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Impacts of ocean warming on kelp forest ecosystems

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Summary

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Kelp forests represent some of the most diverse and productive habitats on Earth, and provide a range of ecosystem goods and services on which human populations depend. As the distribution and ecophysiology of kelp species is strongly influenced by temperature, recent warming trends in many regions have been linked with concurrent changes in kelp populations, communities and ecosystems. Over the past decade, the number of reports of ocean warming impacts on kelp forests has risen sharply. Here, I synthesise recent studies to highlight general patterns and trends. While kelp responses to climate change vary greatly between ocean basins, regions and species, there is compelling evidence to show that ocean warming poses an unequivocal threat to the persistence and integrity of kelp forest ecosystems in coming decades.

I. Introduction

Kelps (large brown macroalgae mostly of the order Laminariales) are distributed along *c.* 25% of the world's coastlines, across temperate and subpolar latitudes in both hemispheres (Fig. 1), where they function as foundation species in coastal marine ecosystems (Teagle *et al.*, 2017; Wernberg *et al.*, 2019). By providing complex biogenic habitat and exhibiting high rates of primary productivity, kelps enhance local biodiversity, fuel inshore food webs and elevate secondary productivity (Smale *et al.*, 2013; Steneck & Johnson, 2013). Kelp forests represent some of the most productive and diverse ecosystems on Earth and underpin critical ecosystem goods and services upon which human societies depend, including nursery habitat for socioeconomically important fisheries

species, biogenic storm defence and nutrient cycling (Smale *et al.*, 2013; Wernberg *et al.*, 2019). The distribution, structure and productivity of kelp forests is, however, influenced by a range of environmental (e.g. light, temperature, nutrients, substrate) and ecological (e.g. grazing, competition, disease) factors, and variability in such factors can lead to rapid and widespread changes at the ecosystem level. In the most comprehensive analysis of temporal trends in kelp populations conducted to date, Krumhansl *et al.* (2016) showed that kelp populations have declined in 38% of the ecoregions examined, and increased or remained stable in 68% of the ecoregions, with various drivers (including ocean warming) interacting across regional and local scales.

Anthropogenic climate change is driving the redistribution of species at a global scale. As the geographic distributions of marine

