Vol. 567: 79–93, 2017
https://doi.org/10.3354/meps12029

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 13

Predicting seagrass recovery times and their implications following an extreme climate event

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ABSTRACT: Extreme temperature events are predicted to become more frequent and intense as climate change continues, with important implications for ecosystems. Accordingly, there has been growing interest in what drives resilience to climatic disturbances. When a disturbance overwhelms the resistance of an ecosystem, it becomes vulnerable during recovery, with implications for ecosystem function and persistence. Understanding what influences ecosystem recovery is particularly important in seagrass ecosystems because of their functional roles, vulnerability, and divergent recovery strategies. Seagrass cover was monitored for 3 yr following a large, heatwave-associated mortality event in Shark Bay, Australia. Although the ecosystem's historically dominant foundational seagrass, *Amphibolis antarctica*, is capable of rapid disturbance recovery, this did not occur, likely because of the failure of mechanisms which have driven rapid recovery in other systems (persistence of rhizome beds, sexual reproduction among neighboring beds). Instead, a tropical early successional seagrass, *Halodule uninervis*, became more common, increasing diversity. These changes in the structure of the Shark Bay seagrass ecosystem, and reduction of biomass and structural complexity, will have important implications for ecosystem services and community dynamics and indicates that this ecosystem is highly vulnerable to future disturbances. More generally, our work suggests that seagrass ecosystems typified by a mix of early and late successional species may be particularly likely to exhibit a mismatch between recovery of cover per se and recovery of function following disturbance. As such, extreme climatic events have the potential to abruptly alter seagrass community dynamics and ecosystem services.

KEY WORDS: Resilience · Disturbance recovery · Climate extremes · Climate change · Seagrass · Disturbance

INTRODUCTION

Although research into the ecological effects of climate change has largely focused on how organisms and ecosystems will respond to changes in average environmental conditions, there is increasing recognition of the ability of extreme climatic events — such as heat waves and droughts — to rapidly alter ecosystems. Climate change is predicted to alter aspects of extreme events, including the frequency and duration of heat waves, heavy precipitation events and droughts, strength of tropical ocean currents, and even the frequency of extremes in the El Niño–Southern Oscillation cycle (Wu et al. 2012, Cai et al. 2014, 2015, IPCC 2014). Such events can induce species range shifts, species die-offs, or changes in community composition, phenology, or primary productivity (e.g. Honnay et al. 2002, Ciais et al. 2005, Inouye 2008, van Mantgem et al. 2009, Augspurger 2013). This has implications for ecosystem functioning and in

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some cases can trigger regime shifts to persistent, fundamentally different ecosystem states (e.g. Bennett et al. 2015). However, there is considerable uncertainty as to the conditions under which ecological disturbances trigger such shifts. In order to predict the occurrence of such shifts, it is first necessary to understand what influences resilience to disturbances.

Resilience is defined as the magnitude of disturbance an ecosystem can withstand without shifting into an alternate state (sensu Holling 1973). For clarity, we define disturbances as 'discrete, extreme events that substantially alter properties of an ecosystem,' while we define stressors as 'continuous or near continuous forces that can change ecosystem properties or prevent recovery of those properties.' Resilience can be broken down into 2 mechanisms: resistance to disturbance and recovery from disturbance (i.e. return time) (Unsworth et al. 2015). Resistance (sensu Carpenter et al. 2001) is the amount of external forcing required to change an ecosystem; ecosystems with higher resistance can withstand stronger forcing with no apparent change. When a disturbance occurs (i.e. resistance has been overcome and the ecosystem has changed), return time, defined as the time it takes for a system to recover from a disturbance (May 1973), becomes the critical mechanism of resilience in a system. Ecosystems that recover rapidly from one disturbance exhibit high stability and are more quickly able to resist subsequent forcing (Plus et al. 2003). It is therefore critical to understand not only how ecosystems respond to extreme events (resistance), but how they recover from them, particularly as climate disturbances become more frequent and the risk of exposure to sequential disturbances increases (Smale & Wernberg 2013, IPCC 2014).

Despite their importance as foundations of coastal ecosystems, seagrass habitats are declining at alarming rates, largely because of impacts from local stressors such as sedimentation and eutrophication (e.g. Short & Wyllie-Echeverria 1996, Waycott et al. 2009). Yet, even remote seagrass ecosystems far removed from local human influence can be vulnerable to large disturbance events such as marine heat waves (e.g. Fraser et al. 2014, Thomson et al. 2015). Such large events, which often cannot be managed at local scales, illustrate the danger climate change and altered thermal regimes pose to marine ecosystems, something already well appreciated by coral reef ecologists (e.g. Glynn 1993, Pandolfi 2015). While the potential for extreme climate events to generate widespread ecosystem shifts is becoming more recognized, many gaps still remain in understanding how ecosystems will respond to and recover from such events (Jentsch et al. 2007, Thomson et al. 2015).

Return time of damaged seagrass beds can range from months to centuries (e.g. Walker & McComb 1992, Plus et al. 2003, Orth et al. 2006, Short et al. 2014). Seagrass life history strategy, in part, heavily influences return time. Seagrass species possess a wide variety of life history traits and inhabit a continuum of successional capabilities, but can often be categorized as late or early successional species (sensu Bazzaz 1979). Late successional seagrasses, such as those in the genera *Amphibolis*, *Posidonia*, *Thalassia*, and *Zostera,* tend to have relatively large and perennial canopies, often with large stores of carbohydrates in their buried rhizome tissue. These energy stores can confer increased resistance to disturbances by providing the capability to rapidly refoliate and regenerate shoots from surviving rhizomes if an extreme event overcomes their initial resistance (e.g. Peterson et al. 2002, Fraser et al. 2014). However, if this initial recovery strategy fails (because of, for example, insufficient rhizome biomass or rhizome death triggered by the disturbance), rapid (<10 yr) return of these seagrasses to pre die-off abundance seems to be heavily dependent on the presence of a seed bank (Preen et al. 1995, Plus et al. 2003, Campbell & McKenzie 2004) or reproductive events from nearby beds (e.g. Larkum et al. 2006, Orth et al. 2006, Tanner 2015). This is because many larger, late successional seagrasses are characterized by excessively slow rhizome elongation rates (Walker et al. 2006), limiting the ability of vegetative expansion to lead recovery, particularly when seagrass loss is widespread. Importantly, many late successional seagrasses lack a dormant seed bank, and some genera, like *Amphibolis*, are viviparous and lack seeds altogether (Larkum et al. 2006). This further highlights how crucial regeneration from below-ground biomass and recruitment from nearby living beds are as mechanisms of rapid return time and resilience of late successional seagrasses.

Unlike late successional species, early successional (sensu Bazzaz 1979) seagrasses have adapted to disturbance through reliance on rapid disturbance recovery and expansion as opposed to resistance to disturbance itself (Unsworth et al. 2015). These species, such as those in the genera *Halophila* and *Halodule*, generally have small energy stores in rhizome tissue, instead relying on fast rhizome elongation rates and dormant seed banks to rapidly recruit and expand after disturbances (Walker et al. 2006). Early successional species also form relatively sparse and short beds, generally with much lower structural complexity and standing biomass than those composed of late successional seagrasses. The plant traits associated with early and late successional species not only influence the recovery trajectories of mixed seagrass beds, but the functions associated with these beds as they change. Because of this, it is important to understand how seagrass assemblages change throughout disturbance recovery so as to better understand not only resilience of the disturbed community, but also implications for ecosystem function.

In addition to life history, other factors like the extent of initial disturbance and local bio-physical and biological features can influence return times and seagrass community shifts throughout ecosystem recovery (i.e. recovery trajectories; Unsworth et al. 2015). Furthermore, density-dependent Allee effects associated with sediment stabilization and pollen limitation can generate feedbacks in disturbed seagrass ecosystems that alter the biological or biophysical features of the ecosystem, further complicating recovery predictions or promoting the maintenance of a seagrass-depauperate state (e.g. Fourqurean & Robblee 1999, van der Heide et al. 2007, Carr et al. 2010, van Tussenbroek et al. 2016). Short return times of functionally critical species can minimize the impacts of such density-dependent feedbacks in seagrass ecosystems and thus maximize the possibility of seagrass functional persistence, with implications for the wider seagrass-associated community.

The purpose of this work was to assess the post-disturbance dynamics of the relatively pristine subtropical seagrass ecosystem of Shark Bay, Western Australia, following a widespread marine heat wave that occurred in 2011 and triggered subsequent catastrophic seagrass loss. Specifically, our goals were to assess changes in cover and occurrence of benthic macrophytes (seagrasses and benthic macroalgae) over a medium time scale (3 yr), to better understand the return times and future disturbance resilience for functionally important seagrass species, and to explore potential implications of the observed post-disturbance state on ecosystem function and seagrass-associated fauna.

