

Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem

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Abstract

Extreme climatic events can trigger abrupt and often lasting change in ecosystems via the reduction or elimination of foundation (i.e., habitat-forming) species. However, while the frequency/intensity of extreme events is predicted to increase under climate change, the impact of these events on many foundation species and the ecosystems they support remains poorly understood. Here, we use the iconic seagrass meadows of Shark Bay, Western Australia – a relatively pristine subtropical embayment whose dominant, canopy-forming seagrass, *Amphibolis antarctica*, is a temperate species growing near its low-latitude range limit – as a model system to investigate the impacts of extreme temperatures on ecosystems supported by thermally sensitive foundation species in a changing climate. Following an unprecedented marine heat wave in late summer 2010/11, *A. antarctica* experienced catastrophic (>90%) dieback in several regions of Shark Bay. Animal-borne video footage taken from the perspective of resident, seagrass-associated megafauna (sea turtles) revealed severe habitat degradation after the event compared with a decade earlier. This reduction in habitat quality corresponded with a decline in the health status of largely herbivorous green turtles (*Chelonia mydas*) in the 2 years following the heat wave, providing evidence of long-term, community-level impacts of the event. Based on these findings, and similar examples from diverse ecosystems, we argue that a generalized framework for assessing the vulnerability of ecosystems to abrupt change associated with the loss of foundation species is needed to accurately predict ecosystem trajectories in a changing climate. This includes seagrass meadows, which have received relatively little attention in this context. Novel research and monitoring methods, such as the analysis of habitat and environmental data from animal-borne video and data-logging systems, can make an important contribution to this framework.

Keywords: *Amphibolis antarctica*, animal-borne video, *Chelonia mydas*, climate change, disturbance, extreme events, green turtle, heat wave

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Introduction

Climate change research typically focuses on variation in ecosystem structure and function associated with gradually increasing mean temperatures (Parmesan & Yohe, 2003). However, extreme events such as hurricanes, floods, droughts, cold snaps, and heat waves can produce high-magnitude, stepwise ecosystem responses that may outpace change associated with gradual climatic trends (Hegerl *et al.*, 2011). To accu-

rately predict ecological responses to climate change, it is therefore necessary to account for both trend- and event-driven variation, the latter of which is currently poorly understood (Katz & Brown, 1992; Jentsch *et al.*, 2007).

Foundation species (e.g., canopy-forming plants, reef-building corals) are habitat-forming species whose presence strongly influences ecosystem structure and function and creates locally stable conditions for other species (Dayton, 1972). In a changing climate, ecosystems where foundation species are susceptible to the direct or indirect effects of elevated temperatures are therefore vulnerable to fundamental reorganization characterized by reduced habitat complexity and disrupted ecosystem services (Ellison *et al.*, 2005; Hoegh-Guldberg & Bruno, 2010). While some of this

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reorganization may be gradual, extreme climatic events can also trigger abrupt ecosystem restructuring via the reduction or elimination of foundation species. For example, reef-building corals may experience mass bleaching and mortality following heat waves (Hoegh-Guldberg, 1999) and overstory trees can suffer large-scale mortality triggered by periods of extreme heat and drought (e.g., Breshears *et al.*, 2005). However, large-scale disturbances associated with stochastic climatic extremes are challenging to predict and the role of these events in determining ecosystem responses to climate change is currently underappreciated (Breshears *et al.*, 2005; Jentsch *et al.*, 2007; Jentsch & Beierkuhnlein, 2008).

The loss of marine foundation species (e.g., corals, kelps, seagrasses) can dramatically alter benthic ecosystems and have marked impacts on marine fauna and human societies (e.g., Pratchett *et al.*, 2008). However, compared with their terrestrial counterparts, relatively few well-studied marine systems exist that allow detailed study of the effects of climatic extremes on foundation species and their associated communities (Hoegh-Guldberg & Bruno, 2010). Seagrasses are marine foundation species that support diverse food webs and provide valuable ecosystem services (e.g., carbon sequestration, habitat for fish and fisheries) (Duarte, 2002; Barbier *et al.*, 2011), but are experiencing rapid, global declines (Orth *et al.*, 2006; Waycott *et al.*, 2009). Concern is growing over the effects of climate change on seagrasses, particularly where temperate species occur near their upper thermal tolerance limits (Jordà *et al.*, 2012). In addition to gradual declines, seagrasses can experience abrupt, large-scale dieback triggered by extreme temperatures (Seddon *et al.*, 2000; Moore *et al.*, 2013). However, the dynamics of climatic disturbance and resilience in seagrass meadows are not well understood owing in part to the relative rarity of long-term monitoring programs (Duarte, 2002). This is a critical shortcoming because the frequency and severity of climatic extremes, and the ecological role of disturbance, are predicted to increase in coming decades (Easterling *et al.*, 2000).

Here, we use the relatively pristine and well-studied seagrass meadows of Shark Bay, Western Australia as a model system to investigate the impacts of extreme temperatures on marine ecosystems supported by thermally sensitive foundation species in a changing climate. Shark Bay provides a unique and valuable model system because of its protected status (an IUCN World Heritage Site) and geographic location in a global marine biodiversity hotspot at the overlap of temperate and tropical zones (Tittensor *et al.*, 2010). Both temperate and tropical seagrasses occur in Shark Bay, but its seascape is dominated by the temperate species *Amphibolis*

antarctica, which constitutes 85% of seagrass coverage and forms large (3700 km²), mostly monospecific meadows with a high canopy (up to 1.3 m) that creates extensive, structurally complex benthic habitat (Walker *et al.*, 1988; Kendrick *et al.*, 2012; Burkholder *et al.*, 2013). The habitat value and ecosystem services provided by *A. antarctica* cannot be matched by the much smaller tropical seagrasses. However, Shark Bay is located at the low-latitude range limit of *A. antarctica*, which probably experiences thermal stress during summer if water temperatures exceed ca. 25 °C (Walker & Cambridge, 1995).

