Resistance, Extinction, and Everything in Between – The Diverse Responses of Seaweeds to Marine Heatwaves

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Globally, anomalously warm temperature events have increased by 34% in frequency and 17% in duration from 1925 to 2016 with potentially major impacts on coastal ecosystems. These "marine heatwaves" (MHWs) have been linked to changes in primary productivity, community composition and biogeography of seaweeds, which often control ecosystem function and services. Here we review the literature on seaweed responses to MHWs, including 58 observations related to resistance, bleaching, changes in abundance, species invasions and local to regional extinctions. More records existed for canopy-forming kelps and bladed and filamentous turf-forming seaweeds than for canopy-forming fucoids, geniculate coralline turf and crustose coralline algae. Turf-forming seaweeds, especially invasive seaweeds, generally increased in abundance after a MHW, whereas native canopy-forming kelps and fucoids typically declined in abundance. We also found four examples of regional extinctions of kelp and fucoids following specific MHWs, events that likely have long term consequences for ecological structure and functioning. Although a relatively small number of studies have described impacts of MHWs on seaweed, the broad range of documented responses highlights the necessity of better baseline information regarding seaweed distributions and performance, and the need to study specific characteristics of MHWs that affect the vulnerability and resilience of seaweeds to these increasingly important climatic perturbations. A major challenge will be to disentangle impacts caused by the extreme temperature increases of MHWs itself from co-occurring potential stressors including altered current patterns, increasing herbivory, changes in water clarity and nutrient content, solar radiation and desiccation stress in the intertidal zone. With future increases anticipated in the intensity, duration and frequencies of MHWs, we expect to see more replacements of large long-lived habitat forming seaweeds with smaller ephemeral seaweeds, reducing the habitat structure and effective services seaweed-dominated reefs can provide.

Keywords: temperature extremes, temperature anomalies, climate variability, extreme climatic events, macroalgae, foundation species, habitat formers, range contraction

INTRODUCTION

Anthropogenic stressors have resulted in widespread changes in coastal marine ecosystems (Perry et al., 2005; Sorte et al., 2010; Pecl et al., 2017), with increased temperature being one of the most pervasive environmental drivers of change (Hoegh-Guldberg and Bruno, 2010; Wernberg et al., 2011a; Smale et al., 2019). It is estimated that >70% of the world's coastlines have experienced significant warming in the past four decades (Lima and Wethey, 2012), with predicted near-surface warming in the order of 2–7°C by the end of the century (Christensen et al., 2007; Lima and Wethey, 2012). As a consequence of continued ocean warming, 46% of the world's coastlines have experienced a significant decrease in the frequency of cold days, whereas 38% of coastlines have experienced an increased frequency of extremely hot days when sea surface temperature (SST) exceed the 95th percentile of standardized anomalies of the raw SST between 1982–2010 (Lima and Wethey, 2012). Recently, Hobday et al. (2016) proposed a framework for describing anomalously warm water events as "marine heatwaves" (MHWs), which included a quantitative definition of periods when SSTs exceed the 90th percentile of the climatological mean for at least five consecutive days. Using this approach, Oliver et al. (2018) empirically showed that MHWs have increased in both frequency and duration since the early 20th century, by 34 and 17%, respectively. The underlying driver of this trend was primarily increased mean ocean temperature (Frölicher et al., 2018; Oliver et al., 2018, 2019), with projections of MHWs under a range of climate change scenarios showing they will likely increase in intensity, frequency and duration with ongoing climate change (Frölicher et al., 2018). Furthermore, MHWs are the direct result of local-scale processes (e.g., ocean heat advection, vertical mixing) which can be suppressed or enhanced by remote influences (e.g., climate modes such as ENSO) (Holbrook et al., 2018). Often, there are multiple drivers that significantly influence the occurrence of a MHW, resulting in temperature extremes being generally accompanied by a multitude of altered environmental factors such as ocean currents, wave action, solar radiation and in the intertidal zone, desiccation stress. This co-occurrence of changes in many environmental conditions makes it difficult to disentangle the interactive effects of different factors during MHWs.

Some MHWs have had significant impacts on marine ecosystems, with substantial ecological and socio-economic consequences (Madin et al., 2012; Pecl et al., 2017; Frölicher and Laufkötter, 2018; Smale et al., 2019). Responses include coral bleaching (Couch et al., 2017; Hoegh-Guldberg and Poloczanska, 2017; Le Nohaïc et al., 2017), loss of kelp forest (Wernberg et al., 2016; Thomsen and South, 2019; Thomsen et al., 2019), increased surface layer stratification (Bond et al., 2015; Schaeffer and Roughan, 2017), mass mortalities of marine invertebrates (Garrabou et al., 2009; Oliver et al., 2017), rapid range shifts (Smale and Wernberg, 2013), restructuring of communities (Wernberg et al., 2013a; Bennett et al., 2015b), and fisheries closures (Caputi et al., 2016, 2019; Oliver et al., 2017). In contrast to the impacts of long-term gradual warming, MHWs can outpace adaptive capabilities and cause sudden and dramatic

regime shifts that are more difficult to predict and manage (Scheffer and Carpenter, 2003; Andersen et al., 2009; Wernberg et al., 2016). Moreover, biological responses to MHWs can have devastating consequences for local economies, in particular affecting commercial fisheries, which rely on healthy ecosystem functioning for their productivity (Mills et al., 2013; Bennett et al., 2016; Caputi et al., 2016; Wernberg et al., 2019). Observations of these extreme events show that MHWs are key drivers of ecosystem-scale change, and demonstrate the drastic consequences MHWs can have on the structure and function of marine communities and ecosystems (Dayton and Tegner, 1983; Pearce and Feng, 2013; Wernberg et al., 2013a).