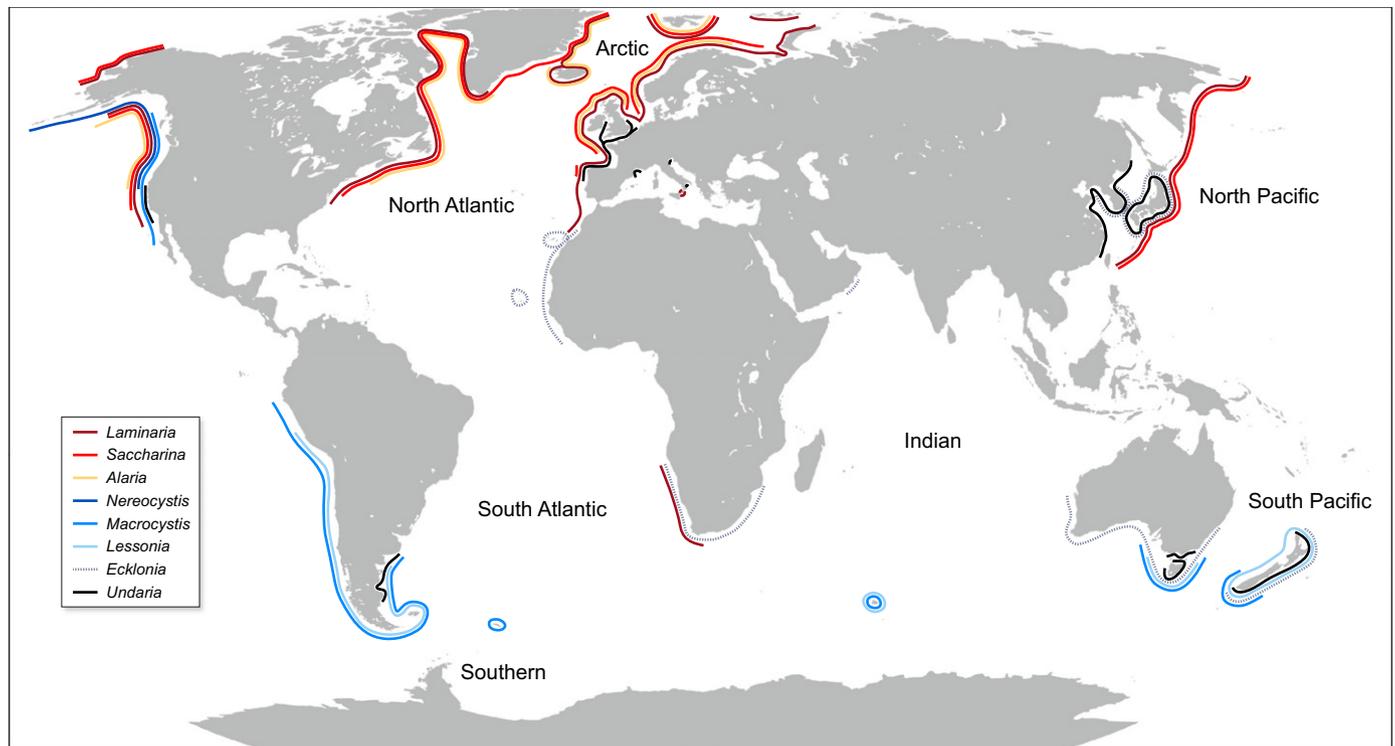


Fig. 1 Approximate global distribution of major kelp genera (Laminariales). Modified and adapted from Steneck & Johnson (2013), Teagle *et al.* (2017) and Wernberg *et al.* (2019).

species is strongly controlled by temperature (Sunday *et al.*, 2012; Pinsky *et al.*, 2019), recent warming trends have caused many species to shift their ranges in order to track optimal thermal habitat (Poloczanska *et al.*, 2013; Wiens, 2016). The distributions of macroalgal species, in particular, are strongly constrained by temperature (Breeman, 1990), and climatic variability has been linked with historical, contemporary and projected range shifts (Straub *et al.*, 2016). In recent years, the number of regional reports of kelp forest reconfiguration or loss linked to ocean warming has increased markedly. Here I collated and synthesized recent (i.e. 2005–2019) field-based observational studies that explicitly examined responses of kelp populations and communities to increased sea temperatures (gradual warming or acute marine heatwaves). The objective of the study was to compare responses across taxa and regions and to explore the wider implications of ocean warming on kelp forest ecosystems.

II. Temperature as a direct and indirect driver of change

Temperature influences processes across all biological scales, from genes to ecosystems. Species occupy defined thermal niches, partly because they are adapted to specific temperature ranges and optima under which cellular and physiological processes can occur (Pörtner & Farrell, 2008). As temperatures increase, populations found towards the upper limit of a given species' thermal distribution (most often those at the equatorward trailing range edge) may be adversely affected by warming as physiological thresholds are exceeded (Wiens, 2016). Acute or chronic thermal stress can

eventually lead to mortality and consequent population-level effects, such as decreased abundance, altered size structure, local extirpation and range contractions. Non-mobile, temperature-sensitive taxa such as macroalgae may be particularly susceptible to the direct effects of increased temperature associated with both chronic gradual warming and acute extreme warming events (i.e. marine heatwaves, *sensu* Hobday *et al.*, 2016). For example, decadal-scale gradual warming trends have been linked with loss of the kelp *Ecklonia cava* in Japan (Tanaka *et al.*, 2012), whereas a short-term marine heatwave led to widespread loss of *Ecklonia radiata* and the furoid *Scytothalia dorcarpa* in Western Australia (Smale & Wernberg, 2013; Wernberg *et al.*, 2016).