In 2010/11, the southeast Indian Ocean along the Western Australian coast experienced an unprecedented marine heat wave that resulted in water temperatures 2–4 °C above long-term averages for ca. 10 weeks during late summer (details in Pearce & Feng, 2013). The heat wave has been attributed to the cooling phase of the Pacific Decadal Oscillation that resulted in warming of the waters of northern Western Australia combined with the second strongest La Niña event this century, and strong easterly winds forcing the warm waters from the Indonesian Archipelago down the Western Australian coast (Feng *et al.*, 2011). This event had myriad short- and long-term impacts on coastal ecosystems including temporary poleward range shifts by tropical fish and megafauna (e.g., whale sharks, manta rays), large-scale fish and invertebrate mortalities, and a likely permanent poleward range shift in a temperate, habitat-forming macroalgae (Wernberg *et al.*, 2012; Pearce & Feng, 2013; Smale & Wernberg, 2013). During the heat wave, Shark Bay experienced the largest deviation from mean temperatures (4 °C in February, 2011) on the mid west coast of Western Australia (Hetzl, 2013), and stocks of scallop and blue crab in Shark Bay declined dramatically shortly after the event (Kangas *et al.*, 2013). However, the effects of the heat wave on the temperate foundation seagrass and large vertebrates in this ecosystem have not yet been investigated in detail.

Expanding on studies of Shark Bay's seagrasses conducted prior to and immediately following the heat wave (Fraser *et al.*, 2012; Burkholder *et al.*, 2013), we used in-water surveys and harvested plants to determine the impact of the heat wave on *A. antarctica* coverage and biomass and assess the responses of other, less common, seagrasses. Concurrently, we used animal-borne video footage to quantify changes in *A. antarctica* condition, a proxy for habitat quality, experienced by seagrass-associated foragers (sea turtles) after the heat wave compared with a decade earlier. While animal-borne video recorders have been widely applied to the study of animal behavior and ecology (Moll *et al.*, 2007), to our knowledge this represents their first use as

a tool for monitoring ecosystem health from the perspective of free-ranging megafauna. Finally, we examined the impact of the heat wave on the health status of largely herbivorous green turtles (*Chelonia mydas*), which occur in Shark Bay in high densities year round (Thomson *et al.*, 2013) and include temperate and tropical seagrasses in their diets (Burkholder *et al.*, 2011; JT, unpublished data). After presenting our findings from Shark Bay, we discuss the need for a generalized framework for assessing the vulnerability of marine ecosystems to abrupt change involving the loss or reduction of foundation species in a changing climate.

Materials and methods

Water temperature

Satellite-derived sea surface temperature (SST) data for a $1/4 \times 1/4$ degree cell located in the Eastern Gulf of Shark Bay adjacent to Guichenault Point (Fig. 1) were derived from satellite measurements (NOAA Reynolds Optimal Interpolation) obtained from the NOAA National Climatic Data Center website (<http://www.ncdc.noaa.gov/sst/>). Mean monthly temperatures from 2001 to 2011 are shown in Fig. 2 to illustrate the magnitude and duration of the 2011 marine heat wave in this ecosystem. More detailed reports on the temperature

anomaly for Shark Bay and Western Australian coastal waters more generally can be found in Pearce *et al.* (2011), Hetzel (2013), and Pearce & Feng (2013).

Seagrass surveys

In-water seagrass surveys were performed at 475 sites throughout Shark Bay between 2007 and 2009, prior to the marine heat wave (Burkholder *et al.*, 2013). These included 63 sites on and around a series of shallow banks offshore of the Monkey Mia Dolphin Resort (Fig. 1), which form the main study area of a long-term ecological research project (Heithaus *et al.*, 2012). The remaining 412 sites were spread throughout the Eastern and Western Gulf of Shark Bay. Each site was surveyed either using snorkel or SCUBA. A 60×60 cm quadrat with grid was dropped haphazardly off the side of the anchored vessel. Percent cover for each seagrass species was visually estimated in the quadrat where it settled on the bottom. The quadrat was then flipped end over end three times moving toward the front of the boat and visually sampled for percent cover of each seagrass. This procedure was then repeated for a third sample at each site. The small number of samples at each site was necessary to allow sampling of enough sites to achieve adequate coverage of the study system.

In 2007–2009, sites in the Monkey Mia Banks region (Fig. 1) were visited 9 or 10 times each while all other sites were



Fig. 1 Google Earth imagery showing the location of Shark Bay (inset), the 113 seagrass cover sampling sites spanning ca. 215 km of coastline and a series of offshore seagrass banks near the Monkey Mia Dolphin Resort (sampling regions: Monkey Mia Banks = red markers/circles, East Peron Peninsula = blue markers/diamonds, West Peron Peninsula = green markers/stars, L'Haridon Bight/Fauré Sill = yellow markers/squares), and the location of five biomass coring locations on the Wooramel Bank (white markers/circles).

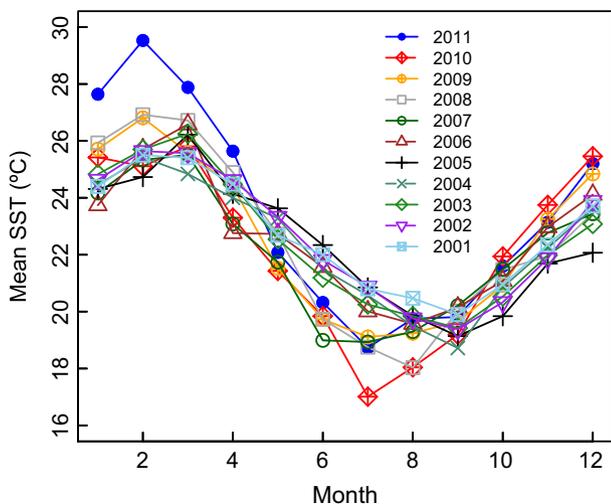


Fig. 2 Mean monthly SST derived from satellite measurements (NOAA Reynolds Optimal Interpolation) in the Eastern Gulf of Shark Bay from 2001 to 2011.

visited twice. In 2012, a subset of these sites was revisited focusing on shallow areas (<8 m deep) where *A. antarctica* was most frequently found in 2007–2009 (Figure S1). These included 42 sites on the Monkey Mia Banks and 71 sites in three other sampling regions spanning ca. 215 km of coastline (Fig. 1). For the Monkey Mia Banks region, percent cover data were collapsed either to a mean for each site in 2007–2009, or separate means for 2007 and 2008/9 (each site was visited only once in January, 2009, so these data were lumped with 2008), for comparison with 2012 data. For the other three regions (hereafter East Peron Peninsula, West Peron Peninsula, and L'Haridon Bight/Fauré Sill), percent cover data were collapsed to a mean value for each site in 2007–2009 for comparison with 2012.