Seaweeds (marine macroalgae) are large, multicellular algae which often dominate shallow-water rocky ecosystems where they can form extensive marine forests (Wernberg and Filbee-Dexter, 2019). Seaweeds represent essential components of coastal habitats and underpin highly diverse ecosystems (Wernberg et al., 2013a; Bennett et al., 2016; Teagle et al., 2017). As important primary producers and habitat formers, seaweeds influence shallow-water communities on rocky reefs globally (Dayton, 1985; Tegner et al., 1997; Bertness et al., 1999; Wernberg et al., 2003; Buschbaum et al., 2006; Tuya and Thomsen, 2009; Egan et al., 2014). Kelp forests, extensive reef systems dominated by large laminarian and fucalean seaweeds (Steneck and Johnson, 2013; Wernberg and Filbee-Dexter, 2019; Wernberg et al., 2019), are especially important for local communities as they directly modify the environment surrounding them and influence adjacent habitats (Gaylord et al., 2007; Wernberg et al., 2018b). Most canopy-forming seaweed species are adapted to thrive in cool, clear, nutrient-rich waters, which makes them vulnerable to anthropogenic stressors influencing water clarity and to ocean warming in warmer parts of their distributions (Fernandez, 2011). Consequently, substantial changes in seaweed distribution and abundance have been observed in various ecoregions over the last five decades due to global change (Lima et al., 2007; Wernberg et al., 2011b; Krumhansl et al., 2016; Filbee-Dexter and Wernberg, 2018; Casado-Amezúa et al., 2019) as well as recent changes due to MHWs (Carballo et al., 2002; Vergés et al., 2014a; Mathiesen, 2016; Reed et al., 2016; Wernberg et al., 2016; Thomsen et al., 2019).

Ocean warming threatens seaweeds as the performance of populations and individuals are affected both directly and indirectly by warming. Warming can directly affect the physiology of seaweeds (Van den Hoek, 1982; Kordas et al., 2011; Tuya et al., 2012; Wernberg et al., 2013b) through sublethal stress leading to reduced performance and increased vulnerability to other stressors (Wernberg et al., 2010). Indirect effects include changes in species interactions, such as shifts in competitive hierarchies and over-consumption by range-shifting herbivores (Haraguchi et al., 2009; Ling et al., 2009; Vergés et al., 2014a; Bennett et al., 2015b; Franco et al., 2015). Pervasive warming of long duration and magnitude, with potential interaction with additional stressors such as solar radiation, desiccation stress and eutrophication, can ultimately exceed a species' lethal thermal limits (Van den Hoek, 1982). Exceeding the sublethal thermal threshold of a species leads to failure to reproduce in marginal populations (causing population

attrition), and can result in local to regional extinctions and ultimately range contractions (O'Brien and Scheibling, 2016; Wernberg and Straub, 2016; Wernberg et al., 2016; Smale et al., 2019).

Overall, increasing temperatures and MHWs directly and indirectly alter the distribution and abundance of seaweeds, their associated species and interactions between species with cascading effects on ecosystem functions and the provision of ecosystem services (Harley et al., 2012; Vergés et al., 2014a; Wernberg and Straub, 2016; Filbee-Dexter and Wernberg, 2018; Thomsen and South, 2019). Given the expected increase in the frequency and duration of MHWs, it is crucial to understand MHW impacts on underlying biological mechanisms which lead to changes in the abundance, distribution and function of foundation species such as seaweeds (IPCC, 2007; Kirtman et al., 2013; Oliver et al., 2018). Recent MHWs have caused substantial ecological changes with economic consequences across marine systems globally (Frölicher and Laufkötter, 2018; Smale et al., 2019). However, little is known about how these extreme events have impacted seaweeds and comprehensive overviews are lacking (but see Smale et al., 2019). Here, we review documented impacts of MHWs on seaweeds, highlighting the diversity of observed responses.

MATERIALS AND METHODS

We conducted a literature search using the library search portal at the University of Western Australia, ResearchGate, Google Scholar and the reference lists of papers returned in the search. We included only MHWs observed in natural ecosystems, not experiments that aimed to mimic MHWs (e.g., Gouvea et al., 2017). Keywords used in the literature search included "marine heatwave*," "marine heat wave," "unusually warm," "abnormally warm," "abnormal temperature," "positive temperature event*," "extreme event*," "hot summer" in combination with "marine," "seaweed*," "macroalga*," "turf" and "crustose coralline alga*." The cut-off date for this general search was 15th of February 2019. News articles were only included where no peer-reviewed journal articles could be found.

The identified literature was screened using the MHW definition (Hobday et al., 2016) for occurrence of an unusual extreme temperature event. Due to the nature of MHWs, the extreme temperature anomalies which define these events (Hobday et al., 2016) co-occur with multiple alterations in the affected ecosystems such as current patterns, increased surface layer stratification, increased desiccation stress in the intertidal zone, altered wave activity and likelihood of strong storms. Contribution of these factors to observed impacts on organisms cannot be disentangled with certainty yet. Hence for the purpose of this paper, reported effects are discussed and categorized as MHW effects on the study organisms and ecosystems.

The observations of seaweed responses to MHW events identified through the literature search were assigned to five broad categories based on the severity of their biological response (**Figure 1**): responses were not observable or confined to negligible sublethal stress (group 1, resistance); visible signs of sublethal stress (group 2, physiological performance, e.g., tissue bleaching); altered ecological interactions (group 3, ecological performance, e.g., changes in reproduction or herbivory affecting competition and consumer pressure); altered abundance (group 4, changes in abundance of native species or arrivals of invasive species), and; widespread seaweed mortality (group 5, range shifts and local to regional extinction).

The observed seaweed species were also categorized into functional groups based on their growth forms: crust (CCA: crustose coralline algae); turf-forming seaweeds (bladed, filamentous and GCA: geniculate coralline algae) and canopy-forming seaweeds (kelp, fucoids). Information was combined to determine how many observations existed per broad response group for each functional group.

RESULTS

A total of 58 observations of seaweed responses to MHWs were identified, reported in 17 peer-reviewed papers and three additional news articles (**Table 1**), often with multiple observations per seaweed group. Resistance ($n = 3$) and extinctions ($n = 4$) were least frequently reported, and bleaching was observed in only one event for six turf-forming red seaweeds and one brown kelp ($n = 7$). The majority of records were changes in abundance; turf-forming seaweeds typically increased in abundance ($n = 18$) whereas large canopy-formers declined in abundance ($n = 17$; **Figure 2**). Overall, 25 observations were found for canopy-forming seaweeds, 29 observations for turf-forming seaweeds and only four observations for CCA. However, there could be a bias in reported observations toward large, conspicuous canopy-formers, with better baseline data availability or because changes are easier to detect for larger species. Additionally, publication bias is likely against reporting resistance or negligent effects with increased likelihood of publication for studies that detect and report large-scale changes.