In addition to the direct physiological impacts of ocean warming, indirect effects of increased temperature have also driven or maintained shifts in the extent and structure of macroalgal-dominated habitats (Harley *et al.*, 2012). It is well known that temperature can mediate the strength and direction of ecological interactions, such as competition and grazing, which in turn can manifest in changes in the structure of populations and communities (Kordas *et al.*, 2011). Evidence from kelp forest ecosystems has shown that grazing pressure may intensify under warmer conditions, due to increased abundances and feeding rates of herbivorous fish and sea urchins, potentially exerting top down control on kelp populations and/or suppressing their recovery following deforestation (Johnson *et al.*, 2011; Vergés *et al.*, 2014; Bennett *et al.*, 2015b). Similarly, increased temperatures may indirectly affect kelp forests by altering the outcomes of competitive interactions between kelps and hard corals, invasive macroalgae or turf-forming algae (Filbee-Dexter & Wernberg, 2018; Kumagai

et al., 2018). Moreover, ocean warming can indirectly influence the distribution of kelp forests by altering habitat availability. This is particularly important in polar regions, where decreased ice cover can lead to increased light and substrate availability in shallow coastal habitats, thereby opening up favourable habitat for expansion of kelp forests in some (but not all) regions (Krause-Jensen & Duarte, 2014; Filbee-Dexter *et al.*, 2019). Rising temperatures may also interact or co-vary with other key structuring factors, such as nutrient availability, ocean currents, overgrowth by epiphytes and the prevalence of pathogens, to drive changes in kelp forest ecosystems (Scheibling & Gagnon, 2009; Campbell *et al.*, 2011; Moy & Christie, 2012; Kumagai *et al.*, 2018).

III. Responses to ocean warming

The literature search returned 33 papers, which examined responses of 25 'kelp' species (some non-Laminariales were included as they provide comparable ecological functions) and spanned all major ocean systems except the Southern Ocean (Table 1; Supporting Information Methods S1). Key illustrative examples are provided in Fig. 2, and all studies are detailed at the ocean basin scale in the sections that follow.

IV. Atlantic Ocean

Compelling evidence of recent impacts of ocean warming on kelp forests stems from the northeast Atlantic region (Table 1). Coastal waters along northwest Europe have warmed considerably in recent decades, with significant increases in both average sea temperatures and the frequency of extreme warming events (Lima & Wethey, 2012; Oliver *et al.*, 2018). Coincident with warming trends are increasing numbers of reports of kelp forest decline or loss, particularly along the Iberian Peninsula, where many species persist at their thermal maxima. For example, several independent studies conducted in Spain and Portugal have documented abundance declines, local extinctions or range contractions for the kelps *Laminaria hyperborea*, *Laminaria ochroleuca*, *Saccharina latissima* and the habitat-forming Tilopteridale *Saccorhiza polyschides* (Table 1). Widespread loss or reconfiguration of kelp forest habitat in the region has affected primary production, biodiversity and provision of fisheries habitat (Diez *et al.*, 2012; Voerman *et al.*, 2013). Interestingly, a previous study on intertidal rocky shore assemblages in Portugal detected no significant changes in the abundances of *L. hyperborea* or *S. latissima* (Lima *et al.*, 2007). Further north, loss of the cold-water species *Alaria esculenta* in Ireland has been inferred from historical records (Simkanin *et al.*, 2005), whilst increased temperature and nutrients were linked with large-scale loss of *S. latissima* in southern Norway (Moy & Christie, 2012). Conversely, *L. ochroleuca* rapidly increased in abundance at its poleward leading range edge, which was reported as the southwest UK (Smale *et al.*, 2015) until it recently spread northwards into climatically favourable habitat in western Ireland (Schoenrock *et al.*, 2019). Kelp forests in the NW Atlantic Ocean have also responded to recent warming trends, perhaps most dramatically off Nova Scotia, Canada, where 85–99% of kelp biomass (primarily *Laminaria digitata* and *S. latissima*) has been