MATERIALS AND METHODS

Study system

This study was performed in the eastern gulf of Shark Bay (25° 45′ S, 113° 44′ E), Western Australia. Shark Bay is a shallow (<15 m), 13 000 km^2 semi-enclosed subtropical embayment situated approximately 800 km north of Perth. The study area, immediately north of Monkey Mia, consists of a series of near-shore shallow (<4 m) seagrass banks separated by deep (6–12 m) seagrass-depauperate channels (Heithaus 2001; Fig. 1). The bay historically contained over 4000 km^2 of seagrass (Walker et al. 1988), making it among the largest remaining seagrass eco-

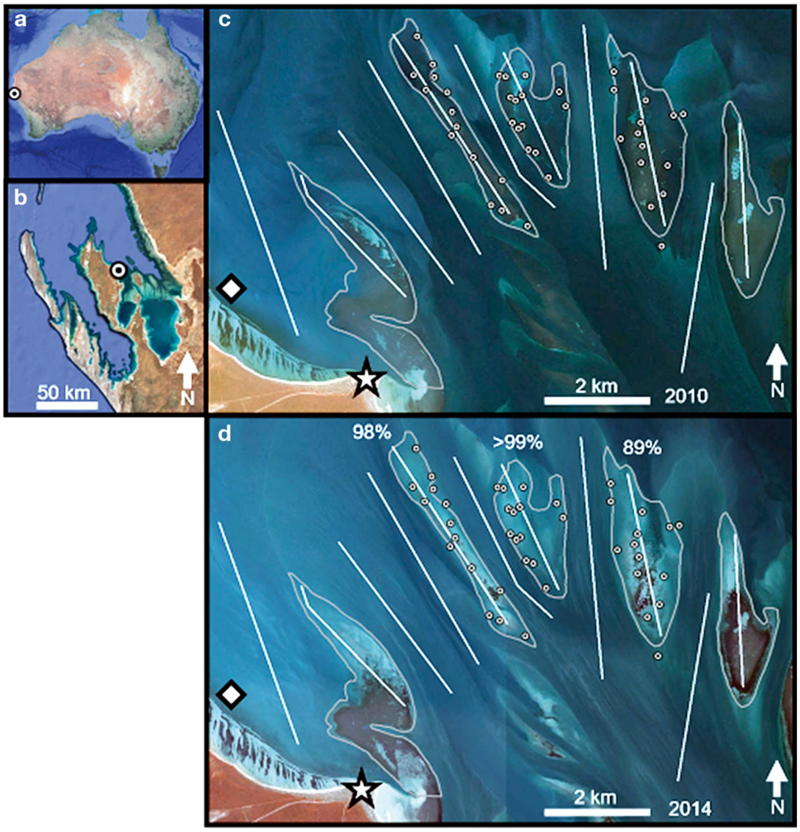

Fig. 1. Location of study area (a) within Australia and (b) the eastern gulf of Shark Bay. Study area (c) pre die-off (March 2010) and (d) post die-off (October 2014). Gray outlines denote the approximate borders of shallow seagrass banks which have been the focus of a long-term research project investigating the role of top-down control in Shark Bay. Dots in panels c and d mark locations of the 42 randomized sampling sites (deep sites excluded). White lines indicate established transects (5 shallow, 6 deep) on which water clarity was assessed. Numbers above banks in (d) describe the percentage of dense vegetation cover lost on that bank between 2010 and 2014, as estimated from the presented satellite imagery. Dark areas on banks are macrophyte cover, traditionally dominated by *Amphibolis antarctica*, while dark areas between banks denote deep water. The star and diamond denote the locations of Monkey Mia and the temperature monitoring station, respectively. Images: Google Earth

systems on earth. Shark Bay's expansive seagrass beds directly or indirectly support a wide variety of megafauna including dugongs *Dugong dugon*, green sea turtles *Chelonia mydas*, and tiger sharks *Galeocerdo cuvier*, a key feature of its status as a UNESCO World Heritage Area. Despite its large size, Shark Bay is almost completely undeveloped with a small human population and relatively few local and regional anthropogenic stressors (Western Australian Department of Environment and Conservation 2008).

Shark Bay hosts 12 species of seagrasses: 8 of tropical and 4 of temperate evolutionary origin (Walker et al. 1988). Of these, only 2 species form large, continuous beds: the temperate species *Amphibolis antarctica* and *Posidonia australis.* Shark Bay's seagrass assemblage has been historically dominated by *A. antarctica,* which accounted for approximately 85% of seagrass cover and often formed dense, monospecific stands of 90–100% cover (Walker et al. 1988, Burkholder et al. 2013a; Fig. 1 and see Fig. 3a.). Because of the height and density of *A. antarctica* beds (200–500 shoots m^{-2}, up to 2 m tall), this seagrass is a structurally complex ecosystem engineer (sensu Jones et al. 1994) that creates extensive benthic habitat, stabilizes sediment, and contributes significant primary production in this ecosystem (Walker 1985, Walker & McComb 1988).

As a subtropical seagrass ecosystem, Shark Bay marks the northern boundary for these temperate seagrasses (Walker et al. 1988). As a result, the seagrass ecosystem is at particular risk from both acute temperature extremes and chronic high temperature stress. One such acute event occurred off the coast of Western Australia in the austral summer of 2011, when ocean temperatures rose 2 to 4°C above average for a 2 mo period (Wernberg et al. 2013). This 'marine heat wave' was associated with almost record strength La Niña conditions and an unusually strong poleward flow of the Leeuwin current, resulting in increased delivery of tropical water down the coast of Western Australia and an extended thermal anomaly of 3.5°C in Shark Bay; typically, monthly temperature anomalies within the Leeuwin Current region are less than ±1.5°C during El Niño and La Niña years (Pearce & Feng 2013). This resulted in widespread changes in algae, fish, and coral communities throughout Western Australia (Pearce et al. 2011, Pearce & Feng 2013, Smale & Wernberg 2013, Wernberg et al. 2013). Following this heat wave, *A. antarctica* in Shark Bay experienced widespread declines in cover that exceeded 90% in many areas (Fraser et al. 2014, Thomson et al. 2015; Fig. 1c,d). A heat wave of this magnitude has not been recorded previously or since in Western Australian waters (Pearce & Feng 2013), and seagrass die-off of this magnitude has not been reported in Shark Bay before (e.g. Fig. 2b).

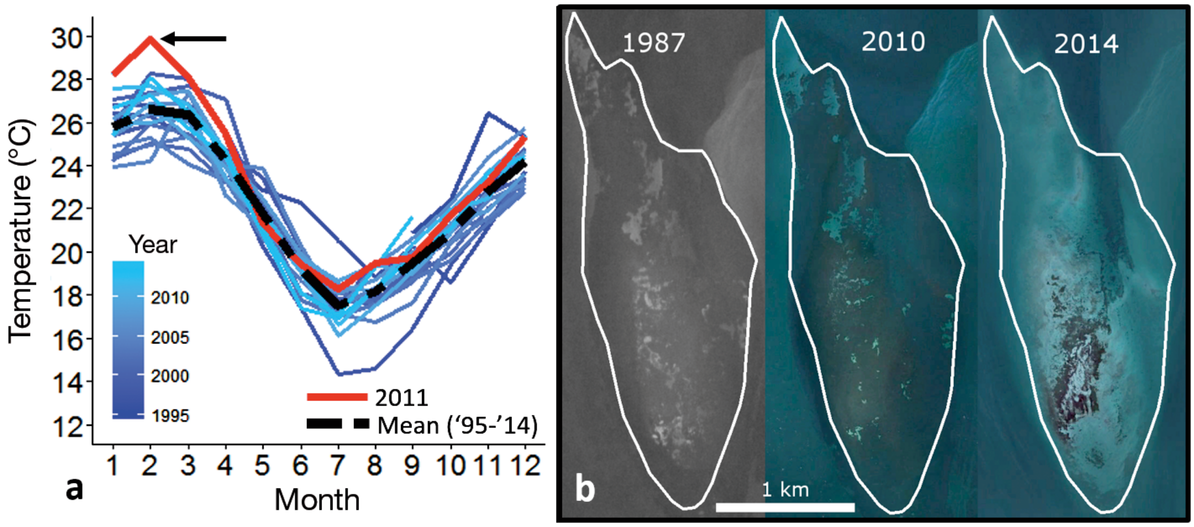

Fig. 2. Long-term data from *in situ* monitoring station illustrating the intensity of the 2011 heat wave and subsequent seagrass die-off. (a) Monthly (mean) water temperature for the study area. Note that mean water temperature for February 2011 (arrow) was 1°C higher than any other February since at least 1995 and 3.5°C above the long-term February average. The second-highest February temperature, in 2014, was associated with a widespread algal bloom in both gulfs of Shark Bay (D. Holley pers. comm., see Fig. 4). (b) Aerial imagery showing the magnitude of change in seagrass cover over decadal time scales compared to change after the heat wave. Anecdotal accounts from local fishermen suggest no seagrass die-off of this magnitude has occurred in the study area in recent history. Image: Google Earth

