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Indirect legacy effects of an extreme climatic event on a marine megafaunal community

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Abstract. While extreme climatic events (ECEs) are predicted to become more frequent, reliably predicting their impacts on consumers remains challenging, particularly for large consumers in marine environments. Many studies that do evaluate ECE effects focus primarily on direct effects, though indirect effects can be equally or more important. Here, we investigate the indirect impacts of the 2011 “Ningaloo Niño” marine heatwave ECE on a diverse megafaunal community in Shark Bay, Western Australia. We use an 18-year community-level data set before (1998–2010) and after (2012–2015) the heatwave to assess the effects of seagrass loss on the abundance of seven consumer groups: sharks, sea snakes (multiple species), Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), dugongs (*Dugong dugon*), green turtles (*Chelonia mydas*), loggerhead turtles (*Caretta caretta*), and Pied Cormorants (*Phalacrocorax* spp.). We then assess whether seagrass loss influences patterns of habitat use by the latter five groups, which are under risk of shark predation. Sharks catch rates were dominated by the generalist tiger shark (*Galeocerdo cuvier*) and changed little, resulting in constant apex predator density despite heavy seagrass degradation. Abundances of most other consumers declined markedly as food and refuge resources vanished, with the exception of generalist loggerhead turtles. Several consumer groups significantly modified their habitat use patterns in response to the die-off, but only bottlenose dolphins did so in a manner suggestive of a change in risk-taking behavior. We show that ECEs can have strong indirect effects on megafauna populations and habitat use patterns in the marine environment, even when direct effects are minimal. Our results also show that indirect impacts are not uniform across taxa or trophic levels and suggest that generalist marine consumers are less susceptible to indirect effects of ECEs than specialists. Such non-uniform changes in populations and habitat use patterns have implications for community dynamics, such as the relative strength of direct predation and predation risk. Attempts to predict ecological impacts of ECEs should recognize that direct and indirect effects often operate through different pathways and that taxa can be strongly impacted by one even if resilient to the other.

Key words: climate change; disturbance ecology; extreme climatic event; marine heat wave; phase shifts; predator–prey interactions; resilience; risk effects.

INTRODUCTION

Most studies of the ecological effects of climate change have focused on how organisms and ecosystems will respond to changes in average climatic conditions as opposed to periodic extreme events (Jentsch et al. 2007, Smith 2011a, Butt et al. 2016). However, extreme

climatic events (hereafter ECEs), including heat waves, cold snaps, storms, droughts, and floods, can rapidly alter ecosystems and significantly influence patterns of biodiversity (Jentsch et al. 2007, Butt et al. 2016). Climate change is predicted to continue to alter properties of extreme events including their frequency, duration, and intensity (Wu et al. 2012, Cai et al. 2014, 2015, Pachauri et al. 2014, Oliver et al. 2018). Therefore, understanding the impacts of these extremes on communities is key to predicting ecosystem trajectories in coming decades.

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Extreme climate events are defined as abrupt disturbances that exert strong effects over a brief duration relative to the lifespan(s) of the organism(s) under investigation (Jentsch et al. 2007). Climate impacts to ecosystems need not be driven by direct physical forcing to be significant, however (Butt et al. 2016). Indeed, indirect biological impacts of gradual change often supercede direct abiotic effects, at least in freshwater and terrestrial systems (Ockendon et al. 2014). Direct and indirect effects have also been documented for ECEs. Direct physical forcing from ECEs can include mortality, sublethal reductions in fitness, reduced resilience, and changes in behavior (e.g., Breshears et al. 2005, Matich & Heithaus 2012, Wernberg et al. 2013, Fraser et al. 2014, Thomson et al. 2014). Much like gradual climatic change, ECEs can also impact species indirectly by abruptly altering patterns of resource availability or modifying species interactions (e.g., Preen and Marsh 1995, Cahill et al. 2013, Ockendon et al. 2014, Bennett et al. 2015). Determining the strength, nature, and relative importance of direct abiotic and indirect biotic (i.e., legacy) effects of ECEs is critical for accurately understanding and predicting their effects on consumers. Although legacy effects of climate extremes have been explored in marine environments (e.g., Bennett et al. 2015), they have less commonly been examined over broad taxonomic and spatial scales (Langtimm and Beck 2003, Cahill et al. 2013, Chapman et al. 2014, Butt et al. 2016).

Species interactions are not only altered by climate change, but alter ecosystem responses to it as well (Zarnetske et al. 2012, Cahill et al. 2013, Taylor et al. 2015, Sanders-DeMott et al. 2018). Not all species interactions are equally influential, however (e.g., Paine 1980, 1992, Power et al. 1996). For example, apex predators may be particularly important biotic multipliers of climate change (sensu Zarnetske et al. 2012), in part because of the scale and scope of their interactions with other species and ability to generate widespread non-consumptive (i.e., “risk”) effects in addition to inflicting mortality via direct predation (Jeffries and Lawton 1984, Schmitz et al. 1997, Lima 1998, Dill et al. 2003, Werner and Peacor 2003, Heithaus et al. 2008). Predation risk can greatly alter the behavior of entire prey populations simultaneously and quickly (Lima and Dill 1990, Sinclair and Pech 1996, Creel and Christianson 2008, Creel et al. 2011, Heithaus et al. 2012), sometimes generating behaviorally mediated indirect interactions (BMIs, also known as behaviorally mediated trophic cascades, or BMTCs; Dill et al. 2003) with strong effects on lower trophic levels (e.g., Schmitz et al. 1997, Ripple and Beschta 2004, Burkholder et al. 2013a). Thus, investigations of the effects of extreme events on species that do not account for impacts on species interactions, especially for strongly interacting species, may fail to predict the overall ecological effects of climate extremes and may hamper understanding of how ecosystems respond to ECEs.

Seagrass ecosystems support diverse consumer communities and provide myriad ecosystem functions including primary production, habitat creation, sediment stabilization, and carbon sequestration and storage (e.g., Costanza et al. 1997, Heck et al. 2003, Orth et al. 2006, Fourqurean et al. 2012, Unsworth et al. 2018). Despite their importance as foundations of coastal ecosystems, seagrass habitats are declining rapidly both because of local stressors (e.g., Short and Wyllie-Echeverria 1996, Waycott et al. 2009) and ECEs (e.g., McKenzie et al. 2012, Fraser et al. 2014, Thomson et al. 2014). Seagrass habitats impacted by ECEs therefore represent a valuable opportunity to test predictions about how resource loss affects abundance and distribution of dependent consumers. For example, are generalist species less vulnerable to ECEs than specialists because of increased adaptive capacity? Do bottom-up stressors from ECEs modify the relative strength of risk effects? And, are species more closely associated with foundational species (e.g., for food or shelter) more at risk from ECEs? Such tests may provide critical insights into our ability to predict how species dynamics will change in response to climate change.

The goal of this study was to investigate the indirect impacts (large-scale seagrass die-off) of an ECE (the 2011 “Ningaloo Niño” marine heatwave) on a taxonomically diverse marine megafaunal community in Shark Bay, Western Australia. Specifically, we analyzed a long-term (18-yr), community-level data set to (1) quantify any legacy effects of the heat wave on the abundance of large sharks and air-breathing marine megafauna and (2) to test whether changes in the resource landscape altered predation-risk-sensitive habitat use patterns of tiger shark (*Galeocerdo cuvier*) prey. We accomplished this by comparing standardized drumline shark fishing and surface-based belt transect survey data before (1997–2010) and after (2012–2015) the heat wave and subsequent seagrass die-off.

