope with the extreme temperatures experienced during the MHW (Smale & Wernberg 2013, Wernberg et al. 2013, Wernberg et al. 2016).

Mobile macroinvertebrates such as echinoderms and molluscs play key roles in the trophic ecology of temperate Australia (Shepherd & Edgar 2013), yet the impact of the 2011 MHW on their distributions and abundances has not yet been analysed in detail. Within the current biogeographical context of southwestern Australia, mobile macro-invertebrates are fairly low in diversity and abundance compared with many other temperate and polar ecosystems, and exhibit highly patchy spatial distributions (Vanderklift & Kendrick 2004, Wernberg et al. 2008, Levitus et al. 2012, Azzarello et al. 2014, Smale & Wernberg 2014). Despite their relatively low diversity and abundances, and an apparent lack of grazing 'fronts' and urchin 'barrens' in the region, densities can be locally high (>8 large inds.m^{-2}, see Vanderklift & Kendrick 2004, Azzarello et al. 2014) and mobile macroinvertebrates represent a conspicuous and characteristic component of kelp forest communities (Vanderklift & Kendrick 2004, Wernberg et al. 2008, Azzarello et al. 2014). Moreover, key species of sea urchins and molluscs may play a critical role in the food web (Vanderklift et al. 2006, Lozano-Montes et al. 2011, MacArthur et al. 2011), linking primary productivity (e.g. drifting and attached macroalgae) to higher trophic levels (e.g. lobsters, finfish).

Off southwest Australia, the reef-associated benthic macroinvertebrate fauna has a predominantly temperate affinity (Vanderklift & Kendrick 2004); the most abundant sea urchin in the region is the purple sea urchin *Heliocidaris erythrogramma* (Valenciennes 1846, hereafter '*Heliocidaris*'), which is widely distributed across southern Australia (Keesing 2001, Smale & Wernberg 2014). The sea urchin *Phyllacanthus irregularis* (Mortensen 1928, hereafter '*Phyllacanthus*'), and the large turbinid gastropod *Lunella torquatus* (Gmelin 1791, recently synonymised with *Turbo torquatus, hereafter* '*Lunella*') are also common, widespread and have cool-temperate affinities. The sea urchin *Centrostephanus tenuispinus* (Clarke 1914, hereafter '*Centrostephanus*') has a warm-temperate distribution (Wernberg et al. 2016), while tropical warm-water species such as the sea urchin *Tripneustes gratilla* (Linneaus 1758, hereafter *'Tripneustes'*) and the cowry gastropod *Monetaria caputserpentis* have occasionally been recorded within kelp forest communities in southwestern Australia (authors pers. obs.). The broad-scale affinities and geographical distributions of common macroinvertebrates observed in previous surveys are shown in Table 1. As such, inter-specific variation in biogeographic and thermal affinities may make some populations more susceptible to temperature variability, such as that experienced during the 2011 MHW.

Here, we conducted geographically extensive surveys and used historical data to test the following hypotheses (1) that the MHW significantly altered the structure of macroinvertebrate assemblages on subtidal reefs in southwest Australia. We also hypothesised (2) that the abundances of more southerly-distributed cool-temperate species would be lower after the MHW, especially at our warmest study locations where thermal physiological tolerances may have been exceeded. Conversely, we predicted that (3) the abundances of more northerly-distributed warm-temperate/tropical macroinvertebrates would be higher after the MHW, particularly at our warmest study locations situated within the tropical-temperate transition zone.

MATERIALS AND METHODS

Study region

The extensive coastline of southwestern Australia is characterized by widespread subtidal rocky reef habitat that supports highly productive, diverse and spatially extensive benthic communities, which are generally dominated by the kelp *Ecklonia radiata* in shallow waters (i.e. <30 m depth). We examined the abundances of benthic macroinvertebrates on kelp-dominated rocky reef habitats within 4 locations off southwest Australia; Hamelin Bay (34.2°S, 115.0°E), Marmion Lagoon (31.8°S, 115.7°E), Jurien Bay (30.2S, 115.0°E) and Kalbarri (27.4°S, 114.1°E). Adjacent locations were situated >200 km apart (Fig. 1) and the study encompassed ~6° latitude and ~800 km of southwest Australian coastline (southeast Indian Ocean). All locations were moderately exposed to the oceanic swell systems that influence the ecology and geomorphology of the region (Searle & Semeniuk 1985, Smale et al. 2011). The study locations encompassed a temperature gradient of ~3°C and fall within a larger regional-scale oceanic temperature gradient that characterizes the west coast of Australia (Fig. 1). Average summer sea temperatures ranged from 20.3°C at Hamelin to 23.2°C at Kalbarri (see Smale & Wernberg 2009, for detailed climatology of the region). The coastline is strongly influenced by the LC which originates in the Indo-Pacific and flows polewards along the coast, before deviating eastwards into the Great Australian Bight (Pearce 1991, Smith et al. 1991). The LC transports tropical (and subtropical) dispersal stages of marine flora and fauna and warm, nutrient-poor water polewards (Ayvazian & Hyndes 1995, Caputi et al. 1996, Smale & Wernberg 2009).

Field surveys

For each location, existing data on the abundance of mobile invertebrates were collated from published studies (Vanderklift & Kendrick 2004, Wernberg et al. 2008) and from authors' unpublished surveys that used identical survey methods. These studies were used to identify sites within each location that could be resurveyed to assess the impacts of the MHW. Multiple comparable study sites, >1 km apart from one another, were selected at random from a larger possible pool for resurveying. All study sites were characterised by extensive limestone reef habitats, at 6-16 m depth, and supported benthic assemblages typical of the wider region (Smale et al. 2010). Two habitat types were defined *a priori*; flat reef platforms (hereafter 'flats') and vertical or steeply-sloping rock faces (hereafter 'slopes'). These habitat types were treated separately because (i) they support distinct invertebrate assemblages (Vanderklift & Kendrick 2004), and (ii) the quantity of available data and the most suitable study sites for resurveying differed between habitat types. For reef flats, 5 sites were selected from each of the 4 locations for resurveying, whereas reef slopes were resurveyed at 3 sites within 3 locations (existing data were not available for reef slopes at Kalbarri). Before the MHW, sites were surveyed between 1 and 3 times between 1999 and 2006 (Table S1). After the MHW, new targeted surveys were conducted for the current study at all sites 3 times (in 2013, 2014 and 2015), with the exception of some sites at Hamelin which were not surveyed in 2014/2015 (Table S1). All surveys were conducted during the austral summer (full details provided in Table S1). Previous research in the region has shown that short-term variability (i.e. seasons to years) in invertebrate assemblage structure is minimal and that densities of dominant macroinvertebrates are generally stable over periods of months to years (Vanderklift & Kendrick 2004, Smale & Wernberg 2014). For example, an examination of *Heliocidaris* abundances from 3 consecutive pre-MHW survey years (between 1999 and 2001) on reef slopes at Marmion indicated minimal inter-annual variability (Fig S1). There was no discernible intensification of localized anthropogenic stressors, such as increased pollution, sedimentation or harvesting, which may have confounded any effects of the MHW, at any of the locations during the study period. Human populations in nearby settlements are relatively small (with the exception of the Perth Metropolitan Area adjacent to our sites at Marmion, which fall within a designated Marine Park) and localized anthropogenic impacts that could potentially confound temperature effects were deemed to be minimal.

All mobile macroinvertebrates (>20 mm) within 5 replicate 5 x 1 m belt transects were counted on SCUBA (by the authors) at each study site. Transects were positioned haphazardly and placed >5 m apart from one another. In total, counts were obtained from 685 transects (395 completed before the MHW and 290 after the MHW) covering ~3425 m^2 of subtidal reef habitat (~1975 m^2 before the MHW and ~1450 m^2 after the MHW).