Sample collection and analysis

In 2007, 475 monitoring locations were established throughout Shark Bay as part of a larger benthic survey (see Burkholder et al. 2013a for details). A subset of these sites were revisited after the 2011 heat wave to assess associated seagrass die-offs (Thomson et al. 2015) and medium-term seagrass status and recovery (this study). Of the 475 original sites visited in 2007 to 2009, 63 were in a smaller, longer-term study area that had been established in 1997 (Heithaus et al. 2012). These sites were revisited 4 times between 2012 and 2014 to assess recovery and changes in the seagrass community. Sites occurred on 3 banks, which were blocked by microhabitat (deep channels generally 6 to 12 m depth, shallow bank interiors >2.5 m depth, and bank edges 2.5–4.5 m depth, Heithaus & Dill 2006). Site placement was randomized within each microhabitat for a total of 7 sites in each microhabitat of 3 banks/channels. The 21 sites in deep channel habitats remained seagrass-depauperate in all surveys and were thus excluded from analysis, leaving 42 sites analyzed. Depth of retained sites ranged from 0.6 to 7.3 m (mean = 2.8 m). At each site, a 60 × 60 cm quadrat was dropped from the research vessel, and percent cover of seagrass (to species) was visually estimated by a diver using either snorkel or SCUBA. The quadrat was then flipped end over end 3 times parallel to the heading of the boat, whereupon another quadrat measurement was taken; this process was repeated for a third quadrat and cover estimates were combined to calculate species richness and mean cover of each species at each site. To minimize observer bias, the majority of post die-off visits were performed by the same 2 individuals (the primary observers were R. J. Nowicki and J. A. Thomson). Furthermore, before collecting data, observers were trained to consistently estimate cover until they arrived at similar estimates to the primary observers, thereby minimizing the impact of observer bias on our results.

Sites were visited 5 times in 2007 (March, May, July, October, December), 4 times in 2008 (April, May, July, November), and once in 2009 (January) for a total of 10 pre die-off visits. These 10 visits, 6 during the warm season (mid-August to mid-May) and 4 during the cold season (mid-May to mid-August), were pooled into a single ‘pre die-off’ value for each site. The first post-heatwave sampling event, occurring 18 mo after the heat wave in October 2012, was considered to mark the end of the die-off event. Sites were visited 4 times after the die-off; October 2012 (warm), May 2013 (cold), October 2013 (warm), and August 2014 (cold). Following the die-off (with the exception of visit 2 in May 2013), benthic macroalgae were also quantified as a single functional group. Similarly, *Posidonia coriacea* was rarely encountered and was pooled with the more common *P. australis,* following previously established collection protocols (Burkholder et al. 2013a). Data were only analyzed for *A. antarctica*, *Halodule uninervis*, and benthic macroalgae; other species were rarely encountered. For each species analyzed, percent occurrence (i.e. percent of sites where that species was present), mean cover when present (i.e. mean percent cover only including sites where that species was present), and mean cover overall (i.e. mean percent cover including all 42 sites) were recorded. When considered together, these 3 metrics provide insight into not only the magnitude, but also the way in which seagrass cover changes. For example, loss of overall cover due to bed thinning results in reductions of mean cover when present, but little or no change in occurrence; conversely, patchy seagrass loss is characterized by little change in mean cover when present, but substantial reductions in occurrence.

In addition to seagrass surveys, changes in the biophysical environment (water temperature, clarity, and salinity) were measured. Water temperature was collected daily at a long-term monitoring station situated in 4 m of water, 3 km NW of Monkey Mia (Fig. 1), from September 1995 to September 2014. Daily estimates were converted to monthly averages (Fig. 2a). Salinity was measured with a refractometer during visits to each seagrass sampling site within the study area. Water clarity was measured indirectly within the study area as bottom visibility when running transect surveys for air-breathing fauna were conducted for a related study. These transects were established in deep habitats (n = 6) or shallow seagrass banks (n = 5) in 1997. Approximately 4 times monthly, transects were run to quantify densities of air-breathing fauna; every time an animal was sighted, depth was recorded and bottom composition was observed from the surface (see Heithaus et al. 2012 for methodological details). Cover data were converted to a binomial variable (1 = bottom visible, 0 = bottom not visible) for analysis. Because transect surveys only occurred under calm conditions (Beaufort scale ≤3), wind conditions are unlikely to have driven the observed patterns of bottom visibility. Due to variability in the way null results were recorded prior to 2008, only data from 2008 to 2014 were included for visibility analysis. Transects run between November and January were also excluded because of generally low sampling effort during these months, and transects run during 2011 were excluded to allow for clear separation of time periods.

Statistical analyses

All statistical analyses were performed in R v.3.2 (R Core Team 2015). Diversity for each visit was calculated using the probability of interspecific encounter (i.e. 1 − the Simpson diversity index, Hurlbert 1971). Because individual seagrass genets could not be differentiated and because seagrasses are often highly clonal, the presence of a species at a site was interpreted as the presence of a single individual. A 1-way repeated measures ANOVA was applied on species richness data to assess changes in richness between 2012 and 2014.

One-way repeated-measures ANOVAs on rank-transformed data were performed on mean cover data of *A. antarctica, H. uninervis* and benthic macroalgae for all 42 sites for each of the 4 post die-off visits (3 for algae). All ANOVAs were run using the 'lme' function in the nlme package (Pinheiro et al. 2016). Additionally, generalized linear mixed models (GLMMs) were used to detect changes in the probability of encountering *A. antarctica, H. uninervis,* and macroalgae in the study area from 2012 to 2014. These models were run as logistic regressions on binomially transformed data using the 'glmmPQL' function in the MASS package (Venables & Ripley 2002). Since the extent of tropical *H. uninervis* can vary seasonally, the *H. uninervis* model included season (warm, cool) and visit number (1–4) as discrete fixed effects, while visit number was the only fixed effect in the *A. antarctica* and macroalgae models. Sampling site was included as a random effect to account for repeated visits.

Water clarity analysis

Bottom visibility (a proxy for water clarity) was converted to a binomial variable (1 = bottom visible from surface, 0 = not visible) and modeled using a logistic regression with the glmmPQL function. Because deep transects were too deep to regularly see the bottom in either time period (see 'Results: Biophysical factors'), only data from shallow transects were included in the model. Fixed effects in the visibility model were depth, time period, and their interaction; transect identity was included as a random effect in the model to account for repeated visits to each transect. A significant ($p \leq 0.05$) interaction of depth and time period on visibility of substrate was interpreted as a change in water clarity since the seagrass die-off.

RESULTS

Average seagrass richness after the die-off did not change over time ($F_{1,125} = 1.98$, $p = 0.16$), though there was a trend of increasing species diversity (Table 1). In total, 7 seagrass species were encountered in surveys of shallow and edge sites from 2012 to 2014 (Table 2). *Amphibolis antarctica* was the only seagrass commonly encountered after the die-off, but at much reduced cover than previously (Table 2, Fig. 3a); indeed, while occurrence decreased from 83% pre die-off to ~60% post die-off, declines in cover were largely driven by dramatic thinning of remaining seagrasses, as evidenced by large reductions in 'cover when present' (Table 2, Figs. 3a & 4a,b). Between 2012 and 2014, overall *A. antarctica* cover remained stable ($F_{1,125} = 3.16$, $p = 0.08$), as did the probability of encountering *A. antarctica* (presence/absence, $t_{124} = 0.95$, $p = 0.34$). Widespread blackening and mortality of *A. antarctica* rhizomes was observed in 2013 (Fig. 4b,c), followed by breakup of beds and transition to bare sand in many habitats by 2014 (Figs. 1d & 4d).