lost over the past 4–6 decades (Filbee-Dexter *et al.*, 2016). However, temperature-related biogeographic range shifts are less clear across the wider NW Atlantic, perhaps due to a lack of monitoring data (Merzouk & Johnson, 2011). Further south, steady warming of the NW Atlantic has been linked with decreased abundance of *S. latissima* near its equatorward range edge (Witman & Lamb, 2018; Feehan *et al.*, 2019). In many cases, the direct physiological effects of increased temperature were compounded by interacting ecological factors (e.g. increased grazing, space pre-emption by turf algae, or fouling by invertebrates) to accelerate kelp decline and suppress recovery (Filbee-Dexter *et al.*, 2016; Witman & Lamb, 2018; Feehan *et al.*, 2019).

In contrast to the North Atlantic, there have been no recent reports of kelp forest loss due to ocean warming in the South Atlantic. This may be because rates of warming are generally lower across much of the South Atlantic, so that kelp populations and communities have been unaffected by temperature variability, or that changes have occurred but remain unreported, perhaps due to lower monitoring effort and/or the fact that fewer temperate reef ecologists are working in the region.

V. Pacific Ocean

Low latitude populations of *Ecklonia* species have declined in abundance or, in some cases, become locally extinct at the trailing range edge in both the southwest and northwest Pacific (Table 1). Coastal waters off southeast Australia are recognised as a hotspot for ocean warming (Sunday *et al.*, 2015), and recent declines in the giant kelp *Macrocystis pyrifera* and the widespread kelp *E. radiata* have been linked with direct and indirect effects of increased sea temperatures (Table 1). A recent marine heatwave in New Zealand led to the local extinction of the bull kelp *Durvillaea antarctica* (taxonomically a furoid), which was often replaced by the invasive kelp *Undaria pinnatifida* (Thomsen *et al.*, 2019). In the northeast Pacific, several kelp species have declined in abundance following decadal-scale gradual warming in British Columbia (Starko *et al.*, 2019), although other kelp populations in the region have exhibited stability despite long-term warming (Pfister *et al.*, 2018). Further south, Californian *M. pyrifera* populations were unexpectedly resilient to a recent extreme warming event (Reed *et al.*, 2016), whereas trailing range edge populations in Baja California were severely impacted (Arafeh-Dalmou *et al.*, 2019). By contrast, there have been no reports of climate-driven changes in kelp forest ecosystems in the southeast Pacific along the western coastline of South America, most likely because the Humboldt Current region has not exhibited a strong warming trend in recent decades (Seabra *et al.*, 2019).

VI. Indian Ocean

The southeast Indian Ocean has warmed dramatically since the turn of the century, at rates far above the global average (Li *et al.*, 2017), and several high-magnitude marine heatwaves have affected marine ecosystems off Western Australia (Wernberg *et al.*, 2016). The most severe marine heatwave occurred in the summer of 2010/2011, when sea temperatures reached record levels of up to 5°C

Table 1 Recent examples of observed changes (or lack of changes) in kelp forest distribution or structure associated with ocean warming.