Statistical analyses were run in R v 2.13.0 or 2.13.1 (R Core Team, 2013) unless otherwise stated. We used nonparametric paired tests of the medians to assess the significance of differences in percent cover before and after the heat wave. First, we conducted a paired Wilcoxon signed-ranks test between 2007–2009 and 2012 for all sites pooled. We then conducted the same test for sites within East Peron Peninsula, West Peron Peninsula, and L'Haridon Bight/Fauré Sill regions separately. For the Monkey Mia Banks region, we ran a Friedman test (the nonparametric equivalent of a repeated-measures ANOVA) with post-hoc comparisons in SPSS v. 21 to test for differences in medians among 2007, 2008/9 and 2012. For the less common seagrasses in Shark Bay, we used mixed effect logistic regression (glmmPQL in the MASS package in R) to analyze the influence of sampling block (2007–2009 vs. 2012) on the probability of observing a species during a given site visit. We analyzed presence–absence data for the temperate species *Posidonia australis* (94 occurrences; rare observations of *P. coriacea* were lumped with *P. australis*) and the tropical species *Cymodocea angustata* (45 occurrences) and *Halodule uninervis* (79 occurrences). We did not analyze presence–absence data for three other tropical seagrasses (*Halophila ovalis*, *H. spinulosa*,

and *Syringodium isoetifolium*), which were encountered rarely (11, 10, and 4 occurrences, respectively). Site was treated as a random effect in the models to account for repeated measures.

Biomass of *A. antarctica* communities ($n = 25$, 1–2 m depth) in the Wooramel Bank region of Shark Bay, located ca. 30 km east of the Monkey Mia banks (Fig. 1), was determined at five sites using 25 cm diameter cores taken three times: during the heat wave (March, 2011), 6 months after the heat wave (September, 2011), and 2 years after the heat wave (March, 2013). Plants were separated into leaves, shoots, rhizomes, and roots, dried at 60 °C, and weighed to determine dry mass. Differences in leaf biomass and belowground biomass over time were determined using ANOVA.

We also assessed the reproductive response of *P. australis* to the heat wave. In 2011, two populations of *P. australis* in Shark Bay were found to be reproductive, one located in the Western Gulf at Useless Loop, the other in the Eastern Gulf at Guichenault Point (Fig. 1). For each population, inflorescence spikes or flowers were counted (density m^{-2}) by randomly allocating five replicate 10 m × 1 m transects within a 0.25 km² area. At each population, three spikes from each transect were harvested and developing fruit was dissected to determine seed availability.

Amphibolis antarctica condition in turtle-borne video footage

In 1999–2003, National Geographic's Crittercam™ was deployed on green and loggerhead turtles in the Monkey Mia banks region and along a stretch of nearshore sandflat extending ca. 15 km northwest of the Monkey Mia Dolphin Resort (Heithaus *et al.*, 2002). Between October and December 2011 and 2012, custom-built turtle-borne video tags with GoPro® HD cameras were deployed on green and loggerhead turtles in the same area (Thomson & Heithaus, 2014), allowing for a comparison of seagrass condition in the two time blocks. We extracted seagrass condition data from videos by viewing a 10 second interval every 3 minutes throughout each deployment. In each interval, the presence of seagrasses was noted and, for *A. antarctica*, seagrass condition was assigned to one of four ordered categories: condition 0, completely or nearly completely defoliated with stems heavily fouled by epiphytic algae or overgrown by benthic algae (Fig. 5a); condition 1, mostly defoliated with stems substantially fouled by epiphytic algae or overgrown by benthic algae (Fig. 5b); condition 2, substantial foliage present, but with some stripped stems still visible and some epiphytic or benthic algae growth (Fig. 5c); or condition 3, full foliage with few to no stripped stems visible and little algae growth (Fig. 5d). If a turtle remained in the same location for multiple intervals, only the first was used. Areas where seagrass coverage was very sparse (i.e., only a few shoots visible) were excluded from analysis. Only intervals where the turtle was resting on or swimming along the sea bottom were analyzed so perspective in the video was relatively consistent. Data for all turtles were pooled for Fig. 5e. We employed cumulative link mixed models using the 'ordinal' package in R to test the effect of time period (before the heat wave = 1999–2003, after the heat wave = 2011–2012) on

the condition of *A. antarctica*. Turtle identity was specified as a random effect. Single-term deletion and a likelihood ratio test were used to assess the significance of the time period parameter.

Green turtle health status

We assessed the health status of green turtles during at-sea captures between 2000 and 2013 using a qualitative ranking of plastron shape (convex = good, flat = fair, concave = poor). This visual assessment method has been validated by comparison with two quantitative indices of condition based on mass and length measurements for green turtles (Thomson *et al.*, 2009), but did not perform as well for loggerhead turtles (*Caretta caretta*). Thus, we restrict our analysis here to green turtles. Only turtles with curved carapace length (CCL) ≥ 70.0 cm were included in this analysis because captures in 2011–2012 focused exclusively on this size range for deployment of animal-borne video recorders. As turtle health status can change over several weeks to months (Heithaus *et al.*, 2007), recaptures of individual turtles ≥ 30 days apart were retained in the analysis. Health status data were analyzed for years in which captures were conducted frequently (>40 captures: 2000, 2002, 2003, 2005, 2006, 2011, 2012, & 2013). Years in which captures were conducted more rarely were excluded to avoid bias resulting from inexperienced field crews, which would catch proportionally more slower moving, poorer condition turtles. We used cumulative link models in the 'ordinal' package in R to confirm that season (June–September = cold, October–May = warm) did not influence turtle health status ($\chi^2 = 0.15$, $df = 1$, $P = 0.7$). This step was necessary because captures were not conducted in both seasons in all years so the effects of season and year could not be simultaneously tested. We then pooled all data for 2011–2013 and 2000–2006 to determine whether turtle health status was lower in years after the heat wave compared with before. Finally, we tested for annual variation from 2011 to 2013 to determine whether turtle health status had decreased with time since the heat wave. Single-term deletions and likelihood ratio tests were used to determine parameter significance.