METHODS

Shark Bay (25°45' S, 113°44' E), Western Australia is a shallow (<15 m), 13,000 km² semi-enclosed subtropical embayment situated approximately 800 km north of Perth. The bay historically contained over 4,000 km² of seagrass (Walker et al. 1988), placing it among the largest seagrass ecosystems on earth. Shark Bay's seagrass assemblage has been historically dominated by the temperate seagrass *Amphibolis 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. 2013b). Indeed, *A. antarctica* is a structurally complex ecosystem engineer (sensu Jones et al. 1994) that creates extensive benthic habitat, stabilizes sediment, and contributes substantial primary and secondary production (Walker 1985, Walker and McComb 1988). Despite its large size, Shark Bay is largely undeveloped with a small human

population and relatively few local and regional anthropogenic stressors (Department of Environment and Conservation 2008), making it a good model ecosystem to study natural community responses to ECEs.

The study area, immediately north of Monkey Mia, consists of a series of nearshore shallow (<4 m) seagrass banks separated by deep, sandy channels (6–12 m, Heithaus 2001; Fig. 1). Since 1997, this study area has been used as a model system to understand the influence of risk effects of tiger sharks on associated prey species and ecosystem structure (Heithaus et al. 2012, Burkholder et al. 2013a, Bessey et al. 2016). Tiger sharks' potential air-breathing prey in this system include megagrazers [dugongs (*Dugong dugon*) and green sea turtles (*Chelonia mydas*)], piscivorous mesopredators [Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), Pied Cormorants (*Phalacrocorax* spp.), sea snakes (subfamily Hydrophiinae)], and benthic invertivores [loggerhead sea turtles (*Caretta caretta*), Heithaus et al. 2012]. Generally, shark abundance varied temporally with consistently high shark abundances during warm months (September–May), and very low abundances during most, but not all, winters (June–August; Heithaus 2001, Wirsing et al. 2006). Moreover, tiger sharks used shallow habitats, where seagrasses are concentrated, to a greater extent than deep ones (Heithaus et al. 2002, 2006). These shallow seagrass habitats were characterized by relatively higher density and quality of food resources for megagrazers (dugongs, green turtles) and mesopredators (sea snakes, Cormorants, dolphins), but also carried an increased risk of predation by tiger sharks (see Heithaus et al. 2012). Before the seagrass die-off, multiple consumer species were distributed in rough proportion to their food supply as would be expected by ideal free distribution (IFD) theory (Fretwell and Lucas

1969) when predation risk was low, but overused resource-poor but relatively safe deeper habitats during dangerous periods (Heithaus et al. 2007a,b,c, Heithaus et al. 2012). These shifts in habitat use result in a behaviorally mediated trophic cascade that structured the seagrass community by reducing herbivory from megagrazers in shallow, risky habitats (Burkholder et al. 2013a).

As a subtropical seagrass ecosystem, Shark Bay marks the northern boundary for the temperate seagrass species *A. antarctica* (Walker et al. 1988). In the Austral summer of 2011, strong La Niña conditions increased the poleward flow of tropical water via the Leeuwin current along the Western Australia coast (Pearce and Feng 2013), generating a strong marine heat wave (MHW; sensu Hobday et al. 2016) that increased water temperatures by 2–4°C for two months (Wernberg et al. 2013, Hobday et al. 2016). Within the study area, average daytime water temperatures for the month of February were 29.8°C (3.5°C above average), and average monthly temperatures remained above the usual yearly maximum from January to March (Nowicki et al. 2017). Following the heat wave, *A. antarctica* cover declined by ~90% in several areas of Shark Bay (Fraser et al. 2014, Thomson et al. 2014), with the magnitude of seagrass die-off increasing at greater depths (J. Thomson, *unpublished data*). Seagrass loss of this magnitude had not been previously reported in Shark Bay and a die-off of this magnitude appears not to exist in local living memory (R. Nowicki, *personal observation*). The seagrass loss was also accompanied by a ~40% decline in benthic fish biomass in shallow habitats and a ~27% decline in deep habitats (Nowicki and Heithaus *unpublished data*), as well as a ~50% reduction in water visibility (Nowicki et al. 2017). *A. antarctica* cover remained very low

FIG. 1. (A) Shark Bay (25°45' S, 113°44' E), Western Australia. The study area is located immediately north of Monkey Mia (star in A, and MM in B) in the Eastern Gulf. (B) The study area is typified by a series of shallow (<4.0 m) seagrass banks (green) separated by deep (6–12 m) sandy channel or plain habitats (blue). Locations of transect surveys are indicated by black lines; brown indicates land. Shark fishing occurred on transects marked with stars, though most sets (~85%) were conducted on the easternmost three transects to reduce bait plume proximity to Monkey Mia. Modified from Heithaus (2005).

following the initial die-off, while the tropical seagrass *Halodule uninervis* recovered by 2013 and surpassed pre-disturbance occurrence and cover estimates by 2014 (Nowicki et al. 2017).

Field methods

Whereas shark fishing and transect surveys occurred in all months, field effort was largely concentrated between February and October to ensure capture of seasonal transitions in shark abundance. Shark abundance was estimated using a standardized top-set drumline method established in 1997 (Heithaus 2001). From 1998 to 2015, we undertook standardized shark sampling via single hook top-set drumlines set in deep channels in the study system (Fig. 1). On each fishing day (approximately 4 d per field month, mean = 3.90, $s = 2.03$), up to 10 baited drumlines were set at dawn. Drumlines were secured to the bottom with a Danforth anchor (Attwood, Lowell, MI, USA) attached to 20 m of line. A 25-L floating drum suspended a single baited 13-0 or 14-0 Mustad Shark Hook (O. Mustad & Son Americas Inc, Miami, FL, USA) 1–2 m below the surface (Heithaus 2001, Wirsing et al. 2006). Some sets were baited with 12-0 sized hooks, but because smaller hooks resulted in lower shark catch rates in this system (Heithaus 2001), these sets were excluded. Drumlines were usually separated by 300 m, though rarely they were set concurrently in two channels with drums 700 m apart. Previous work has shown these differences in deployment to not influence catch rates (Wirsing et al. 2006) so results from both deployment types were pooled.

Drumlines were baited with ~1.5 kg of fish. Bait species varied but was dominated by Australian salmon (*Arripis trutta*, 37.0% of soak time), pink snapper (*Pagrus auratus*, 15.7%), emperor (*Lethrinus* spp., 14.4%), tailor (*Pomatomus saltatrix*, 13.7%), and sea mullet (*Mugil cephalus*, 8.8%), which collectively made up ~90% of soak time. Bait species does not significantly influence shark catch rates in this system (Wirsing et al. 2006), so a correction factor for bait species was not applied. Lines were checked every 2–4 h; soak time was calculated as time between bait entry and bait removal. For hooks from which bait was missing or a shark was captured, bait removal was assumed to occur halfway between checks. Hooked sharks were brought along the 4.5–5.5 m research vessel and were allowed to swim freely to minimize stress while the vessel idled forward. Sharks were identified to species, sexed, and measured (total length, TL) before being fitted with a numbered roto-tag and released (see Heithaus [2001] for details).