The only seagrass species that showed significant evidence of expansion after the die-off was *Halodule uninervis.* The logistic regression model indicated an increased probability of encountering *H. uninervis* with time ($t_{124} = 6.94$, $p < 0.0001$), an effect that did not change seasonally ($t_{124} = 0.28$, $p = 0.78$, Fig. 3b). *H. uninervis* occurrence increased from 2% of visits

Table 1. Seagrass diversity and species richness over time in Shark Bay, Western Australia. Pre die-off values are pooled. Diversity values are expressed as $(1 - \lambda)$, where λ is Simpson's diversity index (Hurlbert 1971), and range from 0 (no diversity) to 1 (maximum diversity). Values are presented with standard error when appropriate

	2007–2009 (10 visits)	2012	May 2013	Oct 2013	2014
Diversity	0.44 ± 0.03	0.43	0.43	0.55	0.59
Richness	1.14 ± 0.02	0.86 ± 0.10	0.76 ± 0.10	1.02 ± 0.10	0.95 ± 0.12

Table 2. Percent occurrence (percent of visits where that species was present), mean cover when present (i.e. mean percent cover only including sites where that species was present), and mean cover overall (i.e. mean percent cover including all 42 sites of seagrass and macroalgae). Values are presented with standard error when applicable. Data include bank and bank edge sites only (n = 42 sites); data from the 2 visits in 2013 are pooled. na: not applicable; –: no data collected

Species	% occurrence				Mean cover (when present) (%)				Mean cover overall (%)			
	2007–2009	2012	2013	2014	2007–2009	2012	2013	2014	2007–2009	2012	2013	2014
Amphibolis antarctica	83	64	62	55	89.5 ± 1.2	4.8 ± 0.9	6.3 ± 1.0	3.8 ± 0.9	75.5 ± 1.9	3.1 ± 0.7	3.9 ± 0.7	2.1 ± 0.6
Posidonia sp.	10	7	7	5	39.5 ± 5.6	5.2 ± 4.9	12.6 ± 7.2	8.4 ± 3.4	3.3 ± 0.7	0.4 ± 0.4	0.9 ± 0.6	0.4 ± 0.3
Halodule uninervis	12	2	12	29	3.1 ± 0.5	1	7.7 ± 5.6	8.5 ± 2.6	0.3 ± 0.1	<0.1	0.9 ± 0.7	2.4 ± 0.9
Halophila ovalis	2	2	2	0	2.5 ± 0.8	1	1.2 ± 0.5	na	<0.1	<0.1	<0.1	0
Halophila spinulosa	2	0	0	2	24.3 ± 8.8	na	na	0.3	0.6 ± 0.3	0	0	<0.1
Cymodocea angustata	7	10	7	5	8.3 ± 1.3	4.2 ± 2.2	5.7 ± 1.9	2.3 ± 1	0.6 ± 0.1	0.4 ± 0.3	0.3 ± 0.2	0.1 ± 0.1
Benthic macroalgae	na	71	48	62	–	14.1 ± 2.7	10.4 ± 3.2	2.9 ± 0.9	–	10.0 ± 2.1	5.2 ± 1.8	1.7 ± 0.6

in 2012 to 29% of visits by 2014, and overall cover also increased significantly with time ($F_{1,125}$ = 23.64, p < 0.0001, Table 2, Figs. 3b & 4f). Other seagrass species (*Posidonia* spp., *Halophila ovalis, H. spinulosa*, and *Cymodocea angustata*) were rarely encountered (Table 2).

Macroalgae cover

Though macroalgae cover was not quantified using the described methods before 2012, several lines of evidence indicate it was at most a minor contributor to submerged aquatic vegetation (SAV) cover in the past. Firstly, *A. antarctica* dominates cover surveys from 2007 to 2009 (Fig. 3a), leaving little room for substantial coverage by other SAV. Secondly, analysis of *A. antarctica* habitats by animal-borne video cameras attached to green turtles before the heat wave (1999–2003) indicate that benthic macroalgae were historically a very minor cover component in the study system, becoming common only after the seagrass die-off (Thomson et al. 2015). Finally, benthic macroalgae were rarely encountered by divers as a substantial component of SAV in the study area prior to the heat wave (D. A. Burkholder and J. A. Thomson pers. obs). Following the seagrass die-off, macroalgae were common but very sparse at sampling sites, as evidenced by high levels of occurrence but relatively low cover when present (Table 2, Fig. 3c). Mean overall cover of benthic macroalgae declined over time ($F_{1,83}$ = 26.7, p < 0.0001), as did the probability of encountering it at a given site (t_{83} = 2.00, p = 0.048, Table 2, Fig. 3c).

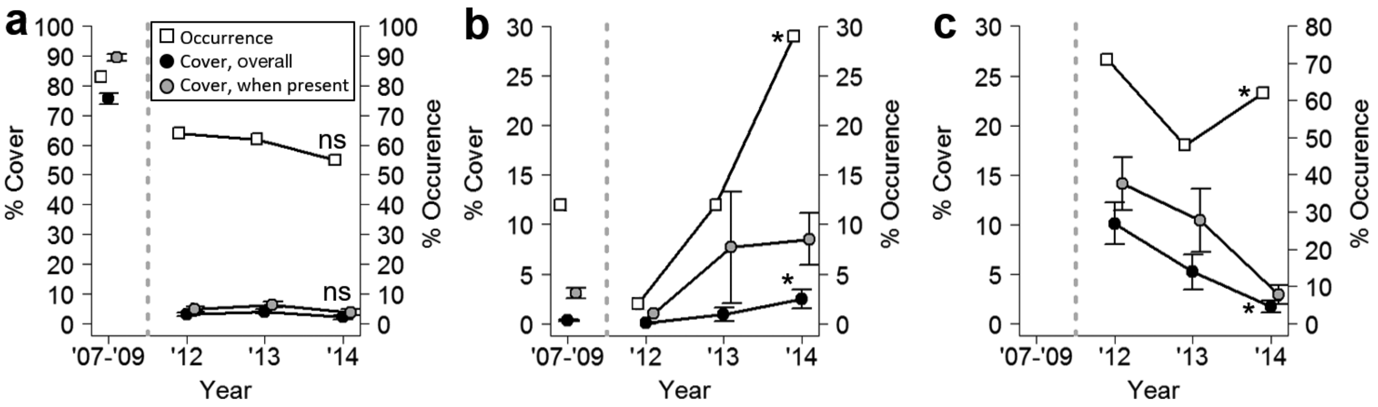

Fig. 3. Change in mean occurrence, mean cover when present, and mean cover overall for the 3 dominant macrophytes in Shark Bay following the heat wave: (a) *Amphibolis antarctica*, (b) *Halodule uninervis*, and (c) benthic macroalgae. Pre die-off values (left of dotted line) are provided when available for reference but are not included in analysis. Data from the 2 visits in 2013 are pooled for consistency with Table 2. Note different scale of *y*-axes in different graphs. Error bars = SE; ns = no significant change; *significant change at p < 0.05 level