Statistical analysis

Differences in invertebrate assemblage structure between pre-MHW and post-MHW surveys was examined with permutational multivariate analysis of variance (PERMANOVA, see Anderson 2001), using PRIMER 6 software (Clarke & Warwick 2001) with the PERMANOVA add-on (Anderson et al. 2008). As macroinvertebrate abundance values per transect were often low, the five transects completed per site/year combination were first pooled (to generate abundance values per 25 m^2) so that a single value was used for each site-year combination. Initially a 'global' analysis was performed on data from all locations, using an orthogonal model with the two factors 'location' (fixed factor) and 'MHW' (fixed factor); each habitat type was analysed separately. Permutations were based on a similarity matrix generated from Bray-Curtis similarity matrix of square-root transformed pooled densities (4999 permutations under a reduced model). As highly-significant ($P \leq 0.001$) interactions between location and MHW were detected for both habitat types (Table S2, Fig. S2), separate *a priori* planned contrasts for each location were conducted to test the prediction that years following the MHW would be distinct from those before the MHW (using the same similarity matrix and data transformation as above, and 4999 unrestricted permutations). In all cases, dummy variables (equal to the lowest transformed abundance value; '1') were included in the similarity matrices to alleviate the overpowering influence of transects with zero abundance values (Clarke & Warwick 2001). Where a significant difference was detected, a SIMPER analysis was performed to determine which taxa contributed most to the observed dissimilarity. PCO plots for each location and habitat type were constructed to examine multivariate partitioning before and after the MHW.

Temporal trends in total abundance (TA), taxon richness (TR) and the abundances of dominant species were examined with univariate permutation-based ANOVA (Anderson et al. 2008), using the planned contrasts described above (all response variables exhibited a significant

Location x MHW interaction term in initial global analyses and so each location was analysed separately). Permutations were based on Euclidean distances between untransformed abundance data (using 4999 unrestricted permutations).

RESULTS

The marine heatwave of 2010/11

At all locations temperature anomalies between +2°C to +3°C persisted for two months (Fig. 1) and absolute sea surface temperatures in the region were the highest on record (Feng et al. 2013, Pearce & Feng 2013, Wernberg et al. 2013). In addition to the extreme warming observed in 2010/2011, sea surface temperatures in early 2012 and (to a lesser extent) early 2013 were also higher than the climatological mean for each location (Fig. 1).

Assemblage-level responses

On reef flats, the composition of mobile invertebrate assemblages was not obviously impacted by the MHW at the coolest study locations (PCO plots showed no clear partitioning in composition before and after the MHW at Hamelin or Marmion: Fig. 2) but were clearly altered by the MHW at the warmest locations (partitioning was evident at Jurien and major shifts in composition occurred at Kalbarri: Fig. 2). Multivariate statistical tests supported inferences from visual inspections of PCO plots, as *a priori* planned contrasts indicated that pre- and post-MHW assemblages at Jurien and Kalbarri were significantly different (Table S3). SIMPER analysis indicated that the observed dissimilarities at Jurien were principally related to lower post-MHW abundances of *Heliocidaris* and *Lunella* and higher abundances of *Centrostephanus* (Table S4). At Kalbarri, the gastropods *Lunella*, *Dicathais orbita* and *Astralium* spp., which were not recorded after the MHW, were the principal contributors to the observed dissimilarities between pre and post-MHW assemblages (Table S4).

On reef slopes, PCO plots indicated that assemblages at Hamelin showed no obvious differences in composition before and after the MHW, whereas partitioning between pre- and post-MHW assemblages was observed at Marmion and Jurien (Fig. 3). These observations were supported by PERMANOVA, as pre and post-MHW assemblages at Hamelin were statistically similar but significant differences in composition were observed at Marmion and Jurien (Table S5). SIMPER analysis indicated that differences at Marmion were related to higher post-MHW abundances of *Heliocidaris* and *Centrostephanus* and lower abundances of the sea star *Petricia vernicina* (Table S6). At Jurien, the sea urchins *Centrostephanus*, *Tripneustes* (both with higher abundances post-MHW) and *Phyllacanthus* (lower abundances post-MHW) were the principal contributors to the observed dissimilarities between pre and post-MHW assemblages (Table S6).

On reef flats total abundance (TA) and taxon richness (TR) did not vary significantly between pre and post-MHW years at the 3 highest latitude locations (Hamelin, Marmion and Jurien, see Fig 4). At Kalbarri, however, TA and TR were significantly lower after the MHW (Table S7) to the extent that not a single macroinvertebrate individual was observed in any of the 75 post-MHW transects (Fig. 4), which covered a habitat area of ~375 m^2. On average at Kalbarri, TA decreased from 2.3 ± 0.8 to 0 inds.25 m^{-2} and TR decreased from 1.3 ± 0.3 to 0 spp.25 m^{-2} (Fig. 4). On reef slopes, TA did not differ significantly before and after the MHW at any location but TR was significantly lower at Jurien after the MHW (Table S8), decreasing from 5.0 ± 0.6 to 2.9 ± 0.3 spp.25 m^{-2} (Fig. 4).

Population-level responses

On reef flats, *Heliocidaris* was the most abundant macroinvertebrate, reaching a maximum average abundance of 8.8 ± 3.0 inds.25m^{-2} at Jurien (Fig. 5). The MHW had no statistically significant effect on *Heliocidaris* abundances at Hamelin, Marmion and Jurien, and it was not recorded at Kalbarri during any survey year (Fig. 5, Table S9). The two most common gastropod taxa, *Lunella* and *Astralium* spp. (*Astralium tentorium* Thiele 1930 and *Astralium squamiferum* Koch 1844) were recorded at all locations before the MHW but were not recorded at the warmest location, Kalbarri, after the MHW (Fig. 5). This marked post-MHW decline was statistically significant for *Lunella* but not for *Astralium* (Fig. 5, Table S9).

On reef slopes, *Heliocidaris* was again the most common macroinvertebrate and did not respond significantly to the MHW (Fig. 6, Table S10). At Jurien, the abundance of the pencil urchin *Phyllacanthus* was significantly lower after the MHW (Fig. 6, Table S10). The most striking observation was the marked increases in the abundance of *Centrostephanus* at both Marmion and Jurien (Fig. 6). Following the MHW, the average abundance of *Centrostephanus* was ~15 times higher at Jurien and also significantly higher at Marmion, increasing from complete absence in transects before the MHW to an average abundance of 1.9 ± 0.7 inds.25m^2 following the event (Fig. 6, Table S10). A marked but statistically non-significant increase in *Centrostephanus* abundance was also observed at Hamelin (Fig. 6, Table S10). The collector urchin *Tripneustes* was not recorded in any pre-MHW transect but was recorded at some sites at Jurien after the MHW, in 2013 and 2014 (Fig. 6). However, the planned contrast between pre- and post-MHW years was not statistically significant because of high variability between sites and years (*Tripneustes* was recorded at 2 sites in 2013, 1 site in 2014 and was absent in 2015), indicating that patterns were variable between sites and years.

Temporal shifts in the relative abundances of sea urchin species on reef slopes (i.e. the percentage of all sea urchin individuals represented by each species, with all 3 sites per location pooled) were also examined (Fig. 7). This analysis showed a consistent clear pattern of higher relative abundance of *Centrostephanus* since the MHW at all 3 study locations (Fig. 7). For example, at Jurien before the MHW *Centrostephanus* represented 3.5% of all sea urchins recorded, yet by 2015 (4 years after the MHW) *Centrostephanus* represented 90.1% of all sea urchin individuals. A similar trend was observed at Hamelin and Marmion (Fig. 7).

Furthermore, at Jurien the relative contributions of *Heliocidaris* and *Phyllacanthus* individuals to the sea urchin assemblage was markedly lower following the MHW, partly as a consequence of the higher abundances of *Tripneustes* (temporarily) and *Centrostephanus* (Fig. 7). The relative abundances of *Heliocidaris* and *Phyllacanthus* at the other study locations were more variable between years and showed no clear trend (Fig. 7).