Ocean	Region	Species	Response	Reference
Atlantic	Norway (65–68°N)	<i>Laminaria hyperborea</i>	Increased abundance	Rinde <i>et al.</i> (2014)
	Norway (58–43°N)	<i>Saccharina latissima</i>	Decreased abundance	Moy & Christie (2012)
	Ireland (54°N)	<i>Alaria esculenta</i>	Decreased abundance	Simkanin <i>et al.</i> (2005)
	Ireland (54°N)	<i>Laminaria ochroleuca</i>	Increased abundance, range expansion	Schoenrock <i>et al.</i> (2019)
	UK (50°N)	<i>L. ochroleuca</i>	Increased abundance, range expansion	Smale <i>et al.</i> (2015)
	UK (50°N)	<i>L. ochroleuca</i>	Increased abundance, range expansion	Teagle & Smale (2018)
	Spain/Portugal (36–43°N)	<i>S. latissima</i> , <i>L. hyperborea</i> , <i>L. ochroleuca</i> , <i>Saccorhiza</i> <i>polyschides</i> *	Decreased abundances, range contractions	Casado-Amezúa <i>et al.</i> (2019)
	Spain (43°N)	<i>L. hyperborea</i> , <i>L. ochroleuca</i>	Decreased abundances	Piñeiro-Corbeira <i>et al.</i> (2016)
	Spain (43°N)	<i>L. ochroleuca</i> , <i>S. polyschides</i> *	Decreased abundances, local extinctions	Diez <i>et al.</i> (2012)
	Spain (43°N)	<i>L. hyperborea</i> , <i>L. ochroleuca</i> , <i>S. polyschides</i> *	Decreased abundances, local extinctions	Voerman <i>et al.</i> (2013)
	Spain (43°N)	<i>L. ochroleuca</i> , <i>S. polyschides</i> *	Decreased abundances, local extinctions	Fernandez (2011)
	Portugal (36–41°N)	<i>S. latissima</i> , <i>L. hyperborea</i>	Stable abundances	Lima <i>et al.</i> (2007)
	Norway (37–39°N)	<i>S. polyschides</i> *	Decreased abundance, range contraction	Assis <i>et al.</i> (2013)
	Northwest Atlantic (42–52°N)	<i>A. esculenta</i> , <i>Laminaria digitata</i> , <i>Saccharina longicuris</i> <i>S. latissima</i>	Stable abundances	Merzouk & Johnson (2011)
	Pacific	Nova Scotia (45°N)	<i>L. digitata</i> , <i>S. latissima</i> , <i>Agarum</i> <i>clathratum</i>	Decreased abundances
Gulf of Maine (43°N)		<i>S. latissimi</i>	Decreased abundances	Witman & Lamb (2018)
Rhode Island (41°N)		<i>S. latissimi</i>	Decreased abundances	Feehan <i>et al.</i> (2019)
Japan (41°N)		<i>Laminaria japonica</i> , <i>Kjellmaniella</i> <i>crassifolia</i> , <i>Costaria costata</i> , <i>Undaria peterseniana</i> , <i>Ecklonia</i> <i>stolonifera</i> , <i>Undaria pinnatifida</i>	Decreased biomass & occurrence of cold water kelps, increased biomass & occurrence of warm water kelps	Kirihara <i>et al.</i> (2006)
Japan (32°N)		<i>Ecklonia</i> spp.	Decreased abundance, range contraction	Kumagai <i>et al.</i> (2018)
Japan (32°N)		<i>Ecklonia</i> spp.	Decreased abundance	Tanaka <i>et al.</i> (2012)
East Australia (30°S)		<i>Ecklonia radiata</i>	Decreased abundance, local extinction	Vergés <i>et al.</i> (2016)
Southeast Australia (38°S)		<i>E. radiata</i>	Decreased abundance	Carnell & Keough (2019)
Tasmania (42°S)		<i>Macrocystis pyrifera</i>	Decreased abundance	Johnson <i>et al.</i> (2011)
Tasmania (42°S)		<i>E. radiata</i>	Decreased abundance	Ling (2008)
New Zealand (43°S)		<i>Durvillaea</i> spp.*	Decreased abundance, local extinction	Thomsen <i>et al.</i> (2019)
British Columbia (49°N)		<i>Alaria marginata</i> , <i>C. costata</i> , <i>Ecklonia</i> <i>arborea</i> , <i>Laminaria setchellii</i> , <i>Nereocystis luetkeana</i> , <i>Lessoniopsis</i> <i>littoralis</i> , <i>Saccharina sessilis</i> , <i>Egregia</i> <i>menziesi</i>	Decreased abundances of most kelps (not at all survey sites), stable abundance of stress tolerant kelps	Starko <i>et al.</i> (2019)
Washington State (48°N)		<i>N. luetkeana</i> , <i>M. pyrifera</i>	Stable abundances	Pfister <i>et al.</i> (2018)
California (34°N)		<i>M. pyrifera</i>	Stable abundance	Reed <i>et al.</i> (2016)
Baja California (30–32°N)		<i>M. pyrifera</i>	Decreased abundance	Arafeh-Dalmau <i>et al.</i> (2019)
Indian	West Australia (30°S)	<i>Scytothalia dorycarpa</i> *	Decreased abundance, range contraction	Smale & Wernberg (2013)
	West Australia (28–32°S)	<i>E. radiata</i>	Decreased abundance, range contraction	Wernberg <i>et al.</i> (2016)
Arctic	Greenland (74°N)	<i>S. latissima</i> , <i>S. longicuris</i>	Increased abundances, Increased biomass	Krause-Jensen <i>et al.</i> (2012)
	Svalbard (78°N)	<i>L. digitate</i>	Increased abundance, Increased biomass	Bartsch <i>et al.</i> (2016)