Transect surveys

Densities of air breathing megafauna (e.g., dolphins, dugongs, green and loggerhead sea turtles, Cormorants, and sea snakes) were assessed via visual belt transects. Eleven transects, ranging in length from 2.9 to 4.5 km, were established in the study area in 1997, with five over

shallow (<4.0 m) seagrass banks and six over deep (6–12 m) channel and sandflat habitats (Heithaus 2001, Fig. 1). Each transect was run between sunrise and sunset approximately four times per month at 6–9 km/h using a 4.5–5.5 m vessel with an outboard motor and approximately three observers (mean = 3.24, SD = 1.05) from 1998 to 2014 (excluding 2000, 2001, and 2005). Because of interspecific differences in size and surface behavior, transect radii varied between species (Table 1). Only individuals at the surface that had not been passed by the boat were counted. At each sighting we recorded depth and bottom cover under the boat, as well as distance and heading to the animal.

Slow vessel speeds, relatively short dive times, and direct comparisons within as opposed to among habitat types and seasons in this study minimized the need for detectability correction factors for most species (Wirsing et al. 2007a, Heithaus et al. 2012). To minimize recounting individuals, transects were not run more than once per day, and were run in haphazard order and direction. Cormorants that fled were noted to minimize recounting. Transects were only run in Beaufort sea state conditions of 3 or lower (when wavelets begin to crest) to minimize sampling bias from reduced visibility (~97% were ≤ 2). To minimize the influence of large animal groups that were very rarely encountered (<0.1% of sighting events), we excluded encounters in which group size exceeded 30 individuals of a species from analysis ($n = 12$ occurrences, all for Cormorants). Furthermore, dolphins were not consistently sampled from 2002 to 2007, so transects run in these years were removed prior to analysis of dolphin data.

Although the dive profiles of marine turtles can result in significant availability bias for these species (Thomson et al. 2012a, 2013), we did not apply correction factors for several reasons. First, turtle dive profiles and proportional surface use are temperature and depth dependent (Thomson et al. 2012a). Transect surveys were controlled for location and season through time, and temperature regimes were similar between the two time periods (2011 excluded, Nowicki et al. 2017). It is therefore unlikely that availability bias would have

TABLE 1. Transect radii for each species recorded on surface transects.

Common name	Scientific name	Transect radius (m)
Indo-Pacific bottlenose dolphin	<i>Tursiops cf. aduncus</i>	200
Dugong	<i>Dugong dugon</i>	100
Green turtle	<i>Chelonia mydas</i>	30
Loggerhead turtle	<i>Caretta caretta</i>	30
Pied Cormorant	<i>Phalacrocorax varius</i>	30
Bar-bellied sea snake	<i>Hydrophis elegans</i>	5
Olive-headed sea snake	<i>Disteria major</i>	5
Shark Bay sea snake	<i>Aipysurus pooleorum</i>	5

significantly changed with time within season or habitat type. Furthermore, the vast majority of transects where turtles were sighted consisted of only one or two sightings, representing sometimes less than 10% of the animals that were likely submerged (Thomson et al. 2012a, 2013). Applying large correction factors when only a single animal is sighted (i.e., without aggregating data to reduce zero inflation) exacerbates overdispersion because no correction factor is applied to transects where no turtle surfaces (but may still be present). We therefore report and analyze uncorrected turtle densities here; actual turtle densities are substantially higher within this system (Thomson et al. 2013). Similarly, because sea turtle surface intervals can be very short, we could not always reliably identify turtles to species. To minimize bias in inferring species-specific turtle response to resource loss, we excluded transects run prior to 1999 (the year identification to species began) and those that included individuals that could not be identified to species. Reliable identification of sea snakes to species was not possible so sea snakes were analyzed as a group.

Data analysis

Data were analyzed in R Studio version 0.99.892 (RStudio Team 2015). The R code used to perform the analyses reported in this paper can be found in Data S1. Data collected in 2011 were excluded from analysis to allow for a clear separation between periods before and after the heat wave. Shark catch per unit effort (CPUE) was expressed as the number of sharks caught per 100 hook soak hours. To reduce zero inflation, all hooks set in a day were pooled to generate a daily CPUE before being summarized (Table 2). Rare days with <10 total hook-hours were excluded. Catch rates appear to be a reliable catch per unit effort (CPUE) measure of tiger shark abundance because sighting frequency of free-swimming sharks is directly related to catch rates and sharks tagged with passive acoustic tags ($n = 8$) have only been detected during periods of high catch rates and high prey abundance (e.g., Heithaus 2001, Heithaus et al. 2012; R. Nowicki, *personal observation*). Furthermore, tiger sharks have been caught even at low winter temperatures, suggesting that changes in catch rates are not because of temperature-induced suspension of feeding (Wirsing et al. 2006; this study).

Shark catch data were analyzed via generalized linear mixed models using the `glmer` function in the `lme4` package (Bates et al. 2015). We calculated CPUE for four subsets of sharks: all sharks, tiger sharks, all “large” sharks (>300 cm TL), and all large tiger sharks (the size at which these animals are thought to become regularly dangerous to dugongs; Wirsing et al. 2007b). In all four models, CPUE was transformed to the 1.5 power to minimize patterns in residuals.

Models had two fixed effects: time period (pre- or post-die-off, 2011 excluded) and a polynomial function

of day of year (DOY) meant to capture seasonal trends in shark abundance. Focal zone (FZ) was included as a random effect to account for repeated visits to the same fishing sites, and year was included as a random effect because it is nested within time period (Zuur et al. 2009). Because all hook sets in a day were pooled, rare days in which multiple focal zones were fished simultaneously ($n = 7$) were assigned their own “mixed” FZ designation. The data were positive, continuous, and included a large proportion of zeroes, so a Tweedie distribution (Tweedie 1984) was applied with a power variance structure that varied by model, based on visual inspection of residual data (packages `tweedie` and `statmod`; Giner and Smyth 2016, Dunn 2017). Because CPUE is already a property of soak time, a fishing effort offset was not applied.

To assess the impacts of seagrass die-off on the abundance of air-breathing fauna abundances at a system-wide scale, we applied linear mixed-effects models to transect count data using the `glmmTMB` function in the `glmmTMB` package (Brooks et al. 2017). In each model, time period was a fixed factor whereas season, habitat, and transect number were included as separate random intercepts (Zuur et al. 2009). The data were positive counts, overdispersed, and often zero inflated. We therefore constructed zero-inflated mixed effects models with three distributions, Poisson, quasi-Poisson (i.e., negative binomial type I), and negative binomial, and used the Akaike information criterion (AIC) to identify the best model for each species following Zuur et al. (2009). Model validation was completed following Zuur et al. (2009) and with the `DHARMA` package (Hartig 2017) using the `simulateResiduals` command with 250 iterations.

To determine whether air-breathing fauna altered habitat use patterns following the seagrass die-off, we used zero-inflated mixed models integrating both transect and shark fishing data. Specifically, we assessed whether a three-way interaction between shark catch rate (expressed as monthly CPUE), habitat (deep, shallow), and time period (pre-die-off, post-die-off) influenced the abundance of each species. CPUE was derived from sets in deep channels and was used as a continuous variable estimate of system-wide shark abundance. Focal zone (Fig. 1) was designated as a random effect to account for repeated transect visits. We interpreted a significant three-way interaction to indicate that a group’s risk-sensitive habitat use patterns had changed in response to the seagrass die-off. When a three-way interaction was not significant, we used backwards model selection to arrive at a final model in which all terms were significant. Sea snakes were excluded from relative habitat use analysis because post-die-off abundance was very low. Because sharks below 300 cm TL are not believed to be dangerous to dugongs in this system, we used the CPUE of large (>300 cm TL) sharks in dugong models.