Results

Amphibolis antarctica coverage and biomass

Prior to the heat wave, in 2007–2009, *A. antarctica* was observed at 93 of 113 sampling sites and median percent cover was 83.4% (mean = 62.8, SE = 3.6). After the heat wave, in 2012, *A. antarctica* was observed at 71 of 113 sites and median percent cover was 1.7% (mean = 13.1, SE = 2.3). For sites with *A. antarctica* present during at least one visit, median cover declined from 87.4% in 2007–2009 to 3.7% in 2012 ($V = 4334.5$, $P < 0.0001$) – a 96% dieback. Within our long-term study site (the Monkey Mia Banks region, Fig. 1), median cover was more than an order of magnitude lower in 2012 than in both 2007 and 2008/9

($\chi^2 = 59.7$, $df = 2$, $P < 0.0001$, Figs 3a, b and 4). Within three other sampling regions (lumped together in Fig. 3c, d), median cover in 2012 was also greatly reduced compared with cover in 2007–2009 (East Peron Peninsula: $V = 91.0$, $P = 0.0002$; West Peron Peninsula: $V = 161.0$, $P = 0.0003$; L'Haridon Bight/Fauré Sill, $V = 216.0$, $P = 0.004$; Figure S2). On the Wooramel bank, widespread defoliation of *A. antarctica* was observed during the heat wave resulting in extremely low leaf biomass (Fig. 3e). In the 2 years following the heat wave, leaf biomass rebounded somewhat ($F_{2,71} = 7.87$, $P < 0.001$; Fig. 3e), but belowground biomass (i.e., rhizomes and roots) decreased sixfold ($F_{2,71} = 22.85$, $P < 0.001$; Fig. 3f).

Responses of other seagrasses

The likelihood of observing the less common temperate species *P. australis*, which covers ca. 200 km² in Shark Bay (Walker *et al.*, 1988), at the 113 sites did not differ between 2007–2009 and 2012 ($t = -0.54$, $df = 558$, $P = 0.59$), and the difference in the physical appearance of *P. australis* and *A. antarctica* after the heat wave was striking (Supporting Videos 1 & 2). However, *P. australis* displayed a catastrophic failure in sexual reproductive effort during the heat wave, as 100% of fruit in the two known reproductive populations aborted seed production despite evidence of successful fertilization. For the tropical seagrasses, the likelihood of observing *C. angustata* at the 113 sites did not differ between 2007–2009 and 2012 ($t = -0.32$, $df = 558$, $P = 0.75$), but *H. uninervis* was less common in 2012 ($t = -3.88$, $df = 558$, $P = 0.0001$).

Habitat degradation revealed by animal-borne video

Video quality was high enough to assess *A. antarctica* condition in 14 green turtle and 16 loggerhead turtle videos in 1999–2003, and 21 green turtle and 19 loggerhead turtle videos in 2011–2012. Footage taken in 1999–2003 showed that turtles spent 97% of their time over the most lush, dense seagrass (Fig. 5c–e). In 2011–2012, after the heat wave, this figure was only 4% and turtles encountered no *A. antarctica* in the highest condition category (Fig. 5e). Instead, turtles spent most of their time swimming over sparse, mostly defoliated seagrass (Fig. 5b) or fully defoliated, dead *A. antarctica* material that often formed thick mats covering the seabed (Fig. 5a, Supporting Videos 1 & 2). Overall, *A. antarctica* was significantly more likely to fall in a lower condition category after the heat wave compared with a decade earlier ($\chi^2 = 119.5$, $df = 1$, $P < 0.0001$) and the change in the appearance of the meadows was stark (Supporting Video 3a, b).