Species marked with an asterisk (*) do not belong to the order Laminariales but serve a similar ecological function as kelps and are therefore included here.

higher than the climatological average (Wernberg *et al.*, 2013). This extreme climatic event, which was superimposed onto a gradual warming trend, had catastrophic ecological consequences along large stretches of temperate and subtropical coastline. Within a few months, the kelp *E. radiata* had significantly declined in

abundance on many rocky reefs (Wernberg *et al.*, 2013), and the furoid *Scytothalia dorycarpa* underwent a range contraction of > 100 km following extirpation of trailing range edge populations (Smale & Wernberg, 2013). These highly productive macroalgal canopies were predominantly replaced by weedy algal turfs, which

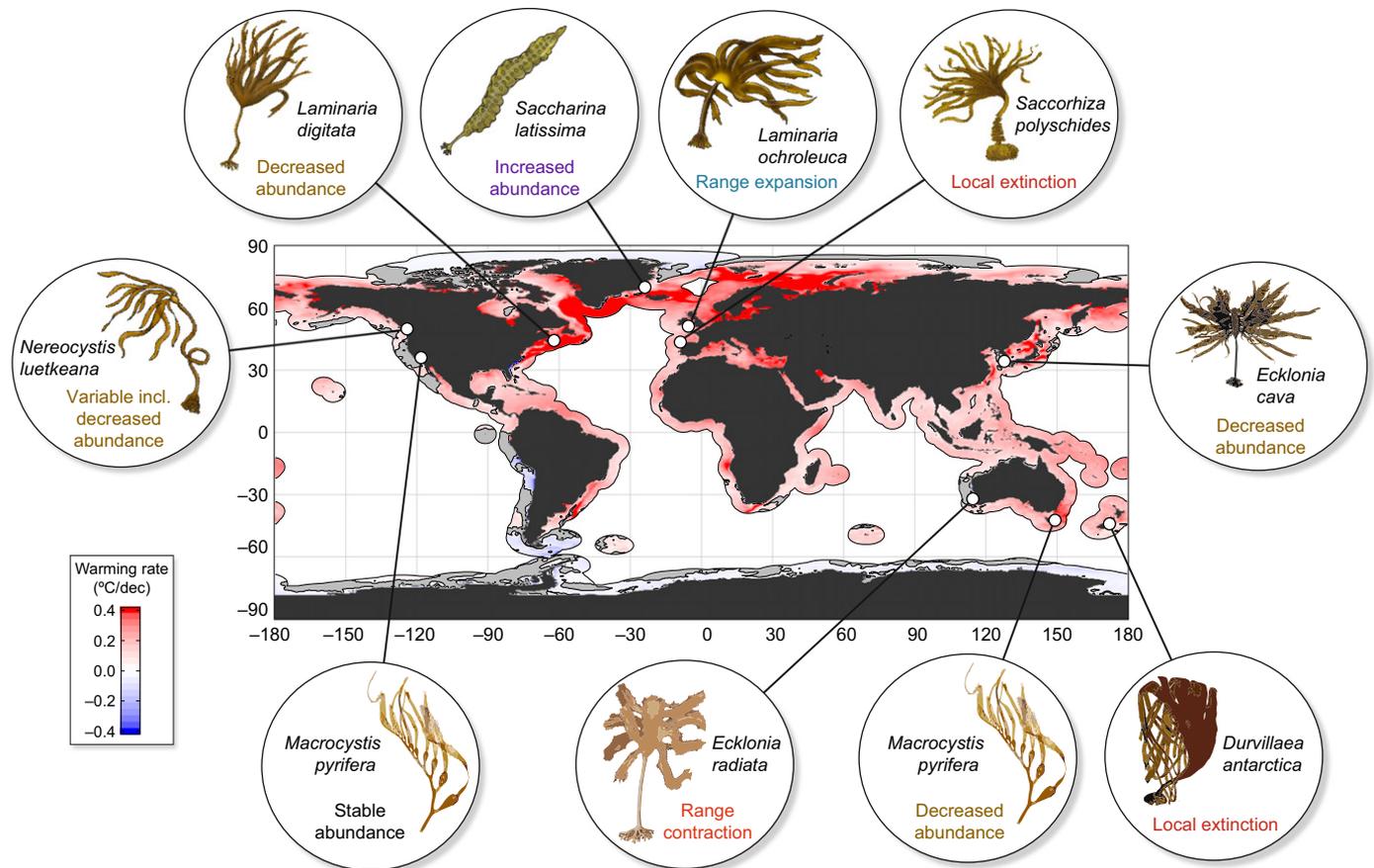


Fig. 2 Selected recent examples of responses of kelp populations and ecosystems to ocean warming. Further details are provided in Table 1. Examples chosen to represent a range of species, responses and regions, not a comprehensive analysis of recent responses. Underlying global map shows rates of sea surface warming in coastal waters (500 km from land), based on 37 yr of daily sea surface temperatures (SSTs; 1982–2018) from National Oceanic and Atmospheric Administration (NOAA) 1/4 arc-degree Daily Optimum Interpolation SST version 2 (dOISST.v2).