Physiological Performance

Tissue bleaching is a good primary indicator of experienced sublethal stress (Hawkins and Hartnoll, 1985). Changes to seaweed condition was categorized as visible discoloration (whitening or turning greenish) of the blade tissue due to loss of surface integrity. This indicates loss or reduction in pigmentation, which in turn is associated with reduced photosynthetic performance (Marzinelli et al., 2015; Xiao et al., 2015). Although changes in physiological performance should be relatively easy to identify, observations for multiple species have only been reported for one MHW and only for turf-forming seaweeds as well as one kelp. During the 1982/83 El Niño in California, changes in coloration from red to unusually green were evident for *Porphyra perforata*, *Iridaea cordata*, *Laurencia spectabilis*, *Prionitis lanceolata*, *Gastroclonium subarticulatum*, and *Gigartina canaliculata* near Point Piedras

Response Group		Response	Examples	MHW
1	Resistance	Not detected	*Ecklonia radiata*[10;12], CCA[12], turf forming algae[12] *Macrocystis pyrifera*[16]	2011 Ningaloo Niño, WA (Hamelin Bay) 2013/14 the blob, Southern California
2	Health	Bleaching	*Egregia menziesii* [3] *Porphyra perforata*[4], *Iridaea cordata*[4], *Laurencia spectabilis*[4], *Prionitis lanceolata*[4], *Gastroclonium subarticulatum*[4], *Gigartina canaliculata* [4]	1982/83 ENSO California
3	Ecological performance	Increased recruitment potential	*Pelvetia fastigiata*[3], *Sargassum muticum* [3]	1982/83 ENSO California
		Increased herbivory	Range-expansion of sub-tropical and tropical herbivores [5, 10]	1997/98 ENSO 2011 Ningaloo Niño; WA
4	Abundance change to altered biodiversity indices	Increased abundance natives	*Ulva spp.*[2], *Enteromorpha spp.*[2], *Iridaea spp.* [2] Geniculate coralline algae [8; 9] CCA[4] and turf-algae cover [7 -10; 13;15] *Chorda filum*[14]	1982/83 ENSO, Chile 2009/10 ENSO, California 2011 Ningaloo Niño; WA
		Increased abundance invasives	*Giffordia mitchelliae* [1] *Agardhiella tenera*[6], *Amphiroa misakiensis*[6], *Caulerpa sertularoides*[6], *Padina durvillaei*[6], *Jania capillacea*[6], *Jania mexicana*[6] *Undaria pinnatifida*[17]	1982/83 ENSO; South America 1997/98 ENSO, Mexico 2017/18 Tasman Sea MHW
		Declined abundance natives	*Sargassum sp.*[1], *Blossevillea galapagensis*[1], *Ulva spp.*[1], *Spermothamnio spp.*[1], *Centroceras spp.*[1] *Lessonia nigrescens*[2], *Macrocystis integrifolia*[2] *Egregia menziesii*[3], *Eisenia arborea* [3] *Mastocarpus papillatus*[4] *Lessonia trabeculata*[5], *Macrocystis pyrifera*[5] *Ecklonia cava*[7] CCA [14] *Saccharina latissima*[15]	1982/83 ENSO; South America 1982/83 ENSO; Chile 1982/83 ENSO; California 1997/98 ENSO; Chile 2011 Ningaloo Niño; WA 1997, 2002, 2006 hot summers, Norway
5	Extinction	Range shift, local to regional extinction	*Ecklonia radiata*[10, 11], *Scytothalia dorycarpa* [10, 11] *Macrocystis pyrifera* [c] *Durvillaea poha* [17]	2011 Ningaloo Niño; WA 2015/16 Tasmanian MHW 2017/18 Tasman Sea MHW
		Global extinction	Not yet observed	

FIGURE 1 | Schematic of different responses of seaweeds with examples to MHWs grouped by severity of the observed response, from no observed effect (e.g., resistance) and less severe impact (e.g., tissue bleaching) at the **top**, to more severe impacts (e.g., local to global extinctions) at the **bottom**. Number/letter in brackets refer to **Table 1**. Several species have multiple observations as their responses differed between locations, e.g., resistance, abundance decline, and regional extinction were observed for *Ecklonia radiata* and *Scytothalia dorycarpa* along the latitudinal gradient in Western Australia.

(Murray and Horn, 1989) and at La Jolla many adult individuals of the kelp *Egregia menziesii* became reddish due to stress (Gunnill, 1985).
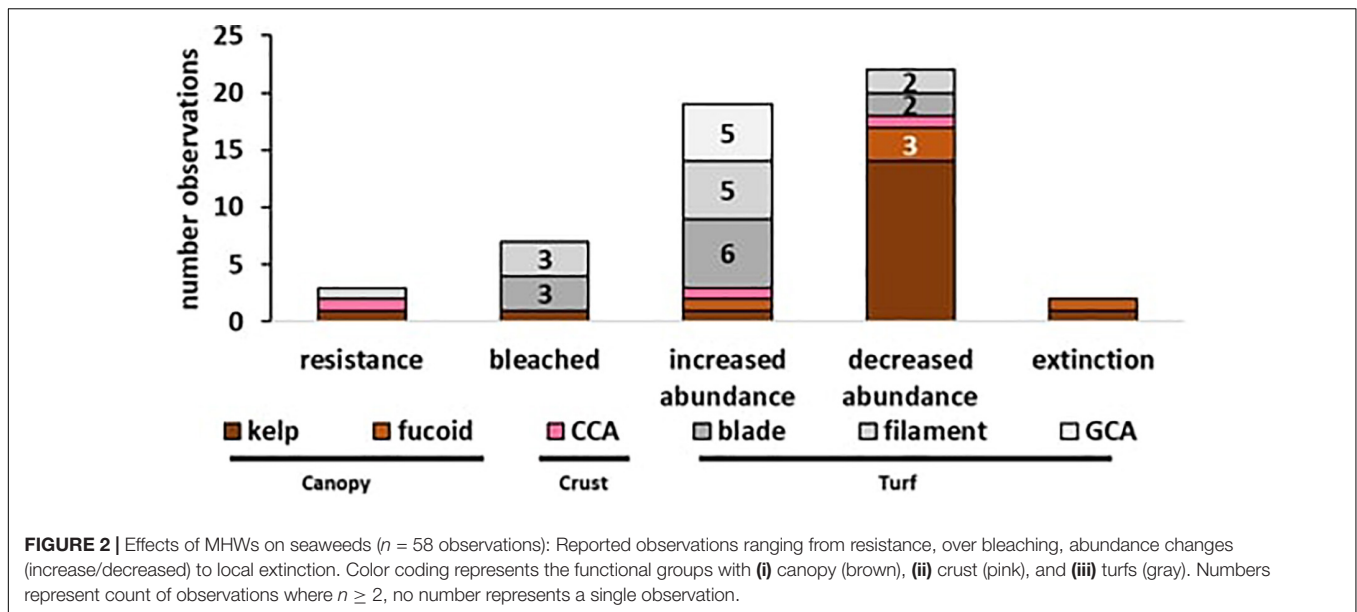
Ecological Performance