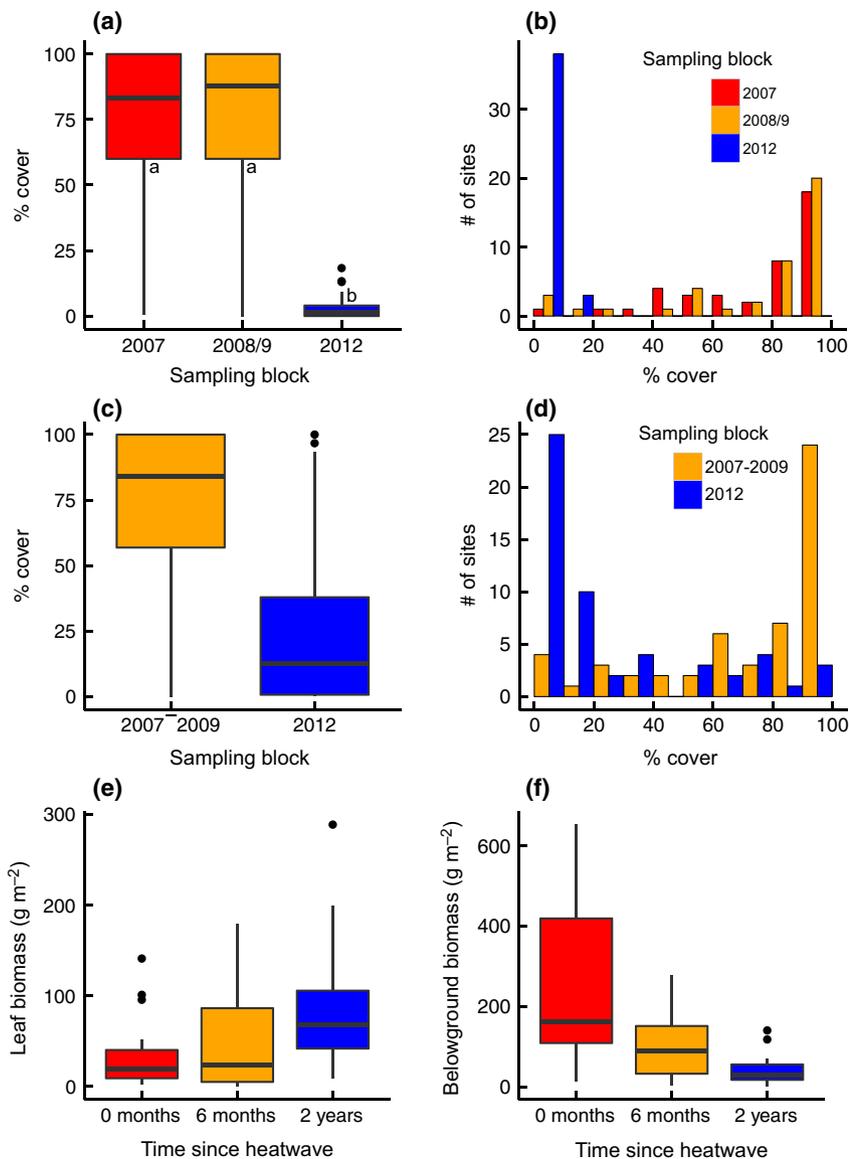


Fig. 3 Boxplots and histograms showing percent cover of *A. antarctica* on the Monkey Mia Banks (a, b) and in three other sampling regions pooled (c, d) before and after the heat wave. Changes in leaf (e) and belowground biomass (f) of *A. antarctica* on the Wooramel Bank since the heat wave.

Declining green turtle health status

The health status of 424 individual green turtles (447 total captures) was assessed between 2000 and 2013. The mean number of captures per year, including recaptures ≥ 30 days apart, was 55.9 ± 5.8 SE. Turtles were more likely to fall in a lower health status category after the heat wave (2011–2013) than before (2000–2006; $\chi^2 = 14.4$, $df = 1$, $P = 0.0001$; Fig. 6a), and turtle health status declined consistently from 2011, the year of the heat wave, to 2013 ($\chi^2 = 10.3$, $df = 2$, $P = 0.006$; Fig. 6b). For example, in 2012, only 6% of turtles fell in

the highest health status category compared to an average of $35\% \pm 6$ (SE) from 2000 to 2006, and by 2013, no turtles fell in this category (Fig. 6b); in contrast, the proportion of turtles in the lowest health status category increased each year after the heat wave. Only 21 individuals were captured multiple times ≥ 30 days apart, and only three of those were captured before and after the heat wave. One turtle that was in fair condition in 2000 declined to poor condition in 2012, and two others were in good condition in both 2003 and 2012. Three turtles were captured once in 2012 and once in 2013. Of these, one was in fair condition and two were in poor

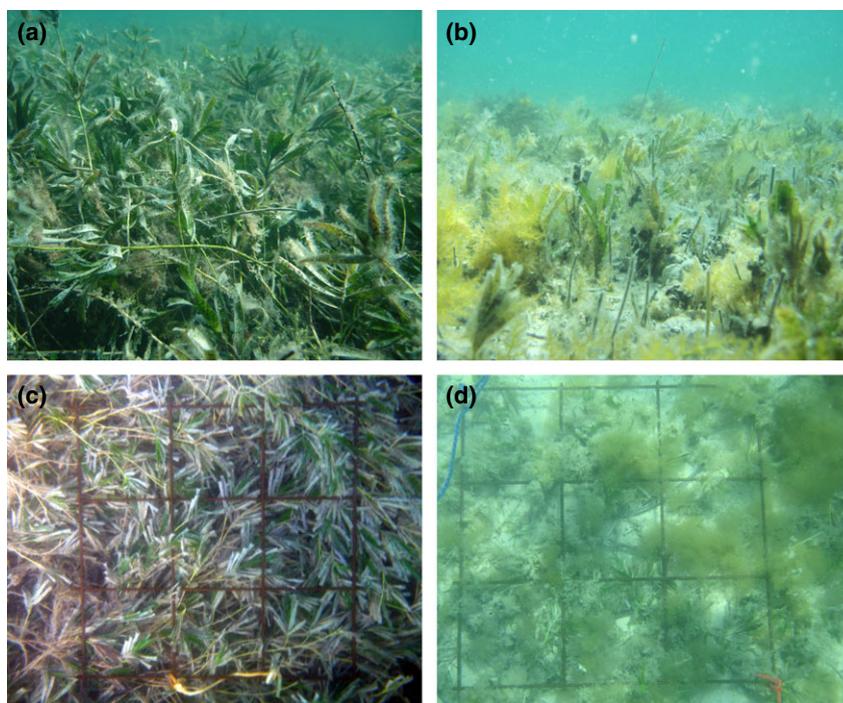


Fig. 4 Horizontal and top-down photos of *A. antarctica* beds in the Monkey Mia Banks region taken before (a, c) and after (b, d) the heat wave. Photos are not from specific sites and are intended as representative examples only.

condition in 2012, and their conditions did not change in 2013.

Discussion

Because of its location in a subtropical transition zone, and the temperate origin of its foundation seagrass, Shark Bay's World Heritage-listed seagrass meadows provide an important model system for investigating the impacts of extreme temperatures on the structure and function of coastal ecosystems in a changing climate. Our data sets provide compelling evidence that stochastic temperature extremes, such as the 2010/11 marine heat wave, have the potential to abruptly restructure ecosystems via the reduction or elimination of thermally sensitive foundation species. This includes habitat-forming seagrasses, which have received relatively little attention in this context. Furthermore, we have shown that extreme temperature events can impact the health status of megafauna that are closely associated with foundation species including large herbivores in seagrass meadows (Hughes *et al.*, 2009). In general, our research in a well-studied, relatively pristine ecosystem supports the growing recognition that, to accurately predict ecosystem trajectories in a changing climate, the potential effects of stochastic extreme events need to be accounted for (Jentsch *et al.*, 2007; Jentsch & Beierkuhnlein, 2008). This is particularly true

if climatic events have the potential to reduce or eliminate key habitat-forming species (Smale & Wernberg, 2013).