TABLE 2. Fishing effort and catch rates of all sharks, all large (>300 cm TL) sharks, tiger sharks (*G. cuvier*), and large tiger sharks, by season and time period (before, during, and after sea-grass die-off).

Fishing effort and catch rates	1998–2010				2011				2012–2015			
	Warm		Cold		Warm		Cold		Warm		Cold	
	Total	SE	Total	SE	Total	SE	Total	SE	Total	SE	Total	SE
Fishing effort												
Total fishing days	220		319		16		7		58		37	
Total hook-hours	13,141		20,106		1,160		495		3,761		3,185	
μ hook-hour/d	59.7		63.0		72.5		70.7		64.8		86.1	
SD	24.5		24.4		22.4		6.4		21.7		17.1	
SE	1.7		1.4		5.6		2.4		2.8		2.8	
All sharks												
Total sharks caught	509		571		57		21		234		41	
μ sharks/100 hook-hour	4.69		3.51		4.81		4.41		6.72		1.63	
SD	3.95		3.80		3.19		2.94		5.44		2.59	
SE	0.27		0.21		0.80		1.11		0.71		0.43	
Large sharks												
Total sharks caught	194		204		17		0		59		8	
μ sharks/100 hook-hour	1.94		1.39		1.41		0.00		1.84		0.42	
SD	2.77		2.46		1.51		0.00		2.32		1.10	
SE	0.19		0.14		0.38		0.00		0.31		0.18	
<i>G. cuvier</i>												
Total sharks caught	465		523		52		20		202		34	
μ sharks/100 hook-hour	4.32		3.23		4.44		4.19		5.84		1.35	
SD	3.86		3.67		3.18		2.55		4.58		2.32	
SE	0.26		0.21		0.80		0.96		0.60		0.38	
Large <i>G. cuvier</i>												
Total sharks caught	194		204		17		0		57		8	
μ sharks/100 hook-hour	1.94		1.39		1.41		0.00		1.78		0.42	
SD	2.77		2.46		1.51		0.00		2.31		1.10	
SE	0.19		0.14		0.38		0.00		0.30		0.18	

Notes: The warm season (Warm) extends from September to May; the cold season (Cold) extends from June to August. Mean, standard deviation (SD), and standard error (SE) of sharks per 100 hook hours are calculated from daily averages and thus differ slightly from a grand arithmetic mean.

RESULTS

Our final data set included 437 d of shark fishing between 1998 and 2015. Exclusion of 2011 data left 27,052 hook hours over 414 fishing days (319 d pre-die-off, 95 d post-die-off) for formal analysis. Daily shark fishing effort before the die-off ($\mu = 63.0$, $s = 24.4$ hook-hours/d) was lower than after the die-off ($\mu = 73.1$, $s = 22.5$ hook-hours/d, two-way ANOVA, $F_{1,411} = 11.1$, $P < 0.001$, Table 2). Daily shark fishing effort was also higher in the cool season ($\mu = 74.6$, $s = 22.4$ hook-hours/d) than the warm season ($\mu = 60.8$, $s = 24.0$ hook-hours/d, two-way ANOVA, $F_{1,411} = 32.5$, $P < 0.0001$). There was a marginally significant interaction between the two (two-way ANOVA on interaction term, $F_{1,410} = 3.58$, $P = 0.059$), with pairwise Tukey tests revealing significantly higher soak times in the cold season post-die-off than any other period (Fig. 2).

We caught 924 sharks from 16 species over the course of the study (2011 inclusive, Tables 2 and 3). The shark community was dominated overwhelmingly by tiger sharks (*Galeocerdo cuvier*, 89.9% of overall catch) in all time periods, followed by the sandbar shark (*Carcharhinus plumbeus*). All other shark species were rarely encountered (Table 3). Tiger sharks were even more dominant among large sharks (those >300 cm TL), making up 99.3% of sharks in this size class (Table 3). Length measurements of 734 tiger sharks (503 pre-die-off, 231 post-die-off) revealed that while average tiger shark length declined from 283.3 cm total length (TL) before the die-off to 264.9 cm TL after the die-off (Welch two-sample t test, $t_{1,455.6} = -4.20$, $P < 0.0001$), the CPUE of the large shark class did not change with time (Tables 2 and 4). Sexing of 664 tiger sharks revealed

that males made up a significantly higher proportion of the population following the die-off: male:female sex ratios changed from 0.29:1 to 0.44:1 (logistic regression, $Z_{663} = 2.41$, $P = 0.016$).

Generalized linear mixed models indicated that overall shark catch rate and seasonal patterns of catch remained similar for all shark groups following seagrass die-off (Table 4, Fig. 3). Because longer soak times yielded lower CPUE both for large sharks (one-way ANOVA, $F_{1,412} = 105.3$, $P < 0.0001$, $R^2 = 0.217$) and sharks in general (one-way ANOVA, $F_{1,412} = 107.0$, $P < 0.0001$, $R^2 = 0.206$), and soak times were longer following the seagrass die-off (Fig. 2), the finding of no significant decline in shark catch is robust.

In total we ran 3,375 transect surveys over the study period (2,661 pre-die-off, 714 post-die-off, Table 5), resulting in 12,477 linear kilometers surveyed and 22,371 animals recorded. Of these, 4.8% (106 of 2,196) of pre-decline transects and 6.7% of post-decline transects (48 of 714) included turtles that could not be identified to species, resulting in 2,756 transects available for turtle analysis (2,090 pre-decline, 666 post-decline).

Abundances and densities of almost all species dropped significantly following the seagrass die-off (Tables 5 and 6, Fig. 4). Dolphin densities dropped by 39.2% (ZINB, $z_{1, 2,142} = 6.02$, $P < 0.0001$), while dugong density was reduced by 67.5% (ZINB, $z_{1, 3,360} = 4.52$, $P < 0.0001$). Similarly, cormorant and green turtle densities declined by 35.3% (ZINB, $z_{1, 3,360} = 9.61$, $P < 0.0001$) and 38.6% ($z_{1, 2,741} = 2.36$, $P = 0.019$), respectively. Sea snakes suffered the largest losses, declining in density by 76.7% (ZINB, $z_{1, 3,360} = 5.46$, $P < 0.0001$). In contrast, loggerhead turtle densities did not significantly differ between time periods (ZIP, $z_{1, 2,741} = 1.67$, $P = 0.097$).

Habitat use of bottlenose dolphins shifted in a manner consistent with increased risk taking following the seagrass die-off (Table 7). Specifically, bottlenose dolphins' use of risky but profitable shallow seagrass bank habitats was inversely related to shark catch rate prior to the seagrass die off, but this relationship disappeared following the seagrass die-off ($t = -3.32$, $P < 0.001$, Table 7, Fig. 5). Conversely, the relationship between shark catch rate and habitat use patterns of cormorants, dugongs, green turtles, and loggerhead turtles did not change significantly following seagrass die-off (Table 7). Instead, loggerhead turtles increased their proportional use of shallow habitats after the die-off independent of shark CPUE, despite a significant influence of CPUE on habitat use generally (Table 7, Fig. 5). Cormorants also increased their relative use of shallow habitats after the die-off, while dugong risk sensitive habitat use patterns remained similarly sensitive to CPUE before and after the die-off (Table 7, Fig. 5). Green turtle habitat use patterns did not appear to be affected by either shark CPUE or time period.