DICUSSSION

The 2011 MHW was extreme in terms of magnitude, duration and spatial extent (Feng et al. 2013, Wernberg et al. 2013). Our data unequivocally demonstrate that the MHW significantly altered the composition of benthic macroinvertebrate assemblages on subtidal reefs in southwest Australia, with the magnitude of impact inversely related to latitude (i.e. the warmest locations were the hardest hit). At the coolest study location, Hamelin, the composition of invertebrate assemblages on reef flats and slopes did not differ between pre and post-MHW years. At the mid-latitude locations, Marmion and Jurien, changes in the relative abundances of macroinvertebrate taxa led to significant alterations in species composition (on reef slopes at Marmion and on both habitat types at Jurien), whereas major shifts in species composition were observed at the lowest latitude location, Kalbarri. This aligns with the responses of fish and macroalgae assemblages (Wernberg et al. 2013), which were impacted by the MHW at a ‘warm’ location (Jurien) but not at a ‘cool’ location (Hamelin). These data support our first hypothesis, that macroinvertebrate assemblage structure in southwest Australia was altered by the 2011 MHW, although responses varied considerably between locations.

The most striking observation of the current study was the decimation of all benthic macroinvertebrates at Kalbarri, which were completely absent after the MHW. The most common mobile invertebrates at Kalbarri before the MHW were all large gastropods (the turban shells *Lunella* and *Astralium* spp. and the carnivorous muricid *Dicathais orbita* Gmelin

1791) which, although not abundant, were commonly recorded before the MHW, being ubiquitous in all surveys prior to 2011. These species exhibit temperate distributions spanning southern Australia, having likely evolved under cool, climatically-stable Tethyan conditions (Williams 2007). Kalbarri is situated towards the equatorward limit of these species' distributions and, although thermal tolerances for these species are unknown, it is very likely that extreme temperatures experienced during the MHW had direct adverse physiological effects and induced high mortality rates. During the MHW, there was 99% mortality of the commercially-important gastropod *Halliotis roei* (Gray 1826, 'Roe's abalone') on inshore reefs at Kalbarri, which represents the equatorward limit of this species' distribution (Caputi et al. 2016). The mass die-offs at Kalbarri were associated with 30°C temperatures, discoloured water and (probably) depleted oxygen levels (Pearce et al. 2011), and deleterious impacts of warming on *H. roei* populations further south in the Perth Metropolitan Area (i.e. near Marmion) were also observed (Caputi et al. 2016). *Lunella* also decreased in abundance after the MHW at Marmion and Jurien (although not significantly), providing further support for the susceptibility of range edge populations to extreme warming.

In addition to direct thermal stress, it is possible that the indirect effects of loss of habitat and food also affected invertebrate populations at Kalbarri and, to a lesser extent, Jurien. The MHW had direct adverse effects on habitat-forming seaweeds such as the dominant kelp *Ecklonia radiata*, which resulted in a 30-40% decline in total canopy cover in Jurien (Wernberg et al. 2013) and the extirpation of the large fucoid *Scytothalia dorycarpa* at its range edge (Smale & Wernberg 2013). At Kalbarri, habitat structure was dramatically impacted by the MHW, as the spatial coverage of the canopy-forming kelp *Ecklonia radiata* decreased from ~75% of the reef's surface (Wernberg et al. 2010) to complete absence after the MHW (Wernberg et al. 2016). It has been shown that *Lunella* has a high affinity with kelp cover, and that sharp declines in *Lunella* abundance are associated with loss of kelp during ENSO events on the East coast of Australia (Ettinger-Epstein & Kingsford 2008). Although *Lunella* and *Astralium* spp. do not primarily feed on kelp, preferring to consume filamentous or foliose algae (Ettinger-Epstein & Kingsford 2008, Wernberg et al. 2008), canopy-forming macroalgae represent a critical resource through shelter provision (Ettinger-Epstein & Kingsford 2008). As such, loss of structural habitat may have indirectly impacted gastropod abundance, as loss of macroalgal shelter can induce behavioural responses and increase vulnerability of invertebrates to predators (Ettinger-Epstein & Kingsford 2008, Stoner 2009). Moreover, drifting kelp fragments are an important food source for benthic macroinvertebrates in the region (Vanderklift & Wernberg 2010), so a decline in food availability may have affected the ecological performance of individuals and the structure of populations.

The post-MHW surveys were conducted 2-4 years after the 2011 event, with invertebrate populations at Kalbarri showing no signs of recovery following apparent widespread mortality. This is unsurprising, as recovery of the gastropod populations formerly recorded at Kalbarri will likely be hampered for 2 reasons; (1) the larval duration for some of these species is presumed to be fairly short (i.e. days to weeks) (Phillips 1969, Joll 1980), so that post-MHW recovery will depend on proximity to source populations, and (2) source populations are likely to be located at higher latitudes, downstream of the main poleward-flowing ocean current, thereby reducing the likelihood of larval transport into impacted locations (Caputi et al. 1996). As Kalbarri is situated towards the equatorward distribution limits for these cool-water species, it is possible that the MHW has induced poleward range contractions (as with a temperate seaweed, see Smale & Wernberg 2013, Wernberg et al. 2016), although additional surveys are needed to confirm species' range shifts. In addition to gastropods at Kalbarri, abundances of the pencil urchin *Phyllacanthus* were markedly lower on reef slope habitats at Jurien after the MHW, which was a major contributor to the observed dissimilarity between pre and post-MHW assemblages. *Phyllacanthus* has a cool-water temperate distribution with its equatorward range edge estimated at the Abrolhos Islands, ~28.5°S (Marsh 1994). As such, its absence at Kalbarri and post-MHW decline at Jurien may be related to recent warming, but thermal tolerance experiments are needed to examine this further. However, we observed no clear trend in the abundance of *Heliocidaris*, which has a similar temperate distribution to *Phyllacanthus*, therefore indicating inter-specific variability in responses to the MHW (as has been shown for seaweed and fish, see Wernberg et al. 2013). In summary, our second hypothesis, which predicted lower post-MHW abundances of more southerly distributed cool-water species, was partially supported as cool-water species at Kalbarri were decimated by the MHW and some, but not all, cool water species exhibited a response at Jurien.

Our third hypothesis – that the relative abundance of more northerly distributed 'warm-water' taxa would increase after the MHW – received some support as the abundance of *Tripneustes* notably increased at some sites at Jurien for the years immediately following the MHW. *Tripneustes* is a warm-water 'collector urchin' that is widely distributed across the Indo-Pacific and extended tropics, where it primarily feeds on drifting seagrass and macroalgae fragments but can actively graze when per capita food supply is insufficient (Ogden et al. 1989, Valentine & Edgar 2010). *Tripneustes* is notoriously 'boom and bust' and intense population outbreaks have been observed in the temperate-tropical transition zone in eastern Australia, with community-level consequences (Valentine & Edgar 2010). *Tripneustes* is common in subtropical waters off Western Australia and, although it has occasionally been recorded further poleward than Jurien (e.g. at Rottnest Island, Vanderklift personal observation), it was extremely rare at all study locations and was not recorded in any transects completed before the MHW. We suggest that the higher abundances of *Tripneustes* at Jurien in 2013 and 2014 was a consequence of the MHW for the following reasons: (1) the enhanced poleward flow of the LC during the MHW would have increased larval supply into cooler locations (Feng et al. 2013, Wernberg et al. 2013); (2) temperatures experienced during the MHW in the Jurien Bay region (i.e. 26-27°C, see Wernberg et al. 2013) would have been favourable for the development of *Tripneustes* larvae (Sheppard Brennand et al. 2010); (3) *Tripneustes* larvae are relatively long-lived and are generally released in the austral summer (Dworjanyn & Pirozzi 2008), which was co-incident with the MHW and the unusually early strengthening of the LC (Pearce & Feng, 2013); and (4) the cohort of sea urchins observed in 2013 were similar in size (test diameters of ~10-12 cm, Smale pers. obs), which according to growth rate estimates (Bacolod & Dy 1986) would have coincided with a recruitment event during or soon after the MHW. However, as no *Tripneustes* individuals were recorded in 2015 the proliferation of the warmer-water species was short-lived, with no indication that the population at Jurien will persist.