Regional implications of the seagrass dieback

As large, temperate seagrasses tend to have slow rates of rhizome elongation and patch formation (Hemminga & Duarte, 2000), we expect the effects of the *A. antarctica* dieback to be prolonged in regions of Shark Bay that experienced the most severe losses. The severity of the dieback varied among the regions sampled, with the smallest decline (58%) observed in an area characterized by high salinity and low turbidity (L'Haridon Bight/Fauré Sill, Figure S2). This suggests a possible combined role of temperature and light limitation in the decline (see also Fraser *et al.*, 2014), which is supported by field and experimental data involving other temperate seagrasses as well (Collier *et al.*, 2011; Moore *et al.*, 2013). In areas where *A. antarctica* experienced complete defoliation and loss of active meristems, recovery will depend on belowground rhizome extension and new shoot growth (Burnell *et al.*, 2013), while in areas where belowground biomass was completely lost, recovery will require recolonization via establishment of seedlings from nearby reproductive populations. Rhizome loss is also likely to reduce the resilience of highly disturbed *A. antarctica* meadows to future

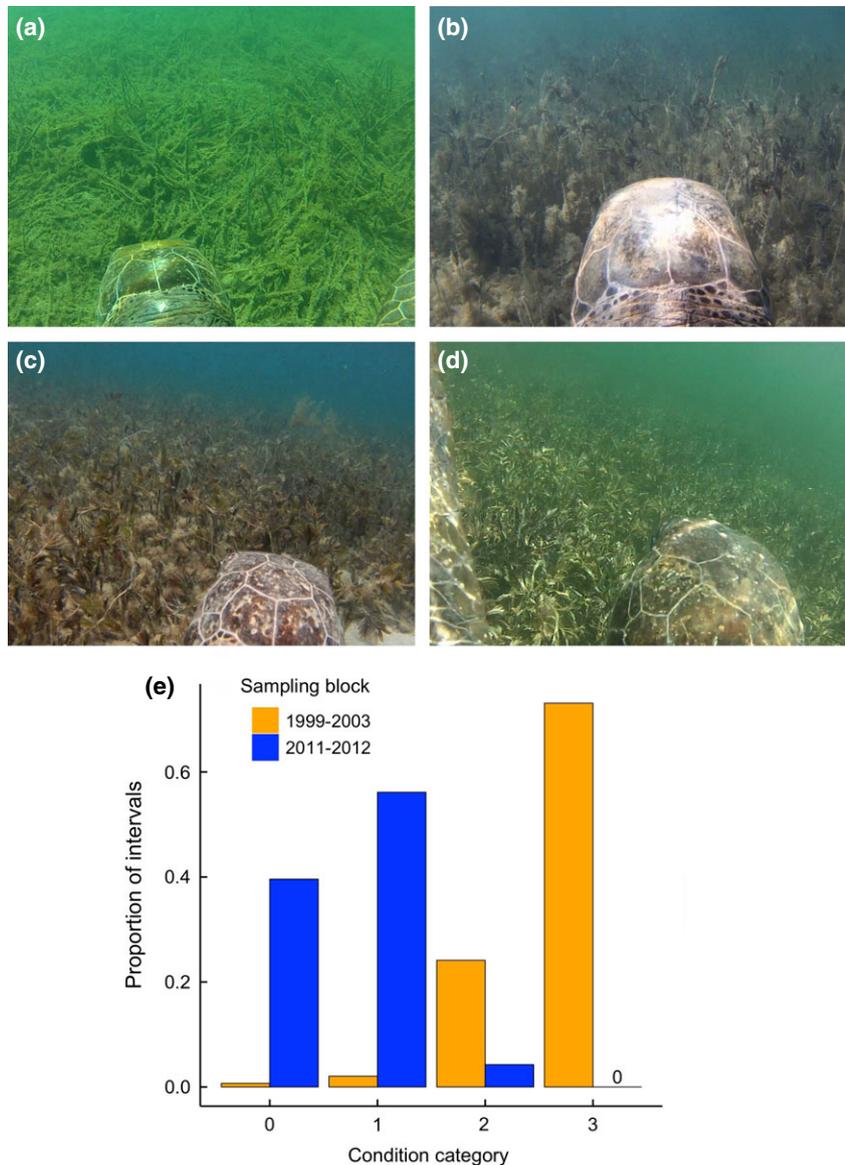


Fig. 5 Examples of *A. antarctica* condition categories 0–3 (a–d, respectively), and the proportion of video intervals (e) in which *A. antarctica* fell into each category in 1999–2003 ($n = 290$) and 2011–2012 ($n = 586$).

disturbances (e.g., cyclones, grazing, additional heat waves), as rhizomes store nutrients and carbohydrates that support seagrasses during unfavorable growing conditions (Pedersen *et al.*, 1997; Alcoverro *et al.*, 2000). Furthermore, the near-complete loss of seagrass coverage in some areas is likely to initiate a feedback that deteriorates growing conditions by destabilizing sediments and increasing turbidity (de Boer, 2007). Indeed, in other ecosystems (e.g., Chesapeake Bay), increased turbidity has been implicated in preventing seagrass recolonization following large-scale dieback triggered by extreme temperatures (Moore *et al.*, 2013).

High seed abortion rates associated with a marine heat wave have been reported for *Posidonia oceanica*, a

congener of *P. australis*, in the Mediterranean Sea (Baletti & Cinelli, 2003). The high abortion of *P. australis* seeds in Shark Bay during the 2011 heat wave indicates that this species is also at the extreme of its thermal tolerance in this region, and high salinities (42ppt) and low nutrient availability (Fraser *et al.*, 2012; Burkholder *et al.*, 2013) probably exacerbate the stress of clonal growth combined with sexual reproduction. Sexual reproduction requires a significant investment of resources from maternal plants (Hocking *et al.*, 1980), and in Shark Bay's nutrient-impooverished embayment, abortion soon after the beginning of development appears to be a strategy to avoid wasting resources (fruit growth, seed development, and nutrient