FIG. 2. Shark fishing effort separated into pre-die-off (1998–2010, green) and post-die-off (2012–2015, gold) periods. Unshaded and shaded areas refer to warm and cool seasons, respectively. Groups that are significantly different from one another (Tukey HSD) are denoted with different letters. Bold lines = medians, box edges = 25th and 75th quartiles, whiskers = 150% interquartile ranges beyond each quartile, individual points = outliers.

TABLE 3. Composition of the large shark community in each time period.

Species	1998–2010		2011		2012–2015		All years	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
<i>Galeocerdo cuvier</i>	523	91.6	72	92.3	236	85.8	831	89.9
<i>Carcharhinus plumbeus</i>	31	5.4	3	3.8	14	5.1	48	5.2
<i>Negaprion acutidens</i>	6	1.1	2	2.6	1	0.4	9	1.0
<i>Carcharhinus amboinensis</i>	2	0.4	0	0.0	7	2.5	9	1.0
<i>Carcharhinus brevipinna</i>	0	0.0	0	0.0	4	1.5	4	0.4
<i>Carcharhinus cautus</i>	3	0.5	0	0.0	0	0.0	3	0.3
<i>Carcharhinus leucas</i>	0	0.0	0	0.0	2	0.7	2	0.2
<i>Carcharhinus limbatus</i>	1	0.2	0	0.0	1	0.4	2	0.2
<i>Carcharhinus obscurus</i>	2	0.4	0	0.0	0	0.0	2	0.2
<i>Isurus oxyrinchus</i>	1	0.2	0	0.0	1	0.4	2	0.2
<i>Sphyrna mokarran</i>	0	0.0	0	0.0	2	0.7	2	0.2
<i>Carcharhinus brachyurus</i>	0	0.0	1	1.3	0	0.0	1	0.1
<i>Carcharhinus falciformis</i>	0	0.0	0	0.0	1	0.4	1	0.1
<i>Carcharhinus sorrah</i>	0	0.0	0	0.0	1	0.4	1	0.1
<i>Nebrius ferrugineus</i>	0	0.0	0	0.0	1	0.4	1	0.1
<i>Sphyrna lewini</i>	1	0.2	0	0.0	0	0.0	1	0.1
<i>Carcharhinus</i> sp.	0	0.0	0	0.0	3	1.1	3	0.3
Species not recorded	1	0.2	0	0.0	1	0.4	2	0.2
Total	571	100	78	100	275	100	924	100

Note: The percentage of the total shark community is shown.

TABLE 4. Output from generalized linear mixed models derived from shark catch rates.

Fixed effects	Estimate	SE	<i>t</i>	<i>P</i>
All sharks				
DOY (second-order polynomial)	−1.14	0.23	−4.883	<0.0001
Time period (pre vs. post)	0.02	1.27	0.02	0.988
All tiger sharks				
DOY (second-order polynomial)	−1.04	0.25	−4.22	<0.0001
Time period (pre vs. post)	0.01	1.18	0.01	0.990
All large sharks				
DOY (second-order polynomial)	−0.88	0.18	−5	<0.0001
Time period (pre vs. post)	−0.03	1.46	−0.2	0.984
All large tiger sharks				
DOY (second-order polynomial)	−0.88	0.18	−4.91	<0.0001
Time period (pre vs. post)	−0.03	1.47	−0.02	0.983

Note: Intercepts and first-order polynomials are not directly interpretable and thus are excluded for brevity. Significance of the second-order day-of-year (DOY) polynomial coefficient is interpreted as a significant seasonal effect on catch rates. Transect ID (i.e., focal zone) and year were random effects. Variance power differed based on data distribution. Significant model terms are highlighted in boldface text.

DISCUSSION

Understanding species responses to extreme climatic events, as well as the factors driving such responses, is one of the great emerging challenges in ecology (Jentsch et al. 2007), and has even been codified into some definitions of ECEs (Smith 2011b). However, our understanding of how consumers respond to extreme events is often poor, particularly at the community level and in marine environments (Langtimm and Beck 2003, Cahill et al. 2013). Studies that do focus on ECEs and their impacts often focus on the direct lethal and sublethal effects from

physiological stress on individual populations (e.g., Marsh 1989, Matich et al. 2011, Wernberg et al. 2013, Oliver et al. 2017) rather than on the indirect effects of such events, despite the significant effects that legacies (e.g., resource loss) can have on consumers (e.g., Preen and Marsh 1995, Gales et al. 2004, Cahill et al. 2013, Butt et al. 2016). Our results demonstrate that indirect effects from an ECE can have significant and variable effects on abundance and habitat use of consumer communities, even when direct effects are minimal. This finding is notable because it is often difficult to disentangle indirect, legacy effects from direct impacts of physical

FIG. 3. Catch rates of (A) all sharks and (B) large (>300 cm TL) sharks by day of year and time period. Temporally restricted data sets only including months in which data were collected in both time periods are shown for (C) all sharks and (D) large sharks. LOESS smoothers (span = 0.75) with 95% confidence intervals (shaded buffers) have been applied to better visualize temporal patterns. Note different scales in both x- and y-axes. The cold season is represented by the shaded vertical bar.

forcing behind an extreme event (e.g., forest fires, hard freezes). Though we did not explicitly measure the impact of the marine heatwave itself on these consumers, the event did not exceed the thermal tolerance ranges of any of the species studied here, the ranges of all of which (except the Shark Bay Sea Snake, *Aipysurus pooleorum*) extend far into tropical waters. As such, we are confident that any major changes in habitat use or population size are driven by legacy effects of this extreme event. Overall, we found that populations of generalists were less likely to be impacted by resource loss, while changes to habitat use were more variable and difficult to predict.

Though we were not able to explicitly test the drivers of population declines, observations and knowledge of the biology and ecology of each taxon allows some conclusions to be drawn about likely factors driving each consumer's response, as well as the potential for impacted populations to recover.

Effects of seagrass loss on consumer abundance

Sharks.—Ecosystem disturbances, including extreme events, can result in direct impacts to shark populations through emigration or mortality (e.g., Heupel et al.

TABLE 5. Densities of potential tiger shark prey before and after the seagrass die-off.

Taxonomic group	Pre-die-off (1997–2010†)				Post-die-off (2012–2014)				Δ relative density (%)
	No. transects	Abundance	Density (km ²)	SE	No. transects	Abundance	Density (km ²)	SE	
Dolphins	1,443	5,152	2.30	0.09	714	1,517	1.40	0.08	–39.2
Dugongs	2,661	921	0.49	0.04	714	77	0.16	0.03	–67.5
Cormorants	2,661	10,915	20.55	0.73	714	1,886	13.29	0.75	–35.3
Loggerhead turtles‡	2,090	371	0.77	0.05	666	89	0.61	0.07	n.s.
Green turtles‡	2,090	355	0.83	0.06	666	72	0.51	0.06	–38.6
Sea snakes	2,661	420	4.69	0.31	714	28	1.09	0.25	–76.7

Note: n.s., not significant.
† Turtle data excludes transects run prior to 1999 and for which turtles could not be identified to species. Dolphin data excludes 2002–2007.
‡ Uncorrected densities (see *Methods*).

TABLE 6. Zero-inflated mixed model results on relative abundance of air-breathing megafauna before and after the marine heatwave.

Taxonomic group	df	Distribution	<i>t</i>	Pr(> <i>z</i>)
Dolphins	1, 2,142	negative binomial I	6.02	<0.0001
Dugongs	1, 3,360	negative binomial II	4.52	<0.0001
Cormorants	1, 3,360	negative binomial II	9.61	<0.0001
Loggerhead turtles	1, 2,741	Poisson	1.67	0.097
Green turtles	1, 2,741	negative binomial I	2.36	0.019
Sea snakes	1, 3,360	negative binomial II	5.46	<0.0001

Note: Significant changes are highlighted in boldface type.