The hypothesis received limited support as there was no evidence of a proliferation of warm-affinity macroinvertebrates at the northernmost location (Kalbarri), where reef habitats were devoid of benthic macrofauna. On the other hand, the principal ‘winner’ of the ecological disturbance was *Centrostephanus*, which increased in abundance by a factor of ~15 at Jurien to outnumber *Heliocidaris* to become the most abundant sea urchin, and significantly increased in abundance at Marmion following the MHW. *Centrostephanus* can be described as a ‘warm-temperate’ species and its proliferation does therefore provide some support for the third hypothesis. Although *Centrostephanus* exhibits a temperate distribution from South Australia to mid-Western Australia, it is far more abundant towards the warm northern limit of its distribution compared with the cooler southern parts of its range (Vanderklift & Kendrick 2004, Wernberg et al. 2016). For example, an unpublished survey based on 90 habitat-scale transects conducted across 18 similar reefs between South Australia (Adelaide) and Marmion in 2005/06 did not find a single *Centrostephanus* individual on these southern reefs (T. Wernberg unpublished data). Moreover, its equatorward range edge extends further north than the other sea urchin species (except *Tripneustes*), with the northernmost population recorded at ~25°S (Marsh 1994, GBIF record 137025088).

Very little is known about the biology of *Centrostephanus tenuispinus*, but its warm-temperate congener on the east coast of Australia, *Centrostephanus rodgersii*, has been extensively studied in recent years (see Byrne & Andrew 2013 for review). *C. rodgersii* has recently extended its range polewards into Tasmania, in response to increased temperature and a strengthening of the East Australian Current, where it has overgrazed kelp forest habitat to create widespread urchin barrens (Ling et al. 2008, Ling et al. 2009). *C. rodgersii* has long-lived planktonic larvae that facilitates long distance dispersal (Byrne & Andrew 2013); it is likely that *C. tenuispinus* also has the potential for widespread dispersal. Increasing abundance of *C. tenuispinus* along the southwest coastline of Australia is congruent with the recent MHW and the longer-term gradual warming trend in the region (Pearce & Feng 2007). Thermal tolerance studies on *C. rodgersii* and *Heliocidaris* on the east coast of Australia would suggest that their thermal windows for fertilisation, development, growth and survival do not differ markedly (Byrne et al. 2010, Wolfe et al. 2013, Pecorino et al. 2014). As such, it is currently unclear whether recent warming has directly (through physiological stress) or indirectly (through temperature-mediated competitive interactions) favoured *C. tenuispinus* over *Heliocidaris* in southwest Australia, and focussed experimental work is needed. It is also not known whether *C. tenuispinus* on the west coast has the potential to modify kelp forest habitat to the extent of its congener on the east coast of Australia.

In conclusion, the 2011 MHW has had profound effects on the marine biota along the southwest coastline of Australia. Rapid changes in the abundance, distribution and condition of organisms representing a wide range of taxonomic and trophic groups have been reported (Pearce et al. 2011, Moore et al. 2012, Smale & Wernberg 2012, Smale & Wernberg 2013, Wernberg et al.

2013, Caputi et al. 2016, Wernberg et al. 2016). This study has shown that the responses of mobile macroinvertebrates assemblages to the warming event varied dramatically with latitude, with greatest impact at the northernmost study locations, even though the magnitude of the warming anomaly was consistent along the latitudinal gradient. Recent modelling approaches based on species distributions and projected temperatures suggest that species' range expansions will be more prevalent than range contractions under climate change scenarios (García Molinos et al. 2016). However, in this 'extreme' example of warming, we primarily observed loss of cooler-water macroinvertebrate species and less evidence for an influx or proliferation of warmer-water species over the timescale of observation. In contrast, observed responses of other taxonomic groups to MHWs, including seaweeds, fish and corals, have included a proliferation of warm-water species (Wernberg et al. 2013, Wernberg et al. 2016). Clearly, better understanding of variability between biogeographic regions and taxonomic groups is needed to improve predictions the effects of climate change on marine ecosystems.

Coastal marine ecosystems along the vast and varied coastline of temperate Australia have responded to longer-term gradual ocean warming and concurrent stressors in complex and unpredictable ways (Wernberg et al. 2011). As short-term climatic variability is superimposed onto longer-term gradual warming trends in southwest Australia as in many other regions around the world, absolute temperatures may now reach unprecedented highs during extreme climatic events (Trenberth 2012). This will increase the likelihood of ecological tipping points being exceeded, triggering rapid phase-shifts in some regions and habitats (Wernberg et al. 2016). Only time will tell, but the 2011 MHW may well have triggered rapid 'tropicalization' (see Vergés et al. 2014) along much of the coastline, by driving widespread loss of temperate flora and fauna and creating opportunities for rapid colonisation by a warm-water biota. Moreover, inter-specific variability in susceptibility and responses to warming trends and events, as shown here, will cause a reshuffling of species and the emergence of novel communities and ecosystems.

Acknowledgements: We thank Scott Bennett, Tiffany Simpson, Emily Gates and Thibaut de Bettignies for assistance in the field. This work was funded by the Australian Research Council through grants to T.W and by a Marie Curie International Incoming Fellowship **(**within the seventh European Community Framework Programme) awarded to D.A.S., who is currently funded by the Natural Environment Research Council of the UK (IRF: NE/K008439/1).

LITERATURE CITED

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32-46

Anderson MJ, Gorley RN, Clarke KR (2008) Permanova+ for primer: guide to software and statistical methods. PRIMER-E, Plymouth, UK

Ayvazian SG, Hyndes GA (1995) Surf-zone fish assemblages in south-western Australia: do adjacent nearshore habitats and the warm Leeuwin Current influence the characteristics of the fish fauna? Mar Biol 122:527-536

Azzarello J, Smale DA, Langlois TJ, Håkansson E (2014) Linking habitat characteristics to abundance patterns of canopy-forming macroalgae and sea urchins in southwest Australia. Mar Biol Res 10:682-693

Bacolod PT, Dy DT (1986) Growth, recruitment pattern and mortality rate of the sea urchin, *Tripneustes gratilla* Linnaeus, in a seaweed farm at Danahon Reef, Central Philippines Phillipine Sci 23:1-14

Bennett S, Wernberg T, Connell SD, Hobday AJ, Johnson CR, Poloczanska ES (2015a) The ‘Great Southern Reef’: social, ecological and economic value of Australia’s neglected kelp forests. Mar Freshwater Res 67:47-56

Bennett S, Wernberg T, Harvey ES, Santana-Garcon J, Saunders BJ (2015b) Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. Ecol Lett 18:714-723

Bergmann N, Winters G, Rauch G, Eizaguirre C, Gu J, Nelle P, Fricke B, Reusch TBH (2010) Population-specificity of heat stress gene induction in northern and southern eelgrass *Zostera marina* populations under simulated global warming. Mol Ecol 19:2870-2883

Byrne M, Andrew N (2013) *Centrostephanus rodgersii*. In: Lawrence JM (ed) Sea urchins: biology and ecology. Elsevier

Byrne M, Soars NA, Ho MA, Wong E, McElroy D, Selvakumaraswamy P, Dworjanyn SA, Davis AR (2010) Fertilization in a suite of coastal marine invertebrates from SE Australia is robust to near-future ocean warming and acidification. Mar Biol 157:2061-2069

Caputi N, Fletcher WJ, Pearce A, Chubb CF (1996) Effect of the Leeuwin Current on the recruitment of fish and invertebrates along the Western Australian coast. Mar Freshwater Res 47:147-155

Caputi N, Kangas M, Denham A, Feng M, Pearce A, Hetzel Y, Chandrapavan A (2016) Management adaptation of invertebrate fisheries to an extreme marine heat wave event at a global warming hot spot. Ecol Evol 6:3583-3593