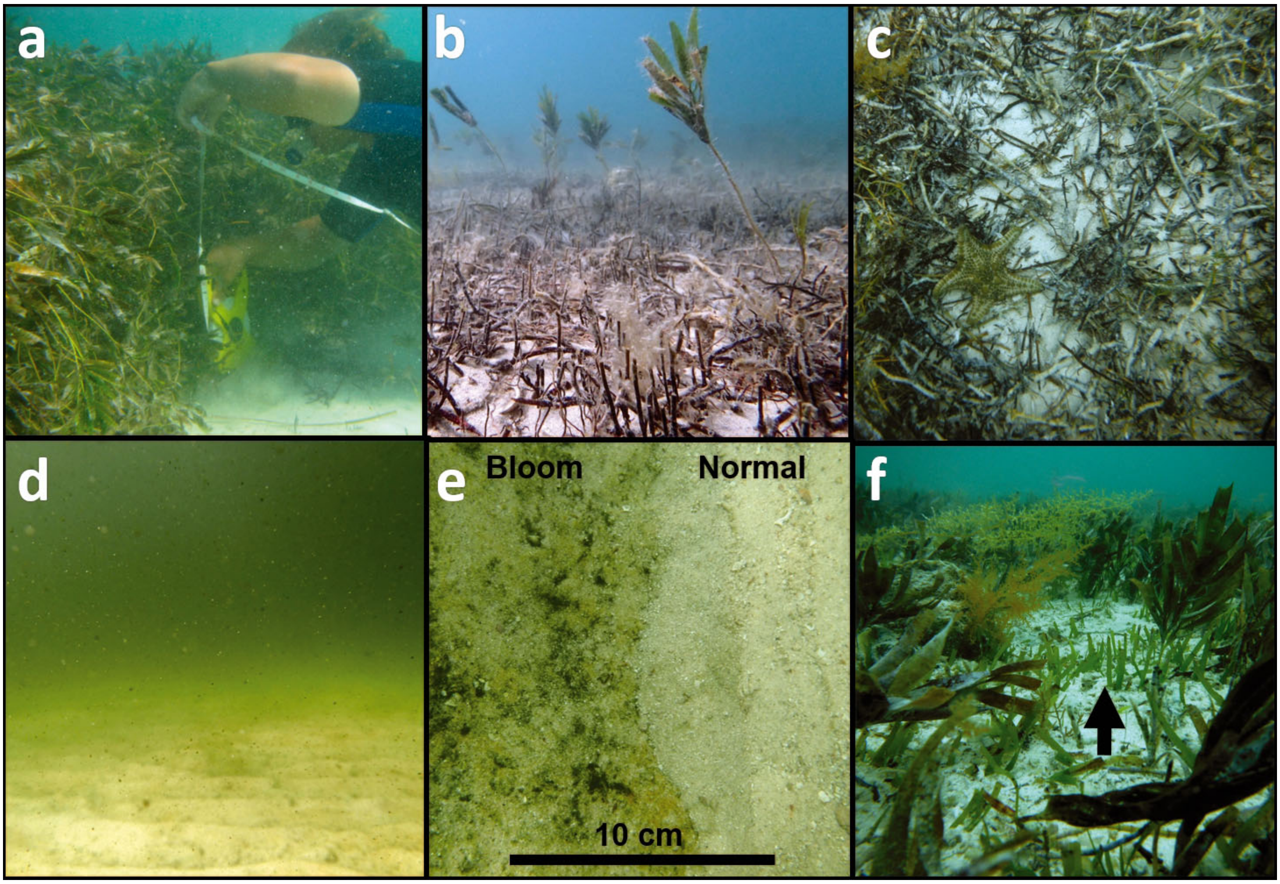

Fig. 4. States of beds of *Amphibolis antarctica* before and after seagrass die-off. (a) Before the heat wave, large, contiguous beds of *A. antarctica* were the most common form of seagrass cover in the study area. (b) After the heat wave, most cover was lost, as were (c) rhizome mats, which began to disintegrate. A phytoplankton bloom in 2014 severely reduced light available to these beds as phytoplankton (d) clouded the water column and (e) covered the benthos. (f) Since 2012, early successional tropical seagrasses such as *Halodule uninervis* (black arrow) have begun expanding into the space left by *A. antarctica*, resulting in a matrix of temperate and tropical seagrasses in some areas. Images: Shark Bay Ecosystem Research Project (SBERP)

Biophysical factors

Water temperatures for February, the warmest month of the year, averaged 26.6°C over the time series, while water temperatures for July, the coldest month, averaged 17.5°C. Monthly averages derived from the time series indicate that the extreme heat wave of 2011, in which surface water temperature averaged 29.8°C in the month of February, has not been repeated (Fig. 2a). In only 2 other years were average February water temperatures within even 2°C of the February 2011 average: 1999 and 2014 (28.3°C and 28.0°C, respectively), illustrating the abnormal magnitude of the heat wave within the study system. Surface water salinity increased significantly from 38.1 ppt (SD = 3.7, n = 418) pre die-off to 40.3 ppt post die-off (SD = 1.9, n = 143, $t_{472.59}$ = 8.85, p < 0.0001), largely driven by relatively high salinity measurements during the 6 d sampling period in August 2014 sampling (mean = 42.1 ppt, *s* = 0.7). Water clarity, as measured by the likelihood of sighting bottom at a given depth, decreased significantly after the seagrass die-off as evidenced by 3750 benthic spot surveys. The probability of being able to see bottom on shallow transects was significantly influenced by the interaction of depth and time period (t_{3738} = 2.41, p = 0.016, Table 3). The percentage of spot surveys on shallow transects in which bottom was observable declined from 97.6% pre die-off (1463 of 1499 surveys) to 68.4% post die-off (1540 of 2251 visits), while chances of sighting bottom in deep habitats remained very low in both time periods (2.0 and 1.3%, Table 4). On average, the depth at which there is a 50% probability of seeing the bottom was reduced from 6.45 m pre die-off to 3.15 m post die-off (Fig. 5).

Table 3. Logistic model results on the impact of depth, time period, and their interaction on probability of being able to identify bottom cover on shallow seagrass banks. Transect identity was included as a random effect to account for repeated visits to each transect. A significant interaction of depth and time period indicates that the influence of depth on probability of sighting bottom has changed since the seagrass die-off (i.e. that water visibility has gotten significantly worse)

Factor	Coefficient	SE	df	*t*	p
Time period	2.00	0.52	3738	3.81	<0.001
Depth	−1.35	0.08	3738	17.77	<0.0001
Time period × Depth	0.38	0.16	3738	2.41	0.016

Table 4. Number of spot surveys conducted and number of surveys in which the bottom was visible from the surface for deep and shallow habitats before and after the seagrass die-off

Time period	Habitat	Bottom surveys (n)	Bottom sightings (n)	Probability of sighting bottom
2008– 2010	Shallow	1499	1463	0.976
	Deep	1024	20	0.02
2012– 2014	Shallow	2251	1540	0.684
	Deep	1199	16	0.013

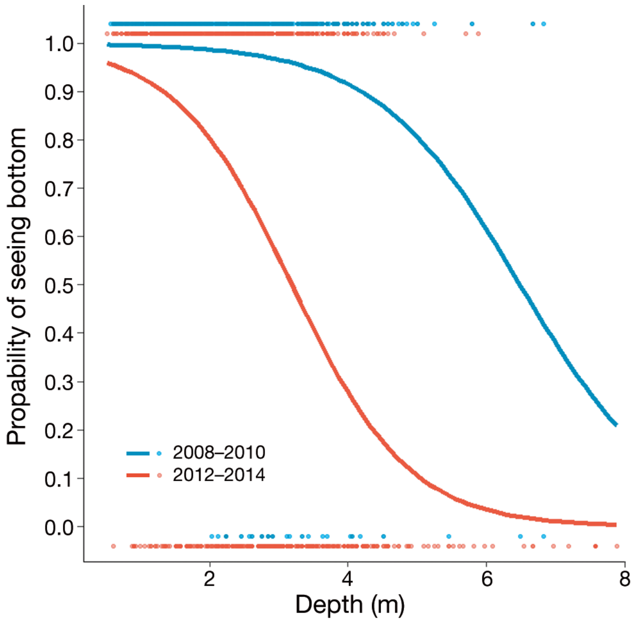

Fig. 5. Logistic regression illustrating significantly reduced water clarity after the seagrass die-off in shallow habitats (t_{3738} = 2.41, p = 0.016). Points (individual sampling events) and trends (regression lines) intentionally jittered on *y*-axis

In addition to chronic reductions in water clarity following the seagrass die-off, a widespread and intense phytoplankton bloom was observed in both gulfs of Shark Bay from February to April 2014, potentially facilitated by sustained high February water temperatures of 28°C (2.3°C above the February average and the second warmest February after 2011 in at least 20 yr, Fig. 2a) and the putative release of nutrients from abundant decaying seagrass tissue (D. Holley pers. comm.). Though not quantified, the bloom had acute but sustained impacts on water quality and clarity; specifically, substantial increase in light attenuation for several weeks (e.g. Fig. 4b vs. 4d, D. Holley pers. comm.), as well as a uniform coating of flocculent matter on the benthos (Fig. 4e).

DISCUSSION

Our results indicate that, over a medium time scale (~3 yr) following an extreme climate event, significant recovery of the previously dominant temperate seagrass *Amphibolis antarctica* has not occurred in Shark Bay. Similarly, although macroalgae can exhibit rapid growth rates and outcompete seagrasses (McGlathery 2001), benthic macroalgae cover declined significantly between 2012 and 2014, indicating that a shift from seagrass to macroalgae dominance is unlikely in the study system. Instead, despite an initial decline likely resulting from smothering by dead *A. antarctica* (Thomson et al. 2015), the tropical early successional seagrass *Halodule uninervis* has expanded following the marine heat wave. This is generally consistent with the life history characteristics of *H. uninervis,* which has rapid rates of rhizome expansion and a dormant seed bank, something which *A. antarctica* lacks (Larkum et al. 2006, Orth et al. 2007). Indeed, patterns of *H. uninervis* expansion described here follow patterns seen in other mixed-*Halodule* spp. systems subject to disturbance, such as *H. uninervis* in Malaysia (Short et al. 2014) and *H. wrightii* in seagrass beds in Florida Bay usually dominated by *Thalassia testudinum* or *Syringodium filiforme* (Robblee et al. 1991, Fourqurean & Robblee 1999, Peterson et al. 2002). The lack of recovery of the late successional *A. antarctica* reflects the post-disturbance behavior of some, but not all, seagrass ecosystems dominated by late successional species (see below). A significant and sustained reduction in water clarity in the years following the seagrass die-off is consistent with a loss of sediment stabilization, an ecosystem function characteristic of intact seagrass beds (Carr et al. 2010, van der Heide et al. 2011). Additionally, the occurrence of a widespread phytoplankton bloom in 2014 is consistent with blooms observed elsewhere following widespread seagrass declines (e.g. Fourqurean & Robblee 1999). Such changes to the biophysical environment, along with seagrass species features (e.g. life history characteristics) and biological features (e.g. connectivity, community trophic structure; Unsworth et al. 2015) have the potential to restrict or inhibit a return to an *A. antarctica*-dominated ecosystem and impact the resilience of this system. The observed shift in the seagrass community has both biophysical and ecological implications.