2003, Matich and Heithaus 2012, Udyawer et al. 2013), though resource loss may also drive shark declines without a triggering extreme event (e.g., Jennings et al. 2008). However, we did not observe an effect of the heat wave or subsequent seagrass die-off on shark abundance. Instead, shark catch rates retained the basic seasonal pattern of this system, with high shark relative abundance in warm months and very low relative abundance in most cool months. Even if demographic impacts of resource loss on predator populations are minimal, however, resource loss can affect other evolutionary and ecological factors impacting predator populations such as predator–prey interactions (Ryall and Fahrig 2006) or phenotypes favored by natural selection (DiBattista et al. 2011). Indeed, tiger sharks captured after the seagrass die-off were on average smaller and more likely to be male than before the seagrass die-off. Importantly, however, the chance of catching large (>300 cm TL) tiger sharks, those most able to consume dugongs in this system, remained constant before and after the event.

The insensitivity of tiger sharks to widespread seagrass die-off in this system is predicted by theory; namely, that generalists are expected to be more resilient to habitat loss than specialists (Ryall and Fahrig 2006). Tiger sharks are generalists at the individual level, feeding on

fish, other elasmobranchs, sea snakes, gastropods, crustaceans, birds, and marine mammals (e.g., Lowe et al. 1996, Castro 2010, Matich et al. 2011, Ferreira et al. 2017), so local declines in one or even several prey species may not greatly affect tiger shark populations in Shark Bay. Instead, seagrass loss could actually increase short-term shark foraging success, especially on energetically stressed prey that take greater risks to obtain food (Heithaus et al. 2007a), prey that use seagrass for refuge like sea snakes (Kerford et al. 2008, Wirsing and Heithaus 2009), or prey that rely on clear water and visual detection of predators to reduce predation risk (i.e., dugongs, Wirsing et al. 2007a). Tiger sharks can also range widely (e.g., Ferreira et al. 2015), and individuals within Shark Bay rarely reside there for extended periods (Heithaus et al. 2007b). This may drive resilience to resource loss in what is effectively only a part of an individual tiger shark’s range.

Sea snakes.—Sea snakes, which are entirely marine, are heavily dependent on seagrass beds to both find prey and seek refuge from predators (e.g., Kerford et al. 2008, Wirsing and Heithaus 2009). This heavy dependence on seagrass, combined with the extremely small home range sizes and limited dispersal potential sea snakes can exhibit (in some cases, one to two orders of magnitude smaller than the study area, e.g., Burns and Heatwole 1998, Lukoschek et al. 2008, Lukoschek and Shine 2012), suggest that the declines we observed were largely driven by mortality, not emigration. It remains unclear, however, the degree to which this putative mortality was driven by starvation vs. predation.

Dugongs.—As obligate seagrass herbivores (Marsh et al. 1982), dugongs are also heavily reliant on seagrass. Though they prefer tropical seagrasses, dugongs in Shark Bay will also crop *Amphibolis antarctica* shoots when tropical seagrasses are rare or difficult to access (Anderson 1986, Wirsing et al. 2007a). Because the marine heat wave resulted in an initial loss of both

FIG. 4. Changes in landscape-level density of dolphins (A), dugongs (B), cormorants (C), loggerhead turtles (D), green turtles (E), and sea snakes (F) within Shark Bay following the seagrass die-off. Significant differences ($P \leq 0.05$) are denoted with asterisks. Turtle density comparisons are based on uncorrected densities and are underestimates of true densities in this system. Values are mean $\pm$ SE.

TABLE 7. Zero-inflated generalized mixed model results on habitat use of air-breathing megafauna before and after the seagrass die-off.

Taxonomic group	Distribution	Model interactions			
		HAB $\times$ TP $\times$ CPUE	HAB $\times$ TP	HAB $\times$ CPUE	TP $\times$ CPUE
Dolphins	negative binomial I	0.001	na	na	na
Dugongs	negative binomial II	n.s.	n.s.	0.011	0.009
Cormorants	negative binomial II	n.s.	<0.001	n.s.	<0.001
Loggerhead turtles	Poisson	n.s.	<0.001	0.032	n.s.
Green turtles	negative binomial I	n.s.	n.s.	n.s.	n.s.

Notes: HAB, habitat (shallow, deep); TP, time period (before or after the heat wave); CPUE, catch per unit effort (number of sharks caught per 100 hook-hours) in deep-channel habitats, used as a continuous estimate of system-wide shark abundance; na, not applicable; n.s., not significant. Two-way interactions were not evaluated when three-way interactions were significant.

FIG. 5. Changes in proportional habitat use of (A) dolphins, (B) dugongs, (C) Cormorants, (D) loggerhead turtles, and (E) green turtles in relation to shark abundance (as measured by shark catch rate; x -axis) and time period (green vs. yellow shading). To facilitate visual interpretation, individual transects were aggregated by month and abundance in each habitat type expressed as a ratio here, with point diameter correlating to the number of transects. Actual statistical analysis occurred on non-aggregated data (see *Methods* and Table 7). Regressions are weighted by number of transects compared within each month. Catch per unit effort (CPUE) in panel B refers to large sharks only. *significant three way interaction ($P < 0.05$).

A. antarctica and some tropical seagrasses (Thomson et al. 2014, Nowicki et al. 2017), the dugong declines observed here are not surprising.

Dugongs are able to choose habitat based on presence of preferred seagrass food resources, and can maintain a spatial memory of highly productive seagrass beds that they revisit over time (Holley 2006, Sheppard et al. 2006). In Western Australia and elsewhere, dugongs often respond to large-scale seagrass dieback events with long-distance emigration to alternative foraging areas

and subsequent reimmigration following recovery of fast-growing tropical seagrasses (e.g., Preen and Marsh 1995, Loneragan et al. 2003, Gales et al. 2004, Holley 2006, Hodgson 2007). When mass dugong mortality does occur, widespread dugong strandings are generally observed (e.g., Marsh 1989, Preen and Marsh 1995, Great Barrier Reef Marine Park Authority 2014). We encountered no dead, dying, stranded, or freshly wounded dugongs during post-heat-wave sampling, and there was no abnormal increase in stranding reports in

Shark Bay (Department of Parks and Wildlife, *personal communication*). As such, dugong declines observed here are likely primarily driven by emigration rather than mass mortality. Generally, it remains unclear what mechanisms determine whether dugongs will emigrate or strand in response to seagrass loss: this would be an important area for future research. Because dugongs are capable of strong top-down control on seagrass ecosystems (e.g., Preen 1995), and because tropical seagrass recovery has already begun (Nowicki et al. 2017), a return of dugongs to Shark Bay seems likely, and may have important implications for the recovery trajectory of the system's degraded seagrass community.