Reproduction potential and early life-history stages of many seaweeds are temperature-sensitive (Bartsch et al., 2013; Andrews et al., 2014), and increased temperatures can both suppress or enhance reproduction and recruitment success (de Bettignies et al., 2018; Muth et al., 2019). Following the 1982/83 El Niño, the turf-forming *Pelvetia fastigiata* and the canopy-forming fucoid *Sargassum muticum* showed increased recruitment success at La Jolla, California (Gunnill, 1985), which led to elevated abundances and likely shifted competitiveness

TABLE 1 | Details of studies (*n* = 20; 17 journal articles[1−17], three news articles[a,b,c]) and species/genera (*n* = 58) found with recorded impacts of MHWs on algae.

MHW	Species	Classification	Functional group	Study number	References
1982/83 ENSO South America	*Sargassum* sp.	Phaeophyceae	Canopy	1	Laurie, 1990
	Blossevillea galapagensis	Phaeophyceae	Canopy		
	Ulva spp.	Chlorophyta	Turf		
	Spermothamnio spp.	Rhodophyta	Turf		
	Centroceras spp.	Rhodophyta	Turf		
	Giffordia mitchelliae	Phaeophyceae	Turf		
1982/83 ENSO Chile	*Lessonia nigrescens*	Phaeophyceae	Canopy	2	Soto, 1985
	Macrocystis pyrifera	Phaeophyceae	Canopy		
	Ulva spp.	Chlorophyta	Turf		
	Enteromorpha spp.	Chlorophyta	Turf		
	Iridaea spp.	Rhodophyta	Turf		
1982/83 ENSO California	*Egregia menziesii*	Phaeophyceae	Canopy	3	Gunnill, 1985
	Ecklonia arborea	Phaeophyceae	Canopy		
	Pelvetia fastigiata	Phaeophyceae	Turf		
	Sargassum muticum	Phaeophyceae	Canopy		
1982/83 ENSO California (Piedras Blancas)	*Porphyra perforata*	Rhodophyta	Turf	4	Murray and Horn, 1989
	Iridaea cordata	Rhodophyta	Turf		
	Laurencia spectabilis	Rhodophyta	Turf		
	Prionitis lanceolata	Rhodophyta	Turf		
	Gastroclonium subarticulatum	Rhodophyta	Turf		
	Gigartina canaliculata	Rhodophyta	Crust		
	CCA	CCA	Turf		
	Mastocarpus papillatus	Rhodophyta			
1997/98 ENSO Chile	*Macrocystis pyrifera*	Phaeophyceae	Canopy	5	Alonso Vega et al., 2005
	Lessonia trabeculata	Phaeophyceae	Canopy		
1997/98 ENSO Pacific Mexican Coast	*Agardhiella tenera*	Rhodophyta	Turf	6	Carballo et al., 2002
	Amphiroa misakiensis	Rhodophyta	Turf		
	Caulerpa sertularoides	Chlorophyta	Turf		
	Padina durvillaei	Phaeophyceae	Turf		
	Jania capillacea	Rhodophyta	Turf		
	Jania mexicana	Rhodophyta	Turf		
1997/1998 ENSO southern Japan	*Ecklonia cava*	Phaeophyceae	Canopy	7	Serisawa et al., 2004
	GCA	Rhodophyta	Turf	8	Tanaka et al., 2012
2009/10 ENSO Southern Mexican Pacific	Turf-forming algae	Turf	Turf	9	López-Pérez et al., 2016
	GCA (*Amphiroa*)	Rhodophyta	Turf		
2011 Ningaloo Niño Western Australia	*Ecklonia radiata*	Phaeophyceae	Canopy	10	Wernberg et al., 2016
	Scytothalia dorycarpa	Phaeophyceae	Canopy	11	Smale and Wernberg, 2013
	Turf-forming algae	Turf	Turf	12	Wernberg et al., 2013a
	CCA	CCA	Crust	13	Smale and Wernberg, 2012
	CCA biofouling (on *E. radiata*)	CCA	Crust		
2011 Ningaloo Niño Western Australia	CCA	CCA	Crust	14	Short et al., 2015
1997, 2002, 2006 hot summers	*Saccharina latissima*	Phaeophyceae	Canopy	15	Moy and Christie, 2012
	Turf-forming algae	Turf	Turf		
	Chorda filum	Phaeophyceae	Canopy		
2013/14 the blob followed by 2015/16 ENSO Southern California	*Macrocystis pyrifera*	Phaeophyceae	Canopy	16	Reed et al., 2016
	understory algae	Turf	Turf		
2017/18 Tasman Sea MHW Christchurch, NZ	*Durvillaea* spp.	Phaeophyceae	Canopy	17	Thomsen et al., 2019
	Undaria pinnatifida	Phaeophyceae	Canopy		
	Colpomenia sinuosa	Phaeophyceae	Turf		
	Dictyota sp.	Phaeophyceae	Turf		
2013/14 the blob followed by 2015/16 ENSO Philippines	Seaweed production drop			a	Galolo, 2016
2013/14 the blob followed by 2015/16 ENSO Northern California	*Nereocystis luetkeana*	Phaeophyceae	Canopy	b	Catton, 2016
2015/16 Tasmanian MHW	*Macrocystis pyrifera*	Phaeophyceae	Canopy	c	Mathiesen, 2016