Rapid recovery of *Amphibolis* spp. in other systems

Although the traits common in late successional seagrasses generally do not favor rapid vegetative expansion or robust reproductive resilience to widespread seagrass loss, rapid recovery of *Amphibolis* spp. is possible if either of the resilience mechanisms mentioned previously (regeneration from rhizomes or recruitment from nearby beds) is successful. For example, *A. antarctica* near the Wooramel delta in Shark Bay (east of this study site) began to refoliate 2 yr after the die-off through use of below-ground energy stores (Fraser et al. 2014, Thomson et al. 2015). On Success Bank, Western Australia, the congener *A. griffithi* is recorded as expanding rapidly (17.6 ha yr^{-1}), partially because of reproduction and gap infilling from nearby beds (Walker et al. 2006). Similarly, in South Australia, a restoration project which provided anchoring points in close proximity (<80 m) to mature *A. antarctica* beds resulted in the establishment of new beds with similar structural characteristics to mature beds within 3 yr (Tanner 2015). Importantly, until below-ground biomass stocks are replenished, merely measuring above-ground biomass of recovering beds may overestimate ecological resilience to future disturbance because the below-ground biomass responsible for resilience is reduced, either because it was spent on rapid recovery or because new recruits have not yet established substantial below-ground stores.

Potential mechanisms of rapid recovery

Although the resilience strategies of *A. antarctica* allow for rapid recovery of above-ground biomass in some cases (e.g. Walker et al. 2006, Fraser et al. 2014), no such recovery occurred in this study. The capability of *A. antarctica* meadows to recover through rhizome regeneration as observed on the Wooramel delta (Fraser et al. 2014) is limited here. This is because the widespread observed death of *A. antarcticas*'s rhizome layer in this study (Fig. 4b,c; see also Thomson et al. 2015) has resulted in large areas of bare sand with no below-ground biomass from which to regenerate. The loss of rhizomes also likely reduced suitable substratum for macroalgae, potentially explaining the continued decline in macroalgae cover. Unlike Success Bank, the magnitude of the initial die-off destroyed or damaged entire seagrass banks (Figs. 1d & 2b), increasing the distance between surviving shoots and potentially inhibiting reproductive capacity through mechanisms such as pollen limitation (e.g. van Tussenbroek et al. 2016). Although formal surveying of *A. antarctica* propagules, seedlings, and reproductive structures was outside scope of this work, signs of sexual reproduction were not apparent during work in these beds between 2012 and 2015 (R. J. Nowicki pers. obs). Importantly, unlike other biophysical feedback loops (i.e. turbidity) which may become less severe if environmental conditions improve, reproductive Allee affects will remain unless plant density itself is restored (van Tussenbroek et al. 2016). Such density-dependence may strengthen continued divergence in post-disturbance cover of *A. antarctica* and *H. uninervis*, as the seed bank of the latter allows for the establishment of widespread new beds, facilitating future reproductive success.

Because the resilience mechanisms that would allow for rapid recovery of *A. antarctica* are unlikely at our study site, vegetative expansion from remaining shoots may now be the most likely mechanism of recovery. Like many late successional seagrasses, *A. antarctica* has slow rhizome elongation rates (20 cm yr^{-1}), i.e. one-fifth that of *H. uninervis* (Marbà & Duarte 1998), meaning the return time of *A. antarctica* will be considerable. This not only increases the vulnerability of *A. antarctica* to future extreme climate events but also means that bio-physical and biological features of the environment (sensu Unsworth et al. 2015) are more likely to play critical roles in determining whether a meaningful recovery of *A. antarctica* will occur in this system at all.

Biophysical factors influencing recovery

In addition to seagrass traits, bio-physical features of the environment (sensu Unsworth et al. 2015) may be particularly critical to mediating the recovery trajectory of seagrasses in Shark Bay. While common anthropogenic alterations to bio-physical features, such as eutrophication, are largely absent in Shark Bay, density-dependent biophysical processes, plankton blooms, and future climate extremes may all be important to shaping recovery trajectories for this system. Seagrasses have high light requirements (Walker & McComb 1992, Dennison et al. 1993) and are well known for their density-dependent capability to trap sediment and increase water clarity. These processes generate positive feedbacks that facilitate seagrass expansion at high seagrass densities, but as seagrass is lost, turbidity increases and light limitation can inhibit the recovery of damaged beds (van der Heide et al. 2007, Carr et al. 2010). In Shark Bay, areas with reduced water clarity appeared to suffer greater declines in response to the initial disturbance (Fraser et al. 2014, Thomson et al. 2015), and water clarity in the study system was significantly reduced in the years following the seagrass die-off (Tables 3 & 4, Fig. 5), suggesting that water clarity reductions may be a strong inhibitor to seagrass recovery in this system. In addition to resulting in a loss of sediment stabilization potential, seagrass losses can also result in nutrient export to the water column, triggering phytoplankton blooms that further reduce water clarity. For example, plankton blooms resulting from an extreme climate event and subsequent seagrass die-off in Florida Bay impacted the local light environment for close to a decade following the initial event, and may have contributed to subsequent seagrass die-offs (Robblee et al. 1991, Fourqurean & Robblee 1999). The significant reduction in water clarity following the seagrass die-off and observed widespread phytoplankton bloom in Shark Bay (despite minimal nutrient runoff) demonstrates the importance of bio-physical features of post-disturbance seagrass ecosystems, even when local anthropogenic impacts to water clarity are minimal.

Salinity of surface waters increased significantly by approximately 2.2 ppt between 2007–2009 and 2012–2014. The drivers of this salinity change are unclear. Shark Bay is only subject to sporadic riverine input, so a reduction in freshwater flow cannot account for the increased salinity. However, this increase in salinity is unlikely to be ecologically significant, as salinity can vary more than twice this amount within the study system in a 24 h period (R. J. Nowicki unpubl. data). Furthermore, salinities measured here remain within historical ranges for the study system (Walker 1985). Finally, although salinity can affect the growth and biology of seagrasses, both *A. antarctica* and *H. uninervis* are commonly found within more interior portions of Shark Bay where salinities regularly exceed 50 ppt (Walker 1985, Burkholder et al. 2013a).

The role of future climate events is also likely to play an increasingly important role in recovery trajectories of disturbed seagrass ecosystems as extreme El Niño and La Niña events become more frequent (Cai et al. 2014, 2015). However, the likelihood of extreme warm events is not spatially homogenous: regions characterized by tropical boundary currents (such as Western Australia) are projected to warm 2 to 3 times faster than the oceanic average (Wu et al. 2012, Vergés et al. 2014). Furthermore, areas where dominant seagrasses are near their temperature thresholds, such as Shark Bay, which sits in a climate transition zone between temperate and tropical regimes, are more likely to be impacted by future acute and chronic warming (Unsworth et al. 2015). Indeed, as gradual warming creates an increasingly hostile biophysical environment for temperate seagrasses at the warm end of their thermal tolerance, local extirpation of temperate species such as *A. antarctica* from Shark Bay may be expected over decadal to centurial scales (Hyndes et al. 2016). Such subtropical regions may be particularly vulnerable to community shifts towards dominance by fast-growing tropical seagrasses because they host a mixed assemblage of temperate late successional and tropical early successional species. Understanding the resilience of late successional seagrasses to climate extremes via resistance, return time, and the mechanisms responsible for each will be critical to determining where and when these foundation species will persist.