generally support lower productivity and biodiversity (Filbee-Dexter & Wernberg, 2018). The marine heatwave was followed by several warm summers and, by 2015, *c.* 43% of kelp forests in southwest Australia had been lost or severely decimated, whilst associated floral and faunal communities had become ‘tropicalized’ (Wernberg *et al.*, 2016). Recent impacts of ocean warming on kelp forest ecosystems in the southeast Indian Ocean have been profound. Conversely, in the southwest Indian Ocean, an eastward range expansion of kelp forests along the coastline of South Africa has been linked with recent ocean cooling trends in the region (Bolton *et al.*, 2012).

VII. Polar Oceans

The Arctic Ocean represents one of the most rapidly changing areas in the world; kelp populations and associated communities are influenced by a range of environmental changes, including reduced sea ice cover, increased freshwater and sediment inputs, altered light regimes, and warming (Krause-Jensen & Duarte, 2014; Filbee-Dexter *et al.*, 2019). While sea ice loss and glacial retreat will open up new areas of coastal habitat for colonisation, concurrent increases in turbidity, freshwater input and sedimentation may limit productivity and the poleward expansion of kelp populations

(Bonsell & Dunton, 2018; Filbee-Dexter *et al.*, 2019). Even so, there is likely to be net gain of kelp forest cover into the Arctic (Krause-Jensen & Duarte, 2014). Indeed, the few empirical studies published so far have recorded increased biomass and productivity in Arctic kelp populations in response to warming, primarily due to decreased ice cover and a longer open water season (Table 1). To date, there have been no reports of kelp expansion or changes from the Southern Ocean or sub-Antarctic Islands.