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E Ltd., Plymouth, UK

Depczynski M, Gilmour JP, Ridgway T, Barnes H, Heyward AJ, Holmes TH, Moore JAY, Radford BT, Thomson DP, Tinkler P, Wilson SK (2013) Bleaching, coral mortality and subsequent survivorship on a West Australian fringing reef. Coral Reefs 32:233-238

Diaz-Almela E, Marba N, Duarte CM (2007) Consequences of Mediterranean warming events in seagrass (*Posidonia oceanica*) flowering records. Glob Change Biol 13:224-235

Dworjanyn SA, Pirozzi I (2008) Induction of settlement in the sea urchin *Tripneustes gratilla* by macroalgae, biofilms and conspecifics: A role for bacteria? Aquaculture 274:268-274

Ettinger-Epstein P, Kingsford MJ (2008) Effects of the El Niño southern oscillation on *Turbo torquatus* (Gastropoda) and their kelp habitat. Austral Ecol 33:594-606

Feng M, McPhaden MJ, Xie S, Hafner J (2013) La Niña forces unprecedented Leeuwin Current warming in 2011. Sci Rep 3:1277

García Molinos J, Halpern BS, Schoeman DS, Brown CJ, Kiessling W, Moore PJ, Pandolfi JM, Poloczanska ES, Richardson AJ, Burrows MT (2016) Climate velocity and the future global redistribution of marine biodiversity. Nature Clim Change 6:83-88

Garrabou J, Coma R, Bensoussan N, Bally M, Chevaldonne P, Cigliano M, Diaz D, Harmelin JG, Gambi MC, Kersting DK, Ledoux JB, Lejeusne C, Linares C, Marschal C, Perez T, Ribes M, Romano JC, Serrano E, Teixido N, Torrents O, Zabala M, Zuberer F, Cerrano C (2009) Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. Glob Change Biol 15:1090-1103

Hansen J, Sato M, Ruedy R (2012) Perception of climate change. Proc Nat Acad Sci USA 109:E2415-E2423

Hobday AJ, Alexander LV, Perkins SE, Smale DA, Straub SC, Oliver EC, Benthuysen J, Burrows MT, Donat MG, Feng M, Holbrook NJ, Moore PJ, Scannell HA, Sen Gupta A, Wernberg T (2016) A hierarchical approach to defining marine heatwaves. Prog Oceanogr 141:227-238

IPCC (2012) Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, and New York, NY, USA

Joll L (1980) Reproductive biology of two species of Turbinidae (Mollusca : Gastropoda). Mar Freshwater Res 31:319-336

Keesing JK (2001) The ecology of Heliocidaris erythrogramma. In: John ML (ed) Developments in Aquaculture and Fisheries Science, Book Volume 32. Elsevier

Lejeusne C, Chevaldonne P, Pergent-Martini C, Boudouresque CF, Perez T (2009) Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. Trends Ecol Evol 25:250-260

Levitus S, Antonov JI, Boyer TP, Baranova OK, Garcia HE, Locarnini RA, Mishonov AV, Reagan JR, Seidov D, Yarosh ES, Zweng MM (2012) World ocean heat content and thermosteric sea level change (0–2000 m), 1955–2010. Geophys Res Lett 39:L10603

Lima FP, Wethey DS (2012) Three decades of high-resolution coastal sea surface temperatures reveal more than warming. Nature Commun 3:704

Ling SD, Johnson CR, Frusher S, King CK (2008) Reproductive potential of a marine ecosystem engineer at the edge of a newly expanded range Glob Change Biol 14:907-915

Ling SD, Johnson CR, Frusher SD, Ridgway KR (2009) Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proc Nat Acad Sci USA 106:22341-22345

Lozano-Montes HM, Loneragan NR, Babcock RC, Jackson K (2011) Using trophic flows and ecosystem structure to model the effects of fishing in the Jurien Bay Marine Park, temperate Western Australia. Mar Freshwater Res 62:421-431

MacArthur LD, Phillips DL, Hyndes GA, Hanson CE, Vanderklift MA (2011) Habitat surrounding patch reefs influences the diet and nutrition of the western rock lobster. Mar Ecol Prog Ser 436:191-205

Marba N, Duarte CM (2010) Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot mortality. Glob Change Biol 16:2366-2375

Marsh LM (1994) Echinoderms of the Houtman Abrolhos Islands, Western Australia and their relationship to the Leeuwin Current. In: David B, Guille A, Feral J-P (eds) Echinoderms through time: Proceedings of the 8th international echinoderm conference, Dijon, France, 6-10 September 1993 A. A. Balkema Rotterdam

Meehl G, Tebaldi C (2004) More intense, more frequent, and longer lasting heat waves in the 21st Century. Science 305:994-997

Moore JAY, Bellchambers LM, Depczynski MR, Evans RD, Evans SN, Field SN, Friedman KJ, Gilmour JP, Holmes TH, Middlebrook R, Radford BT, Ridgway T, Shedrawi G, Taylor H, Thomson DP, Wilson SK (2012) Unprecedented mass bleaching and loss of coral across 12° of latitude in Western Australia in 2010–11. PLoS ONE 7:e51807

Normile D (2016) El Niño's warmth devastating reefs worldwide. Science 352:15-16

Ogden NB, Ogden JC, Abbott IA (1989) Distribution, abundance and food of sea urchins on a leeward Hawaiian reef. Bull Mar Sci 45:539-549

Pearce A, Feng M (2007) Observations of warming on the Western Australian continental shelf. Mar Freshwater Res 58:914-920

Pearce A, Lenanton R, Jackson G, Moore J, Feng M, Gaughan D (2011) The “marine heat wave”off Western Australia during the summer of 2010/11. Fisheries Research Report No. 222. Department of Fisheries, Perth, Australia

Pearce AF (1991) Eastern boundary currents of the southern hemisphere. J Roy Soc West Aust 74:35-45

Pearce AF, Feng M (2013) The rise and fall of the “marine heat wave” off Western Australia during the summer of 2010/2011. J Mar Syst 111–112:139-156

Pecorino D, Barker MF, Dworjanyn SA, Byrne M, Lamare MD (2014) Impacts of near future sea surface pH and temperature conditions on fertilisation and embryonic development in *Centrostephanus rodgersii* from northern New Zealand and northern New South Wales, Australia. Mar Biol 161:101-110

Phillips B (1969) The population of the whelk *Dicathais aegrota* in Western Australia. Mar Freshwater Res 20:225-266

Rahmstorf S, Coumou D (2011) Increase of extreme events in a warming world. Proc Nat Acad Sci USA 108:17905-17909

Rose T, Smale DA, Botting GC (2012) The 2011 marine heat wave in Cockburn Sound, southwest Australia. Ocean Sci 8:545-550

Searle DJ, Semeniuk V (1985) The natural sectors of the inner Rottnest Shelf coast adjoining the Swan Coastal Plain. J Roy Soc West Aust 67:116-136

Shepherd S, Edgar G (2013) Ecology of Australian temperate reefs: the unique South. CSIRO publishing, Clayton, Victoria, Australia

Sheppard Brennand H, Soars N, Dworjanyn SA, Davis AR, Byrne M (2010) Impact of ocean warming and ocean acidification on larval development and calcification in the sea urchin *Tripneustes gratilla*. . PLoS ONE 5:e11372

Smale DA, Kendrick GA, Wernberg T (2010) Assemblage turnover and taxonomic sufficiency of subtidal macroalgae at multiple spatial scales. J Exp Mar Biol Ecol 384:76-86

Smale DA, Wernberg T (2009) Satellite-derived SST data as a proxy for water temperature in nearshore benthic ecology. Mar Ecol Prog Ser 387:27-37

Smale DA, Wernberg T (2012) Ecological observations associated with an anomalous warming event at the Houtman Abrolhos Islands, Western Australia. Coral Reefs 31:441

Smale DA, Wernberg T (2013) Extreme climatic event drives range contraction of a habitat-forming species. Proc Roy Soc B Biol Sci 280:20122829

Smale DA, Wernberg T (2014) Population structure of the purple sea urchin *Heliocidaris erythrogramma* along a latitudinal gradient in southwest Australia. J Mar Biol Assoc UK 94:1033-1040