News articles were only included if results were not yet published in peer-reviewed journals. MHW, marine heatwave, CCA, crustose coralline algae, GCA, geniculate coralline algae, ENSO, El Niño Southern Oscillation. Effects are recorded in **Figure 1***.*

FIGURE 2 | Effects of MHWs on seaweeds (*n* = 58 observations): Reported observations ranging from resistance, over bleaching, abundance changes (increase/decreased) to local extinction. Color coding represents the functional groups with **(i)** canopy (brown), **(ii)** crust (pink), and **(iii)** turfs (gray). Numbers represent count of observations where *n* ≥ 2, no number represents a single observation.

between species. Furthermore, grazing pressure on seaweeds is likely increased when tropical and subtropical herbivores shift their ranges (Vergés et al., 2014a; Smale et al., 2017; Zarco-Perello et al., 2017) due to MHWs. Altered grazing pressure can result in the collapse of seaweed populations and reinforcement of ecosystem transitions (Haraguchi et al., 2009; Vergés et al., 2014a,b, 2016; Bennett et al., 2015b; Franco et al., 2015). During the 1997/98 El Niño, an increase in grazing pressure occurred simultaneously at lower latitudes (10–23°S) of both hemispheres, and the combination of thermal anomalies and migration of grazers produced a synergistic effect. In northern Chile, two canopy-forming kelps were negatively affected, with local disappearance of *Macrocystis pyrifera* at shallow depths and a decreased abundance of *Lessonia trabeculata* at its depth limit (Halpin et al., 2004; Alonso Vega et al., 2005). During the following 1998–2000 La Niña event, kelp productivity was minimal due local disappearance of *M. pyrifera* and decreased densities of *L. trabeculata*, however, recovery occurred post La Niña during the mild 2002/03 El Niño event (Alonso Vega et al., 2005).

In Western Australia, the 2010/11 MHW led to increased herbivory due to the range expansion of tropical and subtropical herbivores, reinforcing the temperature-driven loss of the kelp *Ecklonia radiata,* and facilitating domination of turf algae, with no signs of recovery 8 years after the event (Wernberg, 2019). Additionally, tropical herbivorous fish expanded their range beyond the areas directly affected by the high MHW temperatures, resulting in a further decline of seaweed canopy cover by up to ∼70% at localized reefs (Zarco-Perello et al., 2017). This MHW also caused heavy biofouling by CCA on *E. radiata* at the Houtman Abrolhos Islands in Western Australia (Smale and Wernberg, 2012), the only report of its kind to date. Thus, indirect effects of MHWs come in an array of forms and can act as important drivers of change within marine systems, with possible long-lasting impacts far beyond the direct MHW impacts itself.

Changes in Abundance

The most commonly recorded effect of MHWs was changes in seaweed abundances (∼79% of all observations). During the extreme 1982/83 El Niño, areas of the Galapagos archipelago in South America experienced declines of fucoids and turf-forming seaweeds, followed by colonization of the invasive turf-forming seaweed *Giffordia mitchelliae*. The fucoids *Sargassum* sp. and *Blossevillea galapagensis* as well as the turfs *Ulva* spp., *Spermothamnio* spp. and *Centroceras* spp. decreased in abundance (Laurie, 1990). In comparison, the same ENSO event led to reduced abundances of the two kelps *Lessonia nigrescens* and *Macrocystis pyrifera* in Chile (Soto, 1985). After the abundance of kelp was reduced, the turf-forming seaweeds *Ulva*, *Enteromorpha* and *Iridaea* spp. all proliferated (Soto, 1985). In California, the ENSO-associated warming event resulted in no drastic changes, but led to reduced abundances of the kelps *Egregia menziesii* and *Ecklonia arborea* at La Jolla (Gunnill, 1985), and a substantial increase of CCA in the low- and mid-intertidal zone near Point Piedras Blancas (Murray and Horn, 1989). Even though there is some uncertainty attributing the effects in California to the warmer sea temperatures *per se* due to the co-occurrence of large waves, the population-level responses were similar to those that occurred due to elevated water temperatures recorded in late summer and autumn of 1976 (Gunnill, 1985).

During the 1997/98 El Niño in northern Chile kelp abundances were maintained due to the continuity of coastal upwelling buffering the warming of the ocean. However, after the 1997/98 El Niño event two kelp species were negatively affected with complete disappearance of *M. pyrifera* at shallow depths and decreased abundance of *Lessonia trabeculata* (Alonso Vega et al., 2005). Along the Pacific Mexican Coast seaweed diversity and biomass fluctuated significantly, with an initial increase in biomass caused by the rise in the abundance of warm water tolerant species such as the small turf species

Agardhiella tenera, Amphiroa misakiensis, Caulerpa sertularoides, Padina durvillaei, Jania capillacea, and *Jania mexicana* (Carballo et al., 2002). Overall, seaweed diversity decreased and net biomass increased during the ENSO, whereas diversity increased, biomass decreased and the assemblage structure were altered following the El Niño mediated MHW (Carballo et al., 2002), highlighting the complexity of impacts that MHWs exert over seaweed communities. In the southern Mexican Pacific coral reef communities, the 2009/10 ENSO increased seaweed cover from 2 to 6% due to an increase in turf-forming algae (López-Pérez et al., 2016). This increase in seaweed cover was coupled with a decrease in coral cover, coral overgrowth and changes in echinoderm and fish species composition, all of which altered the overall reef community (López-Pérez et al., 2016). Significant increases of turf-forming algae also occurred in southwestern Australia following the 2010/11 MHW, after drastic declines and range-contractions of canopy forming seaweeds (*E. radiata* and *Scytothalia dorycarpa*) at their northern range edge (Smale and Wernberg, 2013; Wernberg et al., 2013a, 2016). The same MHW in Western Australia negatively affected CCA, suppressing seasonal growth patterns and increasing mortality rates (Short et al., 2015). In comparison, a shift toward CCA dominated barrens followed widespread loss of seaweed forests (*Ecklonia cava*) in Japan after the 1997/98 ENSO and particularly poor growth of *E. cava* in 1999 and 2001 (Serisawa et al., 2004; Tanaka et al., 2012). Also, the 2017/18 Tasmanian Sea MHW resulted in mid-range extinctions and declines in abundances of bull kelp, *Durvillaea* spp. while the percent cover of the weedy macroalgae *Undaria pinnatifida, Colpomenia sinuosa* and *Dictyota* sp. increased in conjunction, most likely due to competitive release (Thomsen et al., 2019).