Biological factors influencing recovery

Alteration of biological features such as top-down control can also be an important driver of return time following disturbance (Unsworth et al. 2015). While historically underappreciated, top-down control by herbivores (and indirectly by their predators) can structure seagrass ecosystems through both facultative and destructive pathways (Nowicki et al. in press). Top-down control by herbivores and their predators influences multiple facets of Shark Bay's seagrass community (Burkholder et al. 2013b), and immigration by novel, tropical herbivores in the future may strengthen consumer control further (e.g. Hyndes et al. 2016). Generally, the importance of top-down control may be high in recovering seagrass ecosystems as herbivores struggle to meet metabolic demands and newly disturbed seagrasses invest in regrowth and regeneration (e.g. Fraser et al. 2014). Top-down control by herbivores is also predicted to become more important to warming subtropical seagrass ecosystems (like Shark Bay), as tropical herbivores such as parrotfish become more able to withstand local thermal regimes (Hyndes et al. 2016). In Shark Bay, food preference experiments indicate that *H. uninervis* is grazed at higher rates and more often than either *A. antarctica* or *Posidonia australis* (both late successional seagrasses, Burkholder et al. 2012), suggesting that increases in top-down control may favor a return of an *A. antarctica*-dominated state by inhibiting expansion of *H. uninervis*. However, the ultimate effect of such herbivory on seagrass return time will depend an interaction between biological features of herbivores (herbivore density, feeding preferences, and feeding tactics) and those of seagrass (nutrient content, grazing tolerance, grazing recovery speed). For example, while tropical early successional seagrasses are often more palatable to (and preferred by) herbivores than late-successional species (Preen 1995, Armitage & Fourqurean 2006, Burkholder et al. 2012, Bourque & Fourqurean 2013, Nowicki et al. in press), the former can also recover quickly from grazing (e.g. Preen 1995). This may shift community composition in favor of early successional seagrasses when they form mixed beds with late successional species, especially if herbivores employ indiscriminate destructive feeding strategies that destroy all seagrasses present, such as grazing fronts by sea urchins or excavation foraging by dugongs (e.g. Preen 1995, Peterson et al. 2002).

In addition to being altered by consumers, the return time of *A. antarctica* could be accelerated by *H. uninervis.* It is possible that expansion of *H. uninervis* may alter the biophysical environment or provide ecosystem functions that could facilitate the regrowth of *A. antarctica*, such as stabilization of sediment (Fonseca & Fisher 1986) or facilitation of attachment for the barbs of *A. antarctica* seedlings (Turner 1983). However, the small size of *H. uninervis* shoots suggests the potential magnitude of such facilitation is likely to be minor.

Ecological implications of extended return time

Complete loss of foundation species has clear implications for ecosystem recovery and community functions. However, multi-species foundation species assemblages can generate more nuanced responses via disturbance-induced changes in assemblage composition. These shifts, which may be driven proximally by differences in return time or environmental tolerance and ultimately by life history traits and ecosystem features, can result in changes to ecosystem function even when seagrass cover per se has recovered. For Shark Bay, increases in *H. uninervis* and losses of *A. antarctica* have led to increased species diversity through increases in species evenness, even as richness has remained relatively constant. This expansion of *H. uninervis*, and increase in diversity, however, does not indicate a functional recovery for this system. *A. antarctica* exceeds the size, standing stock, and productivity of *H. uninervis* by 1 or more orders of magnitude (Walker 1985, Walker et al. 1988). As such, *H. uninervis* is unlikely to be able to provide the same magnitude of ecosystem function as the much larger *A. antarctica*, such as the generation of large amounts of structurally complex habitat (Borowitzka et al. 2006) or primary production (Walker 1985), provision of food through facilitation of epiphytes (Borowitzka et al. 2006), sediment accumulation (Fonseca & Fisher 1986), or carbon storage (Fourqurean et al. 2012).

While some functional losses (such as loss of primary production) may be relatively straightforward to calculate, the ecological implications for consumers can be particularly complex and difficult to predict. For example, seagrass loss will almost certainly reduce food supplies for species that directly feed on seagrass or its epiphyte community, but may result in a temporary prey pulse for predators that consume animals that use seagrass as a refuge. Similarly, resource loss can result in either expansion or restriction of a species' trophic niche (Jones & Post 2016), which may lead to trophic restructuring and changes in top-down control. In Shark Bay, expansions of *H. uninervis* and losses of *A. antarctica* and associated epiphytes are likely to lead to shifts in resource availability and utilization, which may result in lowered standing biomass of algae and tropical seagrasses, even if primary production is high. This may also have implications for residency, movement, or behavior of consumers as they deal with a changing seascape of food availability, refuge, and predation. While investigations into the effects of seagrass die-offs on specific seagrass-associated fauna are not uncommon, relatively little is known about whether or how such declines alter species interactions at the community level — an important gap given the magnitude of global seagrass loss and the importance of species interactions to structuring ecosystems.

The results presented in this study, together with the findings in other studies, i.e. rhizome elongation rates (Marbà & Duarte 1998), loss of sediment stabilization potential, and thermal vulnerability (Walker & Cambridge 1995) of *A. antartcica* suggests that

Shark Bay's mixed seagrass community is changing to reflect a shift to tropical seagrass, and that any return to a state dominated by *A. antarctica* is likely to be lengthy and tenuous. During this time, *A. antarctica* will be vulnerable to subsequent disturbance from future climate extremes, changes in biophysical features, and alteration of biological features such as top-down control. More generally, this work suggests that predicting the recovery trajectory of seagrass ecosystems based only on initial magnitude of decline may be difficult, especially in mixed-species beds where life history strategies and mechanisms of recovery differ. Knowledge of the life history of the species of interest (particularly likely mechanisms of recovery) and repeated post-disturbance monitoring is necessary to assess whether such recovery mechanisms are successful in facilitating recovery in the short term. Integration of studies such as this into a general framework for resilience will be vital to predicting how vulnerable marine communities (and the functions they provide) will change in the context of climate change.

Acknowledgements. Thanks to R. Sarabia, J. Olson, A. Macy, A. Morgan, K. Gastrich, J. Johnson, N. Norton, M. Jew, T. Code, C. Morgan, and H. Neutzel for aid in data collection. We also thank the Staff of Monkey Mia Dolphin Resort and Dave Holley at Department of Parks and Wildlife WA for considerable logistical support and Blue Lagoon Pearls for access to their temperature records. R.J.N. was supported by NSF GRF No. DGE-1038321. Research support was provided by NSF grants OCE0745606 and OCE1329408. Special thanks to R. Sarabia, D. Churchill, and C. Cáceres for reviewing earlier versions of the manuscript. This is contribution No. 84 to the Shark Bay Ecosystem Research Project and No. 23 to the Marine Education and Research Initiative of the Institute for Water and the Environment at FIU.

LITERATURE CITED

Armitage AR, Fourqurean JW (2006) The short-term influence of herbivory near patch reefs varies between seagrass species. J Exp Mar Biol Ecol 339:65–74

Augspurger CK (2013) Reconstructing patterns of temperature, phenology, and frost damage over 124 years: Spring damage risk is increasing. Ecology 94:41–50

Bazzaz FA (1979) The physiological ecology of plant succession. Annu Rev Ecol Syst 10:351–371

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

Borowitzka M, Lavery P, van Keulen M (2006) Epiphytes of seagrasses. In: Larkum A, Orth R, Duarte C (eds) Seagrasses: biology, ecology, and conservation. Springer, Dordrecht, p 441–461

Bourque AS, Fourqurean JW (2013) Variability in herbivory in subtropical seagrass ecosystems and implications for seagrass transplanting. J Exp Mar Biol Ecol 445:29–37

Burkholder DA, Heithaus MR, Fourqurean JW (2012) Feeding preferences of herbivores in a relatively pristine subtropical seagrass ecosystem. Mar Freshw Res 63: 1051–1058

Burkholder DA, Fourqurean JW, Heithaus MR (2013a) Spatial pattern in seagrass stoichiometry indicates both N-limited and P-limited regions of an iconic P-limited subtropical bay. Mar Ecol Prog Ser 472:101–115

Burkholder DA, Heithaus MR, Fourqurean JW, Wirsing A, Dill LM (2013b) Patterns of top-down control in a seagrass ecosystem: Could a roving apex predator induce a behaviour-mediated trophic cascade? J Anim Ecol 82: 1192–1202

Cai W, Borlace S, Lengaigne M, Van Rensch P and others (2014) Increasing frequency of extreme El Niño events due to greenhouse warming. Nat Clim Change 4:111–116

Cai W, Wang G, Santoso A, McPhaden MJ and others (2015) Increased frequency of extreme La Niña events under greenhouse warming. Nat Clim Change 5:132–137

Campbell SJ, McKenzie LJ (2004) Flood related loss and recovery of intertidal seagrass meadows in southern Queensland, Australia. Estuar Coast Shelf Sci 60:477–490

Carpenter S, Walker B, Anderies JM, Abel N (2001) From metaphor to measurement: resilience of what to what? Ecosystems 4:765–781

Carr J, D'Odorico P, McGlathery K, Wiberg P (2010) Stability and bistability of seagrass ecosystems in shallow coastal lagoons: role of feedbacks with sediment resuspension and light attenuation. J Geophys Res 115:G03011