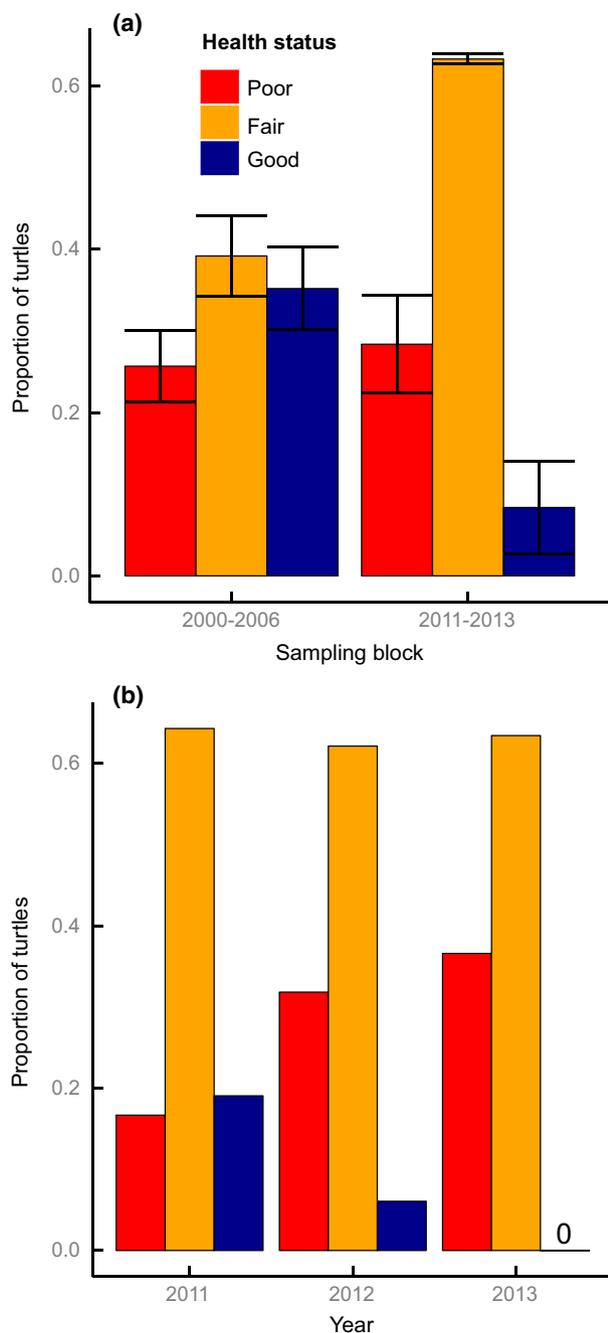


Fig. 6 Health status of 424 green turtles captured in a long-term, at-sea research program in Shark Bay in 2000–2006 and 2011–2013 (a), and annual changes in turtle health status from 2011 to 2013 (b).

reserves). While the short-term impacts on the Shark Bay ecosystem from this reproductive failure are likely to be limited, if these temperature events become more frequent, a decrease in sexually produced propagules by *P. australis* could result in a positive feedback for inbreeding depression, leading to reduced demographic

resilience for this species via lower fitness and genetic variability as determined in genetic assessments that have included Shark Bay (Waycott *et al.*, 1997).

The different responses of two tropical seagrasses to the heat wave are difficult to interpret. However, the reduction in the occurrence of *H. uninervis* may have resulted in part from shading or smothering of its small shoots, which often grow within or near *A. antarctica* stands, by dead or dying *A. antarctica* material that formed thick, algae-covered mats on the sea bottom (Supporting Videos 1 & 2; Fig. 5a). Supporting this hypothesis is the fact that nine sites that were dominated by *A. antarctica* (>50% cover) in 2007–2009 also had *H. uninervis* while only four also had *C. angustata*, whose likelihood of occurrence did not change after the heat wave. However, the trajectories of the tropical seagrasses will only become clear as dead *A. antarctica* degrades and/or washes away, exposing newly available substrate for recolonization. It will be particularly interesting to determine whether fast-recruiting tropical seagrasses will successfully establish in areas formerly occupied by *A. antarctica* or whether the competitively dominant but slower-growing climax species will gradually recover to its predisturbance level. Indeed, the tropicalization of marine communities in this region of Western Australia has been predicted based on bioclimatic envelope modeling (Cheung *et al.*, 2012) and these events in Shark Bay may portend a transition toward a purely tropical state in this ecosystem in coming decades. As mean sea surface temperatures along the southwestern Australian coast are increasing by ca. 0.01–0.02 °C yr⁻¹ (Pearce & Feng, 2007), increased levels of temperature-related disturbance, including heat waves, should be expected in this region in the future.

Some immediate impacts of the heat wave on marine fauna in Shark Bay have already been reported including scallop and blue manna crab (*Portunus armatus*) declines, both of which led to fishery closures (Hetzl, 2013; Kangas *et al.*, 2013). However, long-term community-level responses to elevated water temperatures are challenging to predict because they may reflect a complex suite of biogeographic distributions, species traits (e.g., dispersal ability, reproductive and life history characteristics), and interspecific interactions (e.g., Schiel *et al.*, 2004). Despite uncertainty surrounding the trajectory of the Shark Bay ecosystem following this disturbance, we expect significant impacts in areas that experienced the most severe seagrass dieback. These may include declines in seagrass-associated teleost fish populations (Heithaus, 2004) with potential knock-on effects on piscivores (e.g., dolphins, seabirds) and top predators (i.e., sharks), impacts on elasmobranchs via the loss of nursery and foraging habitat (Vaudo & Heithaus, 2009), changes in the distributions, abundances,

and possibly sizes of large herbivores (green turtles and dugongs, *Dugong dugon*), deterioration of water quality and benthic growing conditions (de Boer, 2007), and a significant loss of carbon sequestration from the formerly dense and expansive meadows, which are among the world's most carbon-rich (Fourqurean *et al.*, 2012a,b). However, additional research is required to determine the extent and magnitude of the *A. antarctica* dieback in unsampled regions of Shark Bay and to track changes in environmental conditions and the abundances/distributions of seagrasses and associated fauna over time.