Overall, we found 22 records both of increased and decreased abundances of seaweeds as a result of MHW events. All 22 records for abundance declines were native species, whereas from the 22 abundance increases reported, 13 were native species and nine were invasive species. Given the fact that invasive species generally have broader temperature tolerances than native species (Sorte et al., 2010) these numbers suggest that the occurrence of MHW events could increase the competitiveness of invasive species.

Interesting differences were also found between growth forms, as 14 records reported a decrease in the abundance of canopy-forming kelps and three reported that fucoids experienced a decline in abundance (see **Figure 2**). For turf-forming species, only one record showed decline in two native turfs, but an invasive turf increased in abundance. In contrast, 18 observations report the increase of turf-forming bladed, filamentous or geniculate coralline algae (GCA). For CCA, no clear trend was obvious, as over four records CCA responses were ranging from resistance to increased abundance, increased abundance as biofouling but also increased mortality. Overall, large conspicuous canopy-formers generally declined following a MHW, whereas for CCA no clear pattern was evident due to a low number of observation, and for turf-forming seaweeds several cases of decreased abundances were observed, but the majority of records showed an increase in abundance.
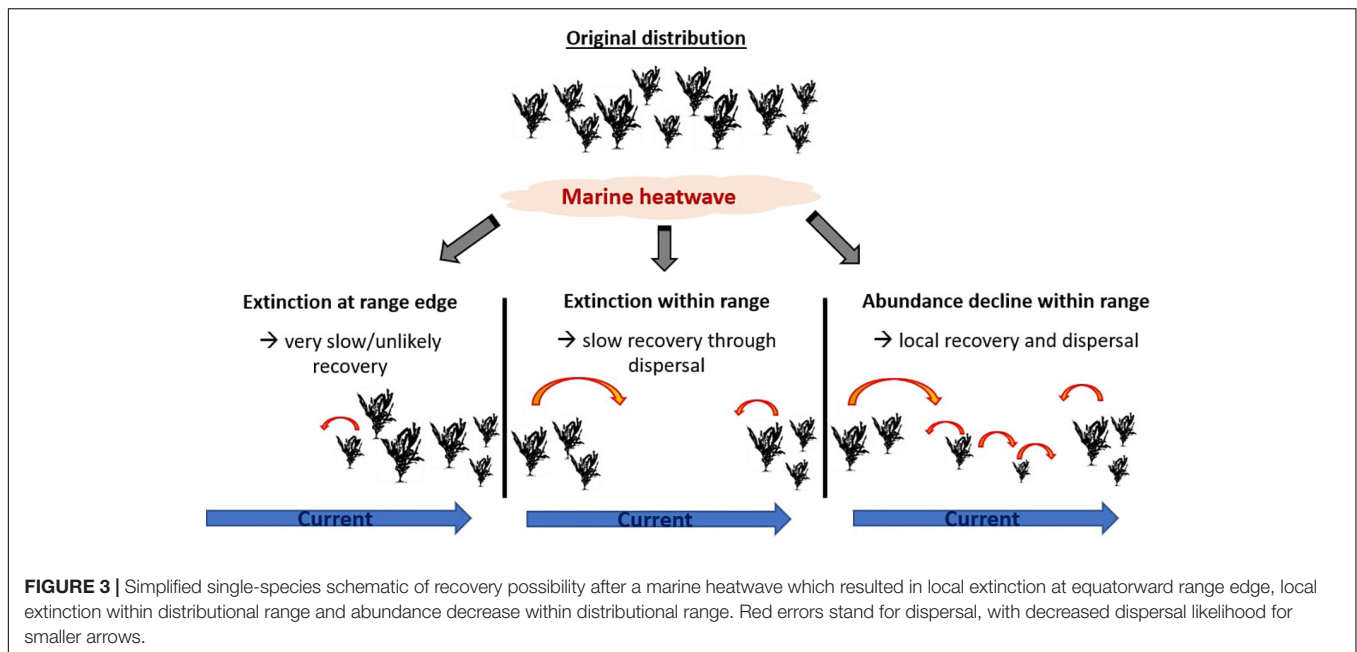
Local and Regional Extinctions

While changes in abundance have been recorded for several species in response to multiple MHWs, only in one instance have regional extinctions along the range edge been observed. The 2010/11 MHW off Western Australia led to a poleward range contraction of ∼100 km for two of the main canopy-forming seaweeds, *Ecklonia radiata* and *Scytothalia dorycarpa*, as marginal populations were extirpated (Smale and Wernberg, 2013; Wernberg et al., 2013a). This contraction culminated in the loss of 43% of the marine forests along >800 km of coastline, and a regime shift toward turf-dominated reefs (Wernberg et al., 2016; Filbee-Dexter and Wernberg, 2018; Wernberg, 2019). Besides extinctions at the trailing range edge, local extinctions of range-center populations have also been observed. The 2015/16 Tasman Sea MHW was associated with localized die-off of *Macrocystis pyrifera* off Tasmania's east coast (Mathiesen, 2016). Over the last few decades, *M. pyrifera* has declined from a 250 km stretch along Tasmania's eastcoast to a last remaining patch in the inner coves of Munroe Bight (Mathiesen, 2016). The 2015/16 Tasmanian MHW, however, stressed *M. pyrifera* individuals which became less resilient to winter storms and were dislodged from the inner coves of Munroe Bight, leading to a local as well as regional extinction of this species along the eastern Tasmanian coast (Mathiesen, 2016). Additionally, following the Tasman Sea MHW in 2017/18, widespread declines in abundance with mid-range local extinctions of bull kelp were observed on the east coast of the South Island of New Zealand (Thomsen et al., 2019). Regional surveys showed a strong reduction in the abundance of *Durvillaea poha* in the region and smaller reductions in *D. willana*. Targeted surveys around Christchurch revealed total elimination of *Durvillaea* spp. on 12 out of 19 local reefs, with reef-wide extinctions observed on the reefs within and immediately north or south of Lyttelton Harbor (Thomsen et al., 2019). Following the elimination of *Durvillaea* spp. densities and cover of weedy macroalgae increased in the area previously inhabited by *Durvillaea* spp. with the potential to suppress future re-colonization by *Durvillaea* spp. into these areas (Thomsen et al., 2019).