Smale DA, Wernberg T, Vance T (2011) Community development on subtidal temperate reefs: the influences of wave energy and the stochastic recruitment of a dominant kelp. Mar Biol 158:1757–1766

Smith RL, Huyer A, Godfrey JS, Church JA (1991) The Leeuwin Current off Western Australia. J Phys Oceanogr 21:323-345

Stoner AW (2009) Habitat-mediated survival of newly settled red king crab in the presence of a predatory fish: Role of habitat complexity and heterogeneity. J Exp Mar Biol Ecol 382:54-60

Thibault KM, Brown JH (2008) Impact of an extreme climatic event on community assembly Proc Nat Acad Sci USA 105:3410-3415

Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, Berghe EV, Worm B (2010) Global patterns and predictors of marine biodiversity across taxa. Nature 466:1098-1101

Trenberth KE (2012) Framing the way to relate climate extremes to climate change. Climatic Change 115:283-290

Valentine JP, Edgar GJ (2010) Impacts of a population outbreak of the urchin Tripneustes gratilla amongst Lord Howe Island coral communities. Coral Reefs 29:399-410

Van De Pol M, Ens BJ, Heg D, Brouwer L, Krol J, Maier M, Exo K-M, Oosterbeek K, Lok T, Eising CM, Koffijberg K (2010) Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? J Appl Ecol 47:720-730

Vanderklift MA, Kendrick GA (2004) Variations in abundances of herbivorous invertebrates in temperate subtidal rocky reef habitats. Mar Freshwater Res 55:93-103

Vanderklift MA, Kendrick GA, Smit AJ (2006) Differences in trophic position among sympatric sea urchin species. Estuarine, Coastal and Shelf Science 66:291-297

Vanderklift MA, Wernberg T (2010) Stable isotopes reveal a consistent consumer-diet relationship across hundreds of kilometers. Mar Ecol Prog Ser 403:53-61

Vergés A, Steinberg PD, Hay ME, Poore AGB, Campbell AH, Ballesteros E, Heck KL, Booth DJ, Coleman MA, Feary DA, Figueira W, Langlois T, Marzinelli EM, Mizerek T, Mumby PJ, Nakamura Y, Roughan M, van Sebille E, Gupta AS, Smale DA, Tomas F, Wernberg T, Wilson SK (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc Roy Soc B 281:20140846

Wernberg T, Bennett S, Babcock RC, de Bettignies T, Cure K, Depczynski M, Dufois F, Fromont J, Fulton CJ, Hovey RK, Harvey ES, Holmes TH, Kendrick GA, Radford B, Santana-Garcon J, Saunders BJ, Smale DA, Thomsen MS, Tuckett CA, Tuya F, Vanderklift MA, Wilson S (2016) Climate-driven regime shift of a temperate marine ecosystem. Science 353:169-172

Wernberg T, Russell BD, Moore PJ, Ling SD, Smale DA, Coleman M, Steinberg PD, Kendrick GA, Connell SD (2011) Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. J Exp Mar Biol Ecol 400:7-16

Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettignies T, Bennett S, Rousseaux CS (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nature Clim Change 3:78-82

Wernberg T, Thomsen MS, Tuya F, Kendrick GA, Staehr PA, Toohey BD (2010) Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. Ecol Lett 13:685-694

Wernberg T, White M, Vanderklift MA (2008) Population structure of turbinid gastropods on wave-exposed subtidal reefs: effects of density, body size and algae on grazing behaviour. Mar Ecol Prog Ser 362:169-179

Williams ST (2007) Origins and diversification of Indo-West Pacific marine fauna: evolutionary history and biogeography of turban shells (Gastropoda, Turbinidae). Biol J Linnean Soc 92:573-592

Wolfe K, Dworjanyn SA, Byrne M (2013) Effects of ocean warming and acidification on survival, growth and skeletal development in the early benthic juvenile sea urchin (Heliocidaris erythrogramma). Glob Change Biol 19:2698-2707

Table 1. Most common macroinvertebrate species recorded during surveys and their affinities and broad-scale distributions within the southwest Australian study region. The proportion of distribution records found either north or south of Jurien Bay (30.3˚S) is provided as an indication of the biogeographical affinities of each species (records were downloaded from The Atlas of Living Australia - http://www.ala.org.au - on 30/01/2017). Additional general information sourced from Edgar (1997). #Indicates few existing records for that species and as such distributions should be treated with caution, but wider affinity determined from best available knowledge.

Species	**Taxa**	**Affinity and distribution**
Centrostephanus tenuispinus	Sea urchin	Warm; warm-temperate, northern range-limit at Shark Bay (25.3 ˚S). #28.3% of 11 records north of 30.3˚S. Family characteristic of tropical reefs
Tripneustes gratilla	Sea urchin	Warm; tropical, northern Australia, 68.8% of 288 records north of 30.3˚S
Phyllacanthus irregularis	Sea urchin	Cool; temperate, #70% of 20 records south of 30.3˚S
Heliocidaris erythrogramma	Sea urchin	Cool; temperate, 92.3% of 607 records south of 30.3˚S.
Lunella torquatus	Gastropod mollusc	Cool; temperate, 87.4% of 372 records south of 30.3˚S
Astralium spp. (*A. tentorium/ A. squamiferum*)	Gastropod mollusc	Cool; temperate, 94.9% of 431 records south of 30.3˚S
Dicathais orbita	Gastropod mollusc	Cool; temperate, 90.9% of 2242 records south of 30.3˚S
Petricia vernicina	Sea star	Cool; temperate, 97.0% of 755 records south of 30.3˚S

Figure legends

Fig 1. Map of southwest Australia indicating the Kalbarri (K), Jurien Bay (J), Marmion Lagoon (M) and Hamelin Bay (H) study locations. The region is characterized by a well-defined oceanic temperature gradient, represented here by average winter isotherms (in °C, 2005–07). Temperature anomalies represent deviations from monthly long-term means (1981-2010), derived from remotely-sensed satellite SSTs.

Fig. 2. PCO plots showing macroinvertebrate assemblage structure on reef flats before and after the MHW at each location. Ordinations are based on Bray-Curtis similarities of square-root transformed abundance data. Dashed circle in Kalbarri plot indicates 16 overlapping samples (15 samples post-MHW and 1 sample pre-MHW) in which macroinvertebrates were absent.

Fig. 3. PCO plots showing macroinvertebrate assemblage structure on reef slopes before and after the MHW at each location. Ordinations are based on Bray-Curtis similarities of square-root transformed abundance data.

Fig. 4. Mean total abundance (left-hand plots) and taxon richness (right-hand plots) of all mobile macroinvertebrates on reef flats and slopes at each location before (blue bars) and after (red bars) the MHW (± SE). Values represent number of individuals/species per 25 m^2 sample area (i.e. 5 transects pooled per site). Significant differences before and after the MHW are indicated with an asterisk (at $P>0.05$, test results shown in Tables S6 and S7).

Fig. 5. Mean abundances (± SE) of dominant species on reef flats before (blue bars) and after (red bars) the MHW. Significant differences before and after the MHW are indicated with an asterisk (at $P>0.05$, test results shown in Table S8).

Fig. 6. Mean abundances (± SE) of dominant species on reef slopes before (blue bars) and after (red bars) the MHW. Significant differences before and after the MHW are indicated with an asterisk (at P>0.05, test results shown in Table S9)

Fig. 7. The relative abundances of sea urchins recorded on reef slopes during each survey year at each location (average of 3 sites per location). The timing of the MHW is also shown.