VIII. Conclusions

Recent climatic changes have unequivocally altered the structure and distribution of kelp forest ecosystems in many regions across the world. In addition to the structural changes described here, it is highly likely that ocean warming has affected key processes, including rates of primary productivity (Pessarrodona *et al.*, 2019), the capture and export of carbon to adjacent habitats (Pessarrodona *et al.*, 2018), resilience to physical disturbance (Wernberg *et al.*, 2010), and habitat provision (Teagle & Smale, 2018). It should be noted, however, that not all kelp populations and ecosystems have responded to warming trends, as many kelp-dominated habitats have exhibited notable long-term stability over decadal scales (Krumhansl *et al.*, 2016; Reed *et al.*, 2016; Pfister *et al.*, 2018).

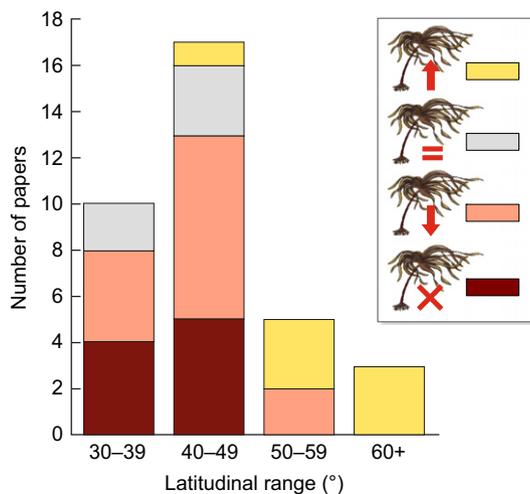


Fig. 3 Number of papers identified in the current review, grouped by latitudinal range. The primary impacts of ocean warming on kelp populations identified in each paper were classified as follows: local extinction/range contraction (brown); decreased abundance/biomass (peach); stable populations/no change (grey); and increased abundance/biomass (yellow).

Moreover, several kelp deforestation events have been attributed to non-climatic stressors, such as overgrazing by sea urchins (Ling *et al.*, 2015) or decreased water quality in coastal habitats (Connell *et al.*, 2008).

Intuitively, some populations of some species will be more susceptible to ocean warming than others, due to intrinsic thermal tolerances and their relative position within a species' thermal range. Typically, equatorward trailing range edge populations are more likely to undergo local extinctions and range contractions, whereas poleward leading-edge populations are more likely to proliferate and extend their range. An examination of the papers highlighted in this review supports this, as low latitude studies have tended to report range contractions and declines in abundance/biomass, whereas high latitude studies have tended to report range expansions and increases in abundance/biomass (Fig. 3). This general pattern will allow for explicit predictions of how and where future warming impacts will occur. While range edge populations are likely to be particularly vulnerable to warming, recent evidence suggests that local thermal adaptation in kelps and other marine macrophytes may be commonplace (King *et al.*, 2019). As such, intra-specific variability in thermal tolerance may render some mid-range populations susceptible to current and future warming trends (Bennett *et al.*, 2015a).

The broader implications of climate-driven shifts and losses of kelp forest ecosystems are far-reaching, with likely consequences for the provision of ecosystem services. Throughout the coming century, average sea temperatures are projected to continue to rise (IPCC, 2013), and the frequency of marine heatwaves will also increase (Frölicher *et al.*, 2018), with ecosystem-level consequences (Smale *et al.*, 2019). Kelp populations and the ecosystems they underpin will almost certainly respond to a warming climate (Assis *et al.*, 2018; Martínez *et al.*, 2018), although the exact nature and wider implications of these ecological changes remain uncertain. What is clear is that some regions (i.e. biogeographic transition zones, warming hotspots, polar areas) and populations (i.e. trailing

range edge, polar leading range edge) will be more vulnerable to continued warming and will likely exhibit the fastest and greatest responses. While significant ecological changes are inevitable, the underlying causes of ocean warming (i.e. anthropogenic climate change) need to be addressed to reduce the risk of irrevocable loss of kelp forest ecosystems in many regions across the global ocean.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Methods S1 Details on the methodological approach used to search the literature and the criteria used to select and include papers in the study are provided.

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