Sea turtles.—The differential response of loggerhead and green turtles to seagrass loss can be explained in part by differences in diet and foraging ecology. Loggerhead turtles in Shark Bay are diet generalists that feed largely on benthic invertebrates and other taxa (Thomson et al. 2012b), though they will also scavenge (Seney and Musick 2007). Therefore, seagrass loss might have little short-term impact, or even a temporarily positive one, if search and handling times for benthic crustaceans and bivalves that use seagrass as cover are reduced. In contrast, green turtles in Shark Bay feed on temperate and tropical seagrasses in addition to macroalgae, gelatinous macroplankton, and benthic macroinvertebrates (e.g., sponges, ascidians), with individual turtles specializing on specific diet mixtures (Burkholder et al. 2011, Thomson et al. 2014, 2018). Indeed, following the seagrass die-off, the body condition of captured green turtles declined markedly (Thomson et al. 2014), and extremely emaciated green turtles were repeatedly encountered in the study system between 2012 and 2015 (R. Nowicki, *personal observation*). This suggests starvation mortality was likely an important driver of the observed decline, though increased risk-taking and reduced escape potential by energetically stressed green turtles in Shark Bay (see Heithaus et al. 2007a) likely also increased mortality to tiger shark predation.

Pied Cormorants.—Cormorants are highly mobile piscivores that use seagrass habitats primarily for foraging. As such, their ~35% decline in abundance is likely to be linked to the significant reduction in the biomass of seagrass-associated fishes in the system (Heithaus 2004; R. Nowicki et al., *unpublished data*) on which they primarily feed (Heithaus 2005). In a contemporary study by Cannell et al. (2012) on Little Penguins (*Eudyptula minor*) on Penguin Island, Western Australia, the 2011 Ningaloo Niño is thought to have driven food reductions and a rise in underweight, dead birds. Cormorant declines in Shark Bay, however, occurred mostly in the cold season (when the breeding season occurs; Dell and Cherriman 2008), suggesting that mortality alone is unlikely to be entirely responsible for observed population reduction.

Bottlenose dolphins.—The mechanism for the ~40% decline in bottlenose dolphin densities is unclear. Extreme events can cause short-term (i.e., several week) dolphin emigration (e.g., Fury and Harrison 2011) and dolphin abundance is in some places correlated with the ENSO cycle (Sprogis et al. 2018). These factors cannot explain the sustained reduction in dolphin abundance when compared to the previous 12 years of data, however, because the La Niña associated with the 2011 marine heat wave ended in March 2012, when we began post-disturbance data collection (Bureau of Meteorology 2012). It is possible that the sustained reduction in dolphin density is a result of emigration because of the thermal forcing from the heat wave itself. We think this unlikely, however, because the range of *Tursiops aduncus* extends far into tropical waters where sea temperatures regularly meet or exceed those encountered at the height of the marine heat wave in Shark Bay.

Tursiops aduncus within the study area have relatively stable home ranges, high philopatry, and inter-individual social bonds that likely play critical roles in reproductive success and fitness (e.g., Smolker et al. 1992, Connor et al. 2001, Krützen et al. 2004, Tsai and Mann 2013). Dolphins are thus likely to remain in the system as long as adequate resources are available. However, abnormal dolphin mortality was not observed during the course of this study or by a contemporary study of mother–calf pairs (Miketa 2018), making it difficult to explain the declines observed here. While dolphins in Shark Bay forage on seagrass-associated fishes, they are less dependent on seagrass for forage than cormorants or sea snakes (Heithaus and Dill 2002, Heithaus 2004, Sargeant et al. 2007, Heithaus et al. 2013).

Drivers of mesoconsumer habitat use patterns following seagrass loss

Myriad factors can influence consumer habitat use, including resource availability, consumer body condition, social factors, physiological effects, and predation risk (Fretwell and Lucas 1969, Clark 1994, Heithaus et al. 2009). Following the seagrass die-off, we observed shifts in habitat use by several species, though habitat shifts consistent with increased risk taking were only observed in bottlenose dolphins. These results highlight the complex nature of species responses to resource loss and emphasize the role of multiple drivers in species-specific disturbance response.

Changes in food supply.—The impact of seagrass loss on food supplies of air-breathing megafauna in this system is likely species specific, and in some cases may be counterintuitive. Net loss of seagrass biomass represents an obvious system-wide food reduction for seagrass herbivores, including dugongs and some green turtles, though expansion by tropical seagrasses in the wake of *Amphibolis* declines (Nowicki et al. 2017) may soften this loss.

However, while the extent of seagrass on shallow banks has been reduced, these banks still represent relatively “resource rich” habitats when compared to seagrass depauperate deep channels. Herbivores that rely on seagrass directly may therefore be forced to continue to spend time in remaining seagrass habitats, even if predation risk in those habitats has increased. This appears to be the case with dugongs, which increased relative use of shallow habitats consistently across shark CPUE following the seagrass die-off (Fig. 5).

Species that rely on seagrass associated prey are likely to exhibit more complex responses to massive seagrass loss. Piscivorous air-breathing megafauna (sea snakes, Cormorants, dolphins) have likely experienced a net reduction in food supply driven by reduced teleost fish biomass in shallow habitats (R. Nowicki et al., *unpublished data*). However, reductions of absolute food supply may be offset somewhat by increased teleost density in remaining vegetated habitats post-die-off (R. Nowicki et al., *unpublished data*), and through reduced refuge for teleosts and increased echolocation and foraging efficiency in newly denuded habitats (Wilson et al. 2013, Miketa 2018). For example, a contemporary study in Shark Bay indicated that while seagrass associated dolphins used seagrass habitats more frequently after the heat wave, they reduced their foraging time in heavily damaged beds, instead foraging in relatively intact seagrass habitats (Miketa 2018). Similarly, cormorants in this system track prey densities even at fine, microhabitat scales (Heithaus 2005), and cormorants were more likely to use shallow habitats after the seagrass die-off. Changes in cormorant foraging efficiency may drive this shift in habitat use independent of shark abundance.

Loggerhead turtles increased their relative use of shallow habitats regardless of shark catch rate after the seagrass die-off. This shift, combined with the lack of numerical response to the seagrass die-off, suggest that as with tiger sharks, seagrass loss may be at least temporarily advantageous for this species. In Shark Bay, loggerhead turtles are most commonly found, and appear to forage most often, in unvegetated habitats where they can locate and consume both epibenthic and infaunal invertebrates more easily (Thomson et al. 2012b). Loggerhead turtles are also known to scavenge opportunistically and to have broad diets at both the individual and population level (Plotkin et al. 1993, Tomas et al. 2001, Casale et al. 2008, Thomson et al. 2012b). Unfortunately, time series data on bivalve abundance and density were not available to test changes in food availability for this species in our study area. In general, stocks of both saucer scallops (*Amusium balloti*) and blue swimmer crabs (*Portunus armatus*) suffered heavy declines in the region following 2011, which has been attributed to both direct effects (temperature related mortality) and indirect legacy effects (seagrass loss) associated with the heat wave (Caputi et al. 2014). As with dolphins and cormorants, however, it is plausible that newly denuded seagrass habitats yield reduced search time, increased

prey encounter rates, or increased turtle foraging success, especially given the capability of loggerhead turtles to scavenge. This would explain shifts in loggerhead turtle habitat use since the seagrass die-off.

Changes to predation risk.—Because tiger sharks dominated the catch both before and after the die-off, we inferred that warm periods remain risky to tiger shark prey at the ecosystem scale, whereas most winters remain relatively safe. Thus, the broad temporal pattern of predation risk that typified this system and drove shifts in prey habitat use patterns prior to the heat wave (Heithaus et al. 2012 and references therein) likely remains fundamentally unchanged despite massive resource loss. However, predation risk is mediated in part by factors other than predator abundance and encounter rate, such as likelihood of detection of both predator and prey and escape probability (Lima and Dill 1990), which are in turn mediated by properties of predators, prey, the environment, and higher order interactions (Clark 1994, Heithaus et al. 2007c, 2009, Wirsing et al. 2010). Furthermore, anti-predator behavior is also balanced with other needs, such as the need to forage. Therefore, changes to other drivers of predation risk may alter the role of tiger shark predation and top down control in this ecosystem.