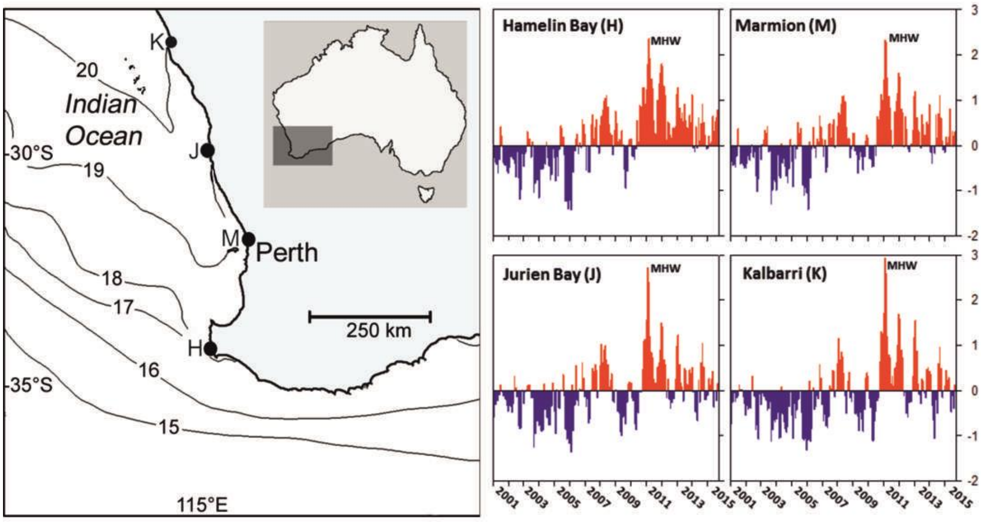
K
20
Indian Ocean
J
30°S
19
M
Perth
18
17
250 km
H
16
35°S
15
115°E
Hamelin Bay (H)
Marmion (M)
Jurien Bay (J)
Kalbarri (K)
MHW
3
2
1
0
-1
-2
2001
2003
2005
2007
2009
2011
2013
2015

Fig. 1

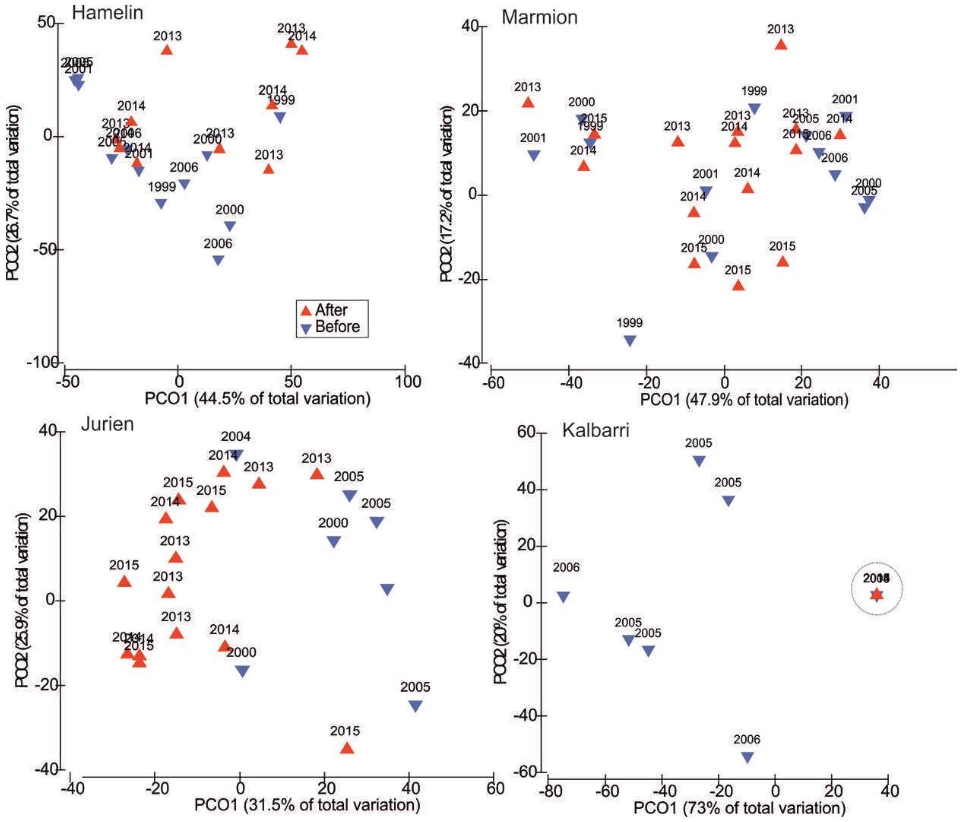
Hamelin
PCO1 (44.5% of total variation)
PCO2 (26.7% of total variation)
-50
0
50
100
-100
After
Before
Marmion
PCO1 (47.9% of total variation)
PCO2 (17.2% of total variation)
-60
-40
-20
0
20
40
Jurien
PCO1 (31.5% of total variation)
PCO2 (25.9% of total variation)
-40
-20
0
20
40
60
Kalbarri
PCO1 (73% of total variation)
PCO2 (20% of total variation)
-80
-60
-40
-20
0
20
40
60
1999
2000
2001
2004
2005
2006
2013
2014
2015

Fig. 2

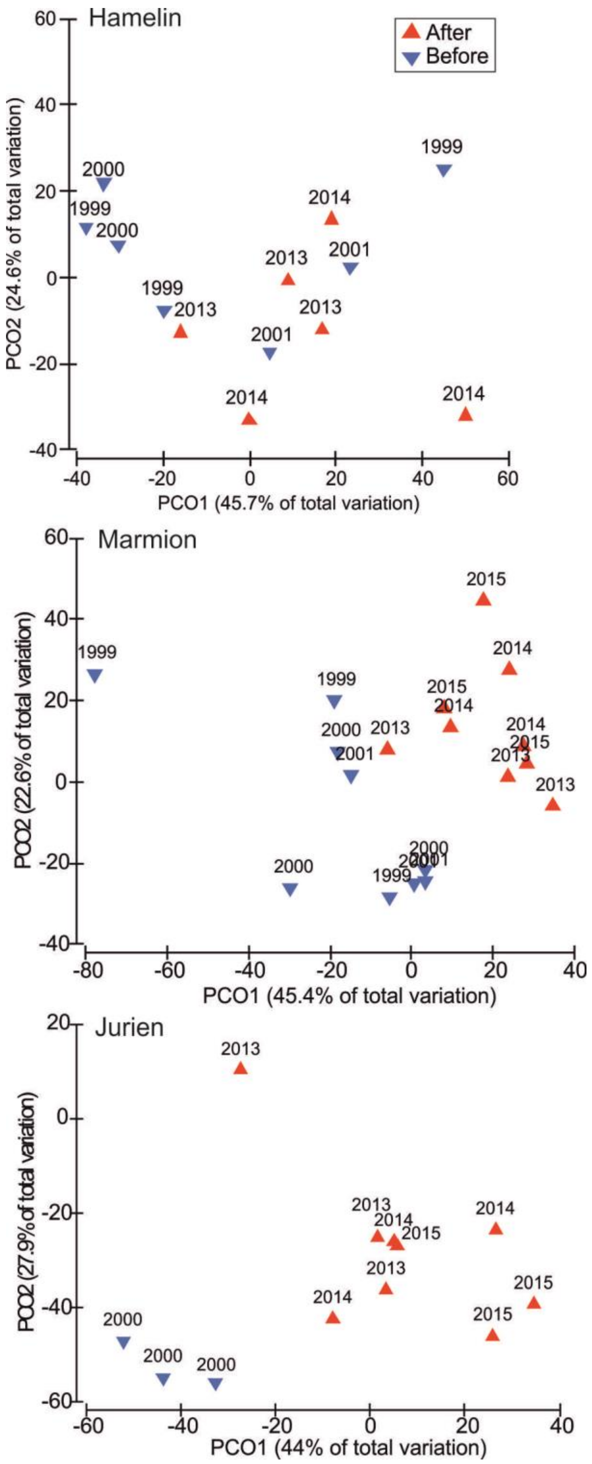
Hamelin
After
Before
PCO2 (24.6% of total variation)
PCO1 (45.7% of total variation)
60
40
20
0
-20
-40
-40
-20
0
20
40
60
2000
1999
2000
1999
2013
2001
2014
2013
2014
2001
2013
1999
2014
2014
Marmion
PCO2 (22.6% of total variation)
PCO1 (45.4% of total variation)
60
40
20
0
-20
-40
-80
-60
-40
-20
0
20
40
1999
1999
2000
2001
2000
1999
2000
2001
2015
2014
2015
2014
2013
2014
2015
2013
2013
Jurien
PCO2 (27.9% of total variation)
PCO1 (44% of total variation)
20
0
-20
-40
-60
-60
-40
-20
0
20
40
2013
2013
2014
2015
2014
2013
2014
2015
2015
2000
2000
2000