Post-MHW Recovery Potential

The potential for affected seaweed populations to recover from MHWs will depend on the severity of the MHW and on species-specific traits of the seaweeds. This includes the location within a species range, species-specific thermal tolerance and reproductive traits, life history (e.g., annual versus perennial) and dispersal capacities. Additionally, recovery trajectories will depend on the severity of alterations in ecosystem structure and local patterns of oceanic currents.

When seaweed abundance declines in the center or poleward parts of the species' range, there is a high chance for population recovery after the MHW due to local reseeding as well as dispersal from adjacent areas (**Figure 3**). In contrast, when propagules are unlikely to disperse into affected areas (Molinos et al., 2017), competitive interactions are altered, or grazing pressure increased, recovery is unlikely or will be very slow. In the more extreme case of local extinctions, recovery will likely be markedly slower as it will depend on re-seeding from less

FIGURE 3 | Simplified single-species schematic of recovery possibility after a marine heatwave which resulted in local extinction at equatorward range edge, local extinction within distributional range and abundance decrease within distributional range. Red errors stand for dispersal, with decreased dispersal likelihood for smaller arrows.

affected populations, which may be separated by considerable distances. In the extreme case of localized to regional extinctions at the equatorward range edge of a species, recovery is predicted to be very slow or unlikely to occur. The 2010/11 MHW in Western Australia demonstrates how recovery is unlikely after extinctions along the range edge. To date, the marine forests that were lost have not recovered (Wernberg et al., 2016; Wernberg, 2019) and the poleward flow of the Leeuwin Current makes natural re-seeding unlikely, as possible source populations are located "downstream." Additionally, recovery will depend on herbivore pressure, as range-expanded as well as local herbivores may suppress any recovery and facilitate domination by turf algae (Bennett et al., 2015b; Wernberg et al., 2016; Filbee-Dexter and Wernberg, 2018).

In all cases, recovery potential is dependent on a return to suitable conditions (e.g., temperature, light, turbidity) after the MHW, competition for space (open settlement ground, species invasions) and herbivore pressure, and the distance from adjacent populations, dispersal properties and current systems (Molinos et al., 2015) for reseeding success. However, it is unlikely that a complete recovery to pre-event conditions will occur, as post-disturbance communities are generally different from the pre-disturbed communities (Sousa, 1984; Shea et al., 2004), resulting in different ecosystem structure and function. Ultimately, declines in abundance and localized extinctions within a species range may be the precursor to projected future range contractions at a species distributional limit (Martinez et al., 2018).

Attribution of Impacts to MHWs

A large proportion of the observed impacts were directly attributed to the events with extreme temperatures identified as the main or one of the key drivers of documented impacts (16 of the 19 studies). Only three studies (Gunnill, 1985; Moy and Christie, 2012; Reed et al., 2016) did not

attribute changes in seaweed performance majorly to MHWs due to the co-occurrence of interacting processes, making it difficult to disentangle the influence of each driver. In these instances, the MHWs were accompanied by storms and long-term eutrophication, or previous impacts in the area surpassed possible MHW effects (e.g., recruitment peaks in prior years, great annual variability). For example, the lack of dramatic long-term effects on seaweeds of the 1982/83 MHW in California is likely to be a consequence of strong storms and high cloud cover which reduced desiccation stress and buffered the possibly negative temperature effects (Gunnill, 1985). Furthermore, seaweed increased in abundance prior to the MHW through recruitment peaks in 1977, 1981, and 1982. As a result, seaweeds persisted during the event (Gunnill, 1985). However, it is likely that the MHW weakened the seaweeds and contributed to the severe loss during storms and strong wave action following the event (Gunnill, 1985). Similarly, multiple stressors, e.g., warm summer temperature, eutrophication and increased sedimentation have been suggested to explain ecosystem shifts in Norway, with large-scale shifts from sugar kelp forests (*Saccharina latissima*) to filamentous red algae on the Skagerrak coast and shifts to a small, functionally different kelp, *Chorda filum*, on the west coast (Moy and Christie, 2012). While the study was not designed to identify the causes of change, severe long-term eutrophication accompanied by reduced light levels was inferred to be the main driver explaining the loss of *S. latissima*. One possible trigger identified for the sudden community shifts were the unusually hot summers in 1997, 2002 and 2006 for 58, 36, and 45 days, respectively, which resulted in SSTs exceeding the thermal tolerance of *S. latissima* (Moy and Christie, 2012). Thus, it is often complicated to establish causal linkages to MHWs as multiple drivers typically occur simultaneously, resulting in complex interactive effects with studies not designed to disentangle possible drivers and

their contributions (Moy and Christie, 2012; Filbee-Dexter and Wernberg, 2018).