Reduced water clarity associated with the die-off (Nowicki et al. 2017) may alter predator–prey interactions by reducing the efficacy of both antipredator behavior (i.e., vigilance, flight initiation) and prey detection by predators. This may result in an altered risk landscape and changes to megafauna antipredator behavior, even for species that do not directly rely on vegetation to reduce predation risk. For example, dugongs, cormorants, and green turtles minimize predation risk by detecting predators early and either fleeing from or outmaneuvering them (Heithaus et al. 2012), and at least some of these escape maximizers avoid profitable behaviors if those behaviors reduce visibility (Wirsing et al. 2007a). This may result in changes to net top-down control, or in the relative importance of direct predation and predation risk to the fitness of these consumers, even if predator abundance has remained constant.

Although decreased visibility is likely to increase predation risk for visually dependent escape maximizers, other prey may benefit from reduced visibility if the effective prey detection radius of tiger sharks is reduced. Loggerhead turtles, for example, rely on a thick, rounded shell instead of speed to survive predator encounters (Heithaus et al. 2002, 2008), an antipredator strategy that may be relatively insensitive to reduced water clarity. Reduced water clarity may alter predation risk on bottlenose dolphins by changing the relative importance of visual and non-visual cues among dolphins and sharks alike. Because dolphins in this system use seagrass banks primarily for foraging and move to deeper areas for resting (Heithaus and Dill 2002), the observed pattern of

increased proportional use of risky interior habitats by dolphins is consistent with several potential (and non-exclusive) drivers, including individuals taking greater risks to obtain foraging rewards because of reduced energetic state and changes in foraging success in remaining seagrass habitats.

Though tiger shark abundance has not changed, changes in dolphin habitat use patterns could also potentially owe to spatial shifts in tiger shark habitat use patterns within the study system. Whereas we were unable to robustly assess microhabitat use patterns of tiger sharks in the study system after the seagrass die-off, in part because logistical constraints (high rates of bait loss) prevent shark fishing in shallow habitats (Heithaus 2001), we think that this explanation is unlikely. Video and active acoustic tracking of sharks before the die-off revealed that tiger sharks spend more time in shallow than deep habitats (Heithaus et al. 2002, 2006). With the increased use of shallow habitats by bottlenose dolphins, cormorants, and loggerhead turtles, it seems unlikely that tiger sharks would reverse previous habitat preferences to instead target deep habitats. Even if tiger sharks have shifted to using shallow habitats less frequently (and reducing shark encounter rates experienced by prey), encounter probability is only one component of predation risk (Lima and Dill 1990, Heithaus et al. 2009), and habitat types can carry intrinsic risk that can alter prey behavior (reviewed in Laundré et al. 2010). Indeed, shallow habitats reduce the vertical maneuverability potential (and thus escape potential) for dugongs (Wirsing et al. 2007c), dolphins (Heithaus and Dill 2002, 2006), and green turtles (Heithaus et al. 2007a), further supporting the notion that tiger sharks should continue to prefer shallow habitats.

Synthesis and broader ecological implications.—Whereas studies manipulating resources, predator, and prey are relatively tractable in terrestrial systems, they are rarely feasible in marine systems, particularly at landscape and community scales. The Ningaloo Niño of 2011 offered a rare opportunity to observe the direct and indirect effects of an extreme climatic event (ECE) on a relatively pristine marine ecosystem at large scales and across multiple trophic levels.

Because direct and indirect effects of ECEs operate through different pathways (i.e., physical forcing vs. resource loss), fauna that are resilient to one kind of effect may still succumb to ECEs through the other. For example, while direct abiotic effects of the Ningaloo Niño were likely uniformly negligible on the populations studied here, indirect effects varied substantially. In agreement with theory and results found in other systems, resource loss most strongly affected specialists, while generalist consumers like tiger sharks and loggerhead turtles remained relatively stable. Unsurprisingly, population declines were highest among species most reliant on seagrasses: dugongs, which are obligate

seagrass herbivores, and sea snakes, which rely on seagrass beds both as a hunting ground and a refuge from their own predators. These patterns reflect differential sensitivity and adaptive capacity to resource loss, two of the components predicted to influence climate vulnerability (Butt et al. 2016).

While tiger sharks were resilient to the ECE as a tropical generalist predator, a temperate generalist predator may have experienced large population declines from direct physical forcing, even if legacy effects would have been minimal. As such, overall vulnerability to ECEs may be broadly predictable if one has information about both a species' physiological constraints and its resource use patterns. Assessments of the vulnerability of consumers to ECEs should therefore incorporate vulnerability to both direct and indirect effects. Furthermore, we demonstrate and caution that just because one pathway has little effect on an assemblage does not guarantee negligible overall effects.

In the absence of direct mortality evidence (such as strandings), it is reasonable to conclude that the mechanism of population decline is likely mediated by dispersal capacity, with low dispersers (like sea snakes) succumbing to mortality and more mobile species like dugongs and cormorants emigrating from the system. This has strong implications for both future population and community dynamics of these species and for the resilience of these populations to future stressors, but needs to be further tested.

A growing number of studies demonstrate that ECEs can have fundamental and lasting effects on marine communities by killing primary producers and altering subsequent species interactions between consumers and producers (e.g., Vergés et al. 2014, Bennett et al. 2015). This illustrates the importance of predicting when and how the direct and indirect effects of extreme events strengthen or weaken top-down control. Changes to the strength and nature of top-down control are likely when disturbance impacts affect different trophic levels unequally and may be mediated by several non-exclusive pathways. First, prey that are energetically stressed are less able to heed predation risk, often resulting in an increase in the relative importance of direct predation. Indeed, both theory and empirical work indicate that resource limitation can mediate the effects of top down control on plant communities through both direct predation and predation risk (Oksanen et al. 1981, Clark 1994, Chase 1996, Werner and Peacor 2006, Heithaus et al. 2007a, Schmitz 2010). Second, changes in the food landscape may change the spatial component of food for safety trade-offs, even if predators populations remain similar. Finally, changes in the physical landscape, such as defoliation and reductions in water clarity, may alter predation risk and direct predation by modifying encounter, attack, and escape rates. These factors in combination make predicting specific changes to predator-prey dynamics challenging. Nonetheless, our data show that in at least some cases, ECEs can change

predation risk dynamics through legacy effects, even when predator populations remain constant.

In conclusion, we argue that a better understanding and prediction of the ecological impacts of ECEs is necessary, and can be obtained through explicit recognition that (1) ECEs generate both direct and indirect effects, which operate via different pathways; (2) a consumer's resilience to one pathway does not inherently convey resilience to the other; (3) first-order predictions about vulnerabilities to ECEs are likely possible given knowledge of a consumer's physiological tolerances and resource use patterns; and (4) ECEs will almost certainly affect different trophic levels unequally, which when combined with changes in landscape may fundamentally alter predator/prey dynamics even if one or both populations remain similar after an ECE occurs. We advocate for greater integration of predator-prey theory and disturbance ecology in the development of frameworks designed to predict how ecosystems will respond to the myriad anthropogenic stressors they face now and in the future. To our knowledge, this is among the first studies to investigate the legacy effects of an ECE on the abundance and habitat use of such a wide variety of marine consumers at the ecosystem scale, and represents a small but important step in integrating disturbance ecology and predator–prey ecology.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1365/full>

DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.7sg523n>