Fig. 3

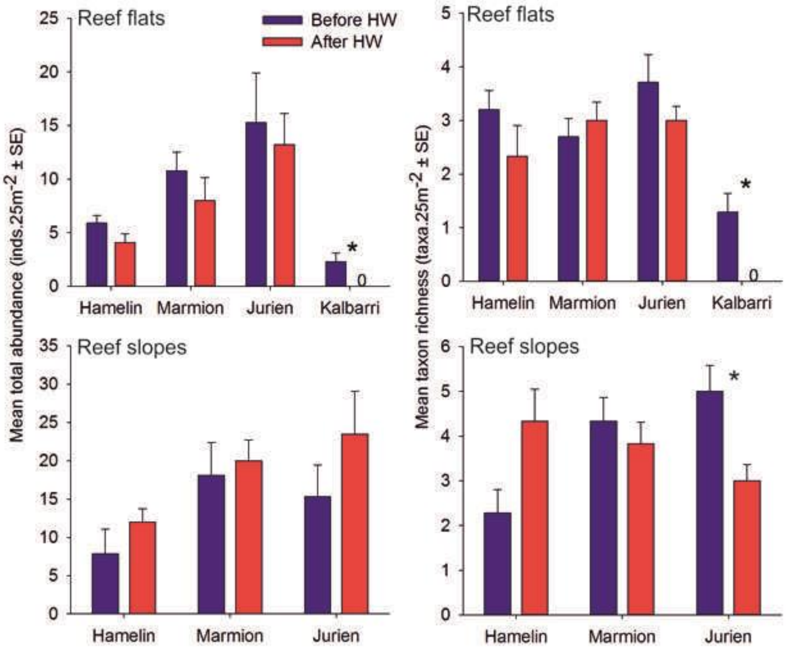
Reef flats
Before HW
After HW
Mean total abundance (inds.25m^{-2} ± SE)
0
5
10
15
20
25
Hamelin
Marmion
Jurien
Kalbarri
*
0
Reef slopes
0
5
10
15
20
25
30
35
Hamelin
Marmion
Jurien
Reef flats
Mean taxon richness (taxa.25m^{-2} ± SE)
0
1
2
3
4
5
Hamelin
Marmion
Jurien
Kalbarri
*
0
Reef slopes
0
1
2
3
4
5
6
*
Hamelin
Marmion
Jurien

Fig. 4

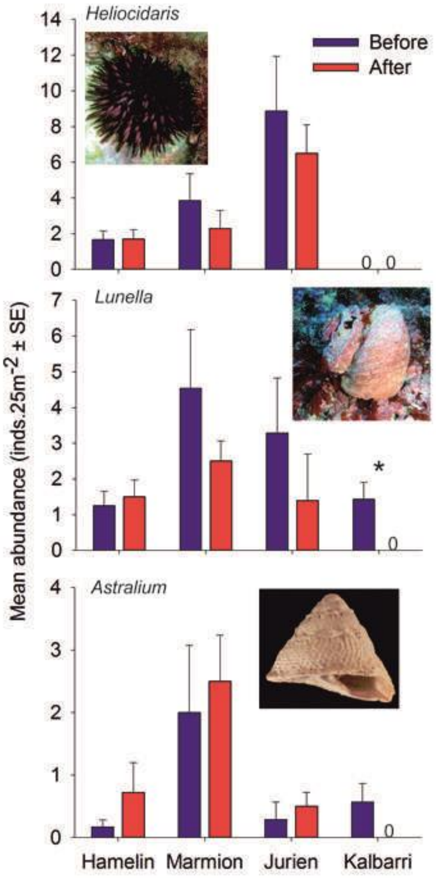
Heliocidaris
Before
After
14
12
10
8
6
4
2
0
0
0
Lunella
7
6
5
4
3
2
1
0
*
0
Astralium
4
3
2
1
0
0
Mean abundance (inds.25m^{-2} ± SE)
Hamelin
Marmion
Jurien
Kalbarri

Fig. 5

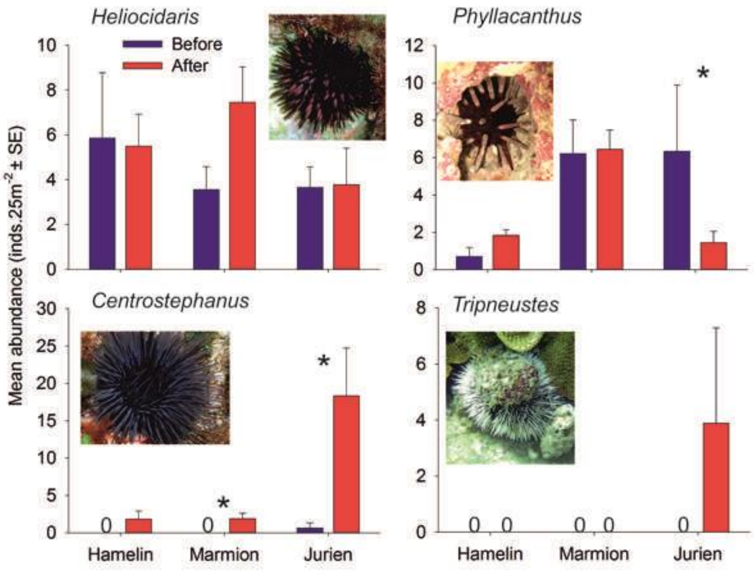
Heliocidaris
Before
After
Phyllacanthus
Centrostephanus
Tripneustes
Mean abundance (inds.25m^{-2} ± SE)
10
8
6
4
2
0
12
10
8
6
4
2
0
30
25
20
15
10
5
0
8
6
4
2
0
*
*
*
0
0
0
0
0
0
0
Hamelin
Marmion
Jurien
Hamelin
Marmion
Jurien

Fig. 6

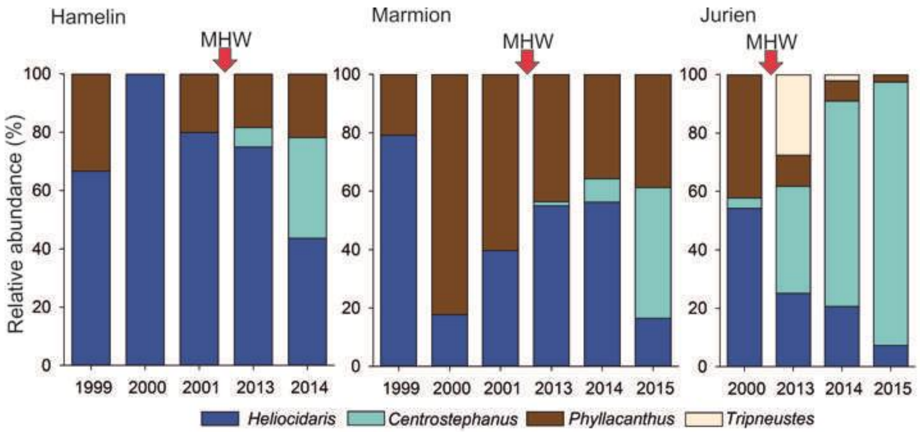
Hamelin
Marmion
Jurien
MHW
MHW
MHW
Relative abundance (%)
0
20
40
60
80
100
1999
2000
2001
2013
2014
2015
Heliocidaris
Centrostephanus
Phyllacanthus
Tripneustes

Fig 7.