It is possible that the effects of MHWs may not be evident during, or immediately after the peaks in temperature, but instead have long time-lags. For example, in California, following the MHW in 1982/83, significant differences in seaweed abundance and diversity were evident in the winter of 1983/84 (Gunnill, 1985). It is possible that standing stocks of the two laminarians *Ecklonia arborea* and *Egregia menziesii* decreased as the MHW weakened the plants resulting in delayed die-offs during the summer of 1983 (Gunnill, 1985). The impact of MHWs can also vary between geographical region. This was observed following the 1997/98 El Niño which caused local extinctions of the kelp *Macrocystis pyrifera* in Peru, southern Chile and California, whereas effects in Japan and northern Chile were delayed and only detected after the event (Edwards, 2004). Similarly, in Western Australia impacts of the 2010/11 MHW ranged from catastrophic for marine temperate communities at warmer locations (Kalbarri, 28°S), severe in central locations (Jurien Bay, 30°S) to absent in cooler locations (Hamelin Bay, 34°S), even though all regions experienced similar temperature anomalies (Wernberg et al., 2013a, 2016, 2018a). Delayed impacts and differential responses over time (season) and space, is likely to depend on the spatial extent and magnitude of the MHW as well as species-specific geographical ranges and potential for local adaptation (Wernberg et al., 2018a), and may cause MHWs to go unrecognized as important drivers of ecological change.

Limitations

The majority of published information on seaweed responses to MHWs are from sites that were subjected to extreme warming conditions and experienced a multitude of ecological impacts. Notwithstanding potential publication bias that encourage reporting significant ecological changes following MHWs, but discourage reports about species resistance (no changes, i.e., non-significant effects), lack of observed impacts at some sites may be the result of limited seaweed research taking place or difficulties in determining impacts due to a lack of long-term baseline data or high natural inter-annual variability. For example, *M. pyrifera* in California showed considerable biomass variation between 2001 and 2015. Although the recorded *M. pyrifera* biomass in 2014 and 15 during and directly after "the blob" were two of the lowest on record, the low biomass was not attributed to the MHW because its biomass is naturally variable and the monitoring sites were well within the species distribution range (Reed et al., 2016). The importance of biogeography was also evident during the 2010/11 MHW in Western Australia, where the more southern (Hamelin Bay, cool region) populations of *E. radiata*, CCA and turf-forming algae showed resistance, whereas northern populations closer to the trailing range edge (Jurien Bay, warm region) were heavily impacted by the MHW despite experiencing similar temperature anomalies (Wernberg et al., 2013a). These different responses at two locations within the area covered by the MHW highlights the need to consider the location of a population within a species range as well as species-specific thermal limits and the potential of resistance when assessing impacts from MHWs (Wernberg et al., 2013a, 2016). Moreover, recent evidence suggests that thermal divergence, either *via* plasticity or adaptation, is common across species distributional ranges in marine macrophytes (King et al., 2017). Range-center seaweed populations could therefore be equally vulnerable to MHWs compared to range-edge populations (Bennett et al., 2015a; King et al., 2019; Thomsen et al., 2019); clearly, further work on intraspecific and inter-regional variability in susceptibility to MHWs is warranted (Bennett et al., 2019).

A key constraint of MHW impact studies is the lack of available historical information about seaweed populations and communities – a prerequisite to disentangle impacts from natural variability and to quantify the magnitude of ecological change (Southward et al., 1995; Wernberg et al., 2016). Without historical baseline data it is particularly difficult to detect resistance as well as immediate to long-term changes, and dramatic large-scale impacts have only been recognized in areas with sustained biological monitoring (Wernberg et al., 2011b; Poloczanska et al., 2013). This limitation can, however, be ameliorated, to an extent, by combining observations with MHW experimental studies. As climate change experimental studies on seaweed are still rare (Wernberg et al., 2012), and even more scarce related to MHWs (Gouvea et al., 2017), we recommend that efforts are directed toward conducting such experiments. Focus should be first on determining susceptibility of key species to different characteristics of MHWs, followed by studies disentangling the interactive nature of temperature, desiccation, solar radiation and eutrophication effect to determine when and if stressors enhance or buffer against impacts of each other. Additionally, we emphasize the invaluable knowledge that baseline data on seaweed biogeography, population structure and physiological performances can provide, both to document and assess future impacts as well as re-analyzing existing datasets to evaluate in more detail resistance and susceptibility of seaweeds to MHWs as well as assess which additional factors could have enhanced or buffered temperature effects.

CONCLUSION

Superimposed on decadal-scale increases in mean oceanic temperatures, MHWs are increasing in frequency and duration (Oliver et al., 2018), and will likely continue to do so in the future (Frölicher and Laufkötter, 2018). These MHWs have impacted marine ecosystems with well-documented effects on seaweeds ranging from resistance, to altered physiological and ecological performances, and drastic shifts in ecosystem structure and functioning and, in a few cases, regime shifts. These regime shifts have led to profound economic and environmental changes (Wernberg et al., 2016; Filbee-Dexter and Wernberg, 2018; Smale et al., 2019). In addition to directly affecting seaweeds, MHWs have facilitated poleward range shifts of subtropical and tropical herbivores, leading to increased grazing pressure (Bennett et al., 2015b; Vergés et al., 2016; Zarco-Perello et al., 2017). This compounded stress favors a shift from canopy-forming kelps and fucoids toward simplified turf-dominated systems that suppresses canopy recovery. Between canopy-formers, turfs and crustose coralline algae, turf-forming seaweeds were the only functional

group with a majority of positive responses. Ultimately, the severity of MHW effects will depend on the resilience, recovery and recolonization traits of the affected seaweeds, their position within their thermal safety margins, interaction with other stressors such as eutrophication and altered currents, modified grazing pressure, and the attributes of the MHWs. Specifically, research about the resilience of seaweeds is required to better understand species-specific sensitivity to MHWs, and to identify which coastal regions are most vulnerable to regime shifts. Further range shifts and local regime shifts in marine forests, as well as within similarly important ecosystems (e.g., coral reefs and seagrasses meadows), seem inevitable in the near future (Takao et al., 2015; Kumagai et al., 2018; Martinez et al., 2018; Smale et al., 2019). However, it remains uncertain how altered ecosystems will impact the provision of ecological services upon which human societies depend.

AUTHOR CONTRIBUTIONS

SS and TW conceived the idea for the manuscript. SS wrote the manuscript. TW, MT, PM, MB, BH, and DS contributed to the concept and writing. All authors approved the submitted manuscript.

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