While the marine heat wave is overwhelmingly likely to have been the main driver of the *A. antarctica* dieback in Shark Bay, other events may also have contributed to the observed declines in cover and biomass. In particular, a large flood event affected the Wooramel River (Fig. 1) in January, 2011 and resulted in river discharge (Figure S3) until mid-March. The flooding of the Wooramel is rare, with flooding generally occurring every 6–8 years for days to weeks usually associated with tropical lows in summer and temperate lows in winter. The scale and duration of flooding observed in summer 2010–2011 are unusual. However, the influence of this flood would probably be limited to nearshore areas surrounding the river mouth, which is located 40–90 km (across a large gulf) from our 113 seagrass coverage sampling sites (Fig. 1). Thus, the Wooramel flooding may have contributed to trends in *A. antarctica* biomass observed at the biomass coring locations on the Wooramel bank (Fig. 1), but would not have significantly affected other regions in Shark Bay where similar large-scale seagrass losses were observed.

Broader implications of a regional event

The temperature-induced decline of a foundation seagrass in a remote and well-protected ecosystem at the overlap of temperate and tropical zones has broad significance. Most large-scale seagrass losses have occurred in highly developed coastal regions where many anthropogenic stressors affect the marine environment (e.g., Chesapeake Bay, Mediterranean Sea), making the role of individual stressors difficult to discern (Duarte, 2002). By contrast, in Shark Bay, we were able to detect a clear fingerprint of a warming event on the severe dieback of a habitat-forming seagrass, demonstrating that extreme temperatures alone are sufficient to produce abrupt, high-magnitude disturbances where foundation seagrasses occur near their upper thermal tolerance limits. The severity of the dieback and its effects on the health status of a resident megagrazer reveal the magnitude of community-level impacts that extreme temperatures can produce. In addition,

our results highlight significant challenges ahead for the management of protected ecosystems in biogeographic transition zones in a rapidly changing climate. Specifically, if the *A. antarctica* dieback in Shark Bay portends a poleward range shift for this species, how will this affect the region's World Heritage status, which is supported by its formerly expansive *A. antarctica* meadows and associated communities? Finally, reduced carbon sequestration in Shark Bay's seagrass meadows, a global 'blue carbon' hotspot, has the potential to exacerbate climate change impacts on ecosystems globally (Fourqurean *et al.*, 2012a,b) and carries significant societal costs (Pendleton *et al.*, 2012).

Toward a predictive framework

Our understanding of the effects of extreme events on ecosystems is in its infancy (Jentsch & Beierkuhnlein, 2008). However, examples of abrupt, temperature-induced ecosystem change involving the loss of foundation species in systems ranging from semiarid woodlands (Breshears *et al.*, 2005) to coral reefs (Hoegh-Guldberg, 1999) and seagrass meadows (Seddon *et al.*, 2000; Moore *et al.*, 2013) make clear that these processes need to be well understood to accurately predict ecosystem trajectories in a changing climate. While these events might be most likely to occur where foundation species occur near the high-temperature extremes of their ranges (e.g., low-latitude or low-altitude range margins) (Smale & Wernberg, 2013), some species are vulnerable to thermal disturbance throughout their range (Hoegh-Guldberg, 1999; Breshears *et al.*, 2005; Jordà *et al.*, 2012). Furthermore, it is essential to determine how increasing levels of event-driven disturbance under climate change will interact with other common, but less acute, stressors (e.g., pollution, over-exploitation, habitat loss/fragmentation) to affect ecosystem structure, function, and resilience (Harley *et al.*, 2006). Evidence from marine ecosystems suggests that climatic extremes can interact in a synergistic manner with additional stressors to produce prolonged or permanent ecosystem state shifts. For example, on coral reefs, fishing-related declines in herbivorous species can interact with thermal disturbance of corals to produce shifts to an algae-dominated state (Hughes *et al.*, 2007). In seagrass meadows, temperature-induced seagrass losses can initiate feedbacks (i.e., sediment destabilization and resuspension) that increase turbidity and degrade benthic growing conditions, facilitating a transition to an unvegetated state (de Boer, 2007; Moore *et al.*, 2013). Abrupt disturbances and long-term transitions involving the loss of foundation species entail significant losses of structural complexity (i.e., habitat opportunities) and therefore represent a major

challenge for the management of ecosystems in a changing climate.

Based on our research in Shark Bay and similar events in diverse ecosystems, we suggest that a generalized framework for predicting ecosystem vulnerability to abrupt change associated with the temperature-induced reduction or loss of foundation species is needed. As a starting point, this framework should include an assessment of foundation species' sensitivities to elevated temperatures, their adaptive capacity and intrinsic ability to recover following disturbance (e.g., reproductive and life history characteristics), the potential for overlapping environmental or anthropogenic stressors to exacerbate temperature effects, and the potential for abiotic or biotic feedback loops to facilitate prolonged or permanent state shifts following a thermal disturbance. Experimental and cross-ecosystem studies conducted in conjunction with long-term monitoring programs are particularly needed to evaluate factors influencing ecosystem resilience in the face of increasing climatic extremes. Improved regional climate modeling is also needed to predict changes in the frequency and severity of specific types of climatic disturbances. Novel research and monitoring techniques, such as analysis of habitat and environmental data collected using animal-borne video and data-logging systems deployed on key species (e.g., large herbivores in seagrass meadows), can provide valuable insights into ecosystem functioning in a rapidly changing climate.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Depth distribution of previously surveyed seagrass sampling sites (Burkholder *et al.*, 2013) with >50% *A. antarctica* coverage.

Figure S2. *Amphibolis antarctica* decline in the four sampling regions identified in Fig. 2. Regions are the Monkey Mia Banks (a, b), East Peron Peninsula (c, d), West Peron Peninsula (e, f), L'Haridon Bight/Fauré Sill (g, h).

Figure S3. A satellite image (courtesy of Curtin University) showing flooding of the Wooramel River (red box) in January, 2011.

Videos S1 & S2. Examples of green turtles swimming across the transition between patches of *P. australis* and *A. antarctica* after the marine heat wave.

Video S3. A series of ten 3-second clips of turtles swimming over *A. antarctica* from (a) Crittercam™ footage taken before the heat wave (1999–2003) and (b) GoPro® footage taken after the heat wave (2011–2012). To select which clips to use in these videos, 15 intervals in which turtles were swimming along the bottom over a predominantly *A. antarctica* substrate were randomly selected from each data set. A 3-second clip was extracted from each interval and the ten clips with the highest video quality in each sample were stitched together.