Ciais P, Reichstein M, Viovy N, Granier A and others (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–533

Dennison WC, Orth RJ, Moore KA, Stevenson JC and others (1993) Assessing water quality with submersed aquatic vegetation. Bioscience 43:86–94

Department of Environment and Conservation (2008) Shark Bay World Heritage Property strategic plan, 2008–2020. Department of Environment and Conservation, Perth

Fonseca MS, Fisher JS (1986) A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. Mar Ecol Prog Ser 29:15–22

Fourqurean JW, Robblee MB (1999) Florida Bay: a history of recent ecological changes. Estuaries 22:345–357

Fourqurean JW, Duarte CM, Kennedy H, Marbà N and others (2012) Seagrass ecosystems as a globally significant carbon stock. Nat Geosci 5:505–509

Fraser MW, Kendrick GA, Statton J, Hovey RK, Zavala-Perez A, Walker DI (2014) Extreme climate events lower resilience of foundation seagrass at edge of biogeographical range. J Ecol 102:1528–1536

Glynn PW (1993) Coral reef bleaching: ecological perspectives. Coral Reefs 12:1–17

Heithaus MR (2001) The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. Environ Biol Fishes 61:25–36

Heithaus MR, Dill L (2006) Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? Oikos 114:257–264

Heithaus MR, Wirsing AJ, Dill LM (2012) The ecological importance of intact top-predator populations: a synthesis of 15 years of research in a seagrass ecosystem. Mar Freshw Res 63:1039–1050

Holling CS (1973) Resilience and stability of ecological systems. Annu Rev Ecol Syst 4:1–23

Honnay O, Verheyen K, Butaye J, Jacquemyn H, Bossuyt B, Hermy M (2002) Possible effects of habitat fragmentation and climate change on the range of forest plant species. Ecol Lett 5:525–530

Hurlbert SH (1971) The nonconcept of species diversity: a critique and alternative parameters. Ecology 52:577–586

Hyndes GA, Heck KL, Vergés A, Harvey ES and others (2016) Accelerating tropicalization and the transformation of temperate seagrass meadows. Bioscience 66:938–948

Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353–362

IPCC (2014) Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva

Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: events, not trends. Front Ecol Environ 5:365–374

Jones AW, Post DM (2016) Does intraspecific competition promote variation? A test via synthesis. Ecol Evol 6: 1646–1655

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Larkum A, Orth R, Duarte C (eds) (2006) Seagrasses: biology, ecology, and conservation. Springer, Dordrecht

Marbà N, Duarte CM (1998) Rhizome elongation and seagrass clonal growth. Mar Ecol Prog Ser 174:269–280

May RM (1973) Stability and complexity in model ecosystems. Princeton University Press, Princeton, NJ

McGlathery KJ (2001) Macroalgal blooms contribute to the decline of seagrass in nutrient-enriched coastal waters. J Phycol 37:453–456

Nowicki RJ, Fourqurean JW, Heithaus MR (in press) The role of consumers in structuring seagrass communities: direct and indirect mechanisms. In: Larkum A, Kendrick GA (eds) Biology of seagrasses. Springer, New York, NY

Orth RJ, Luckenbach ML, Marion SR, Moore KA, Wilcox DJ (2006) Seagrass recovery in the Delmarva coastal bays, USA. Aquat Bot 84:26–36

Orth RJ, Harwell MC, Inglis GJ (2007) Ecology of seagrass seeds and seagrass dispersal processes. In: Larkum A, Orth R, Duarte C (eds) Seagrasses: biology, ecology, and conservation. Springer, Dordrecht, p 111–133

Pandolfi JM (2015) Incorporating uncertainty in predicting the future response of coral reefs to climate change. Annu Rev Ecol Evol Syst 46:281–303

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

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. Western Australian Fisheries and Marine Research Laboratories, North Beach

Peterson BJ, Rose CD, Rutten LM, Fourqurean JW (2002) Disturbance and recovery following catastrophic grazing: studies of a successional chronosequence in a seagrass bed. Oikos 97:361–370

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2017) nlme: linear and nonlinear mixed effects models. R package version 3.1-131. https://CRAN.R-project.org/package=nlme

Plus M, Deslous-Paoli JM, Dagault F (2003) Seagrass (*Zostera marina* L.) bed recolonisation after anoxia-induced full mortality. Aquat Bot 77:121–134

Preen A (1995) Impacts of dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing. Mar Ecol Prog Ser 124:201–213

Preen AR, Lee Long WJ, Coles RG (1995) Flood and cyclone related loss, and partial recovery, of more than 1000 km^2 of seagrass in Hervey Bay, Queensland, Australia. Aquat Bot 52:3–17

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Robblee MB, Barber TR, Carlson PR Jr, Durako MJ and others (1991) Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida Bay (USA). Mar Ecol Prog Ser 71:297–299

Short FT, Wyllie-Echeverria S (1996) Natural and human-induced disturbance of seagrasses. Environ Conserv 23: 17–27

Short FT, Coles R, Fortes MD, Victor S and others (2014) Monitoring in the Western Pacific region shows evidence of seagrass decline in line with global trends. Mar Pollut Bull 83:408–416

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

Tanner JE (2015) Restoration of the seagrass *Amphibolis antarctica* — temporal variability and long-term success. Estuaries Coasts 38:668–678

Thomson JA, Burkholder DA, Heithaus MR, Fourqurean JW, Fraser MW, Statton J, Kendrick GA (2015) Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. Glob Change Biol 21:1463–1474

Turner T (1983) Facilitation as a successional mechanism in a rocky intertidal community. Am Nat 121:729–738

Unsworth RKF, Collier CJ, Waycott M, Mckenzie LJ, Cullen-Unsworth LC (2015) A framework for the resilience of seagrass ecosystems. Mar Pollut Bull 100:34–46

van der Heide T, van Nes EH, Geerling GW, Smolders AJ, Bouma TJ, van Katwijk MM (2007) Positive feedbacks in seagrass ecosystems: implications for success in conservation and restoration. Ecosystems 10:1311–1322

van der Heide T, van Nes EH, van Katwijk MM, Olff H, Smolders AJ (2011) Positive feedbacks in seagrass ecosystems — evidence from large-scale empirical data. PLOS ONE 6:e16504

van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD and others (2009) Widespread increase of tree mortality rates in the western United States. Science 323:521–524

van Tussenbroek BI, Soissons LM, Bouma TJ, Asmus R and others (2016) Pollen limitation may be a common Allee effect in marine hydrophilous plants: implications for decline and recovery in seagrasses. Oecologia 182: 595–609

Venables W, Ripley B (2002) Modern applied statistics with S, 4th edn. Springer, New York, NY

Vergés A, Steinberg PD, Hay ME, Poore AG and others (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc R Soc B 281:20140846

Walker DI (1985) Correlations between salinity and growth of the seagrass *Amphibolis antarctica* (Labill.) Sonder & Aschers., in Shark Bay, Western Australia, using a new method for measuring production rate. Aquat Bot 23: 13–26

Walker DI, Cambridge ML (1995) An experimental assessment of the temperature responses of two sympatric seagrasses, *Amphibolis antarctica* and *Amphibolis griffithii*, in relation to their biogeography. Hydrobiologia 302: 63–70

Walker DI, McComb AJ (1988) Seasonal variation in the production, biomass and nutrient status of *Amphibolis antarctica* (Labill.) Sonder ex Aschers. and *Posidonia australis* Hook. f. in Shark Bay, Western Australia. Aquat Bot 31:259–275

Walker DI, McComb AJ (1992) Seagrass degradation in Australian coastal waters. Mar Pollut Bull 25:191–195

Walker DI, Kendrick GA, McComb AJ (1988) The distribution of seagrass species in Shark Bay, Western Australia, with notes on their ecology. Aquat Bot 30:305–317

Walker D, Kendrick G, McComb A (2006) Decline and recovery of seagrass ecosystems — the dynamics of change. In: Larkum A, Orth R, Duarte C (eds) Seagrasses: biology, ecology, and conservation. Springer, Dordrecht, p 553–565

Waycott M, Duarte CM, Carruthers TJ, Orth RJ and others (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc Natl Acad Sci USA 106:12377–12381

Wernberg T, Smale DA, Tuya F, Thomsen MS and others (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nat Clim Change 3:78–82

Wu L, Cai W, Zhang L, Nakamura H and others (2012) Enhanced warming over the global subtropical western boundary currents. Nat Clim Change 2:161–166

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Submitted: June 8, 2016; Accepted: December 19, 2016
Proofs received from author(s): February 20, 2017