



## Tansley insight

# Impacts of ocean warming on kelp forest ecosystems

Author for correspondence:

Dan A. Smale

Tel: +44 1752 426489

Email: dansma@mba.ac.uk

Received: 14 May 2019

Accepted: 28 July 2019

Dan A. Smale 

The Laboratory, Marine Biological Association of the United Kingdom, Citadel Hill, Plymouth, PL1 2PB, UK

## Contents

Summary	1447	VI. Indian Ocean	1449
I. Introduction	1447	VII. Polar Oceans	1451
II. Temperature as a direct and indirect driver of change	1448	VIII. Conclusions	1451
III. Responses to ocean warming	1449	Acknowledgements	1452
IV. Atlantic Ocean	1449	References	1452
V. Pacific Ocean	1449		

## Summary

*New Phytologist* (2020) **225**: 1447–1454  
doi: 10.1111/nph.16107

**Key words:** climate change, coastal ecosystems, ecosystem services, kelp forests, ocean warming, seaweed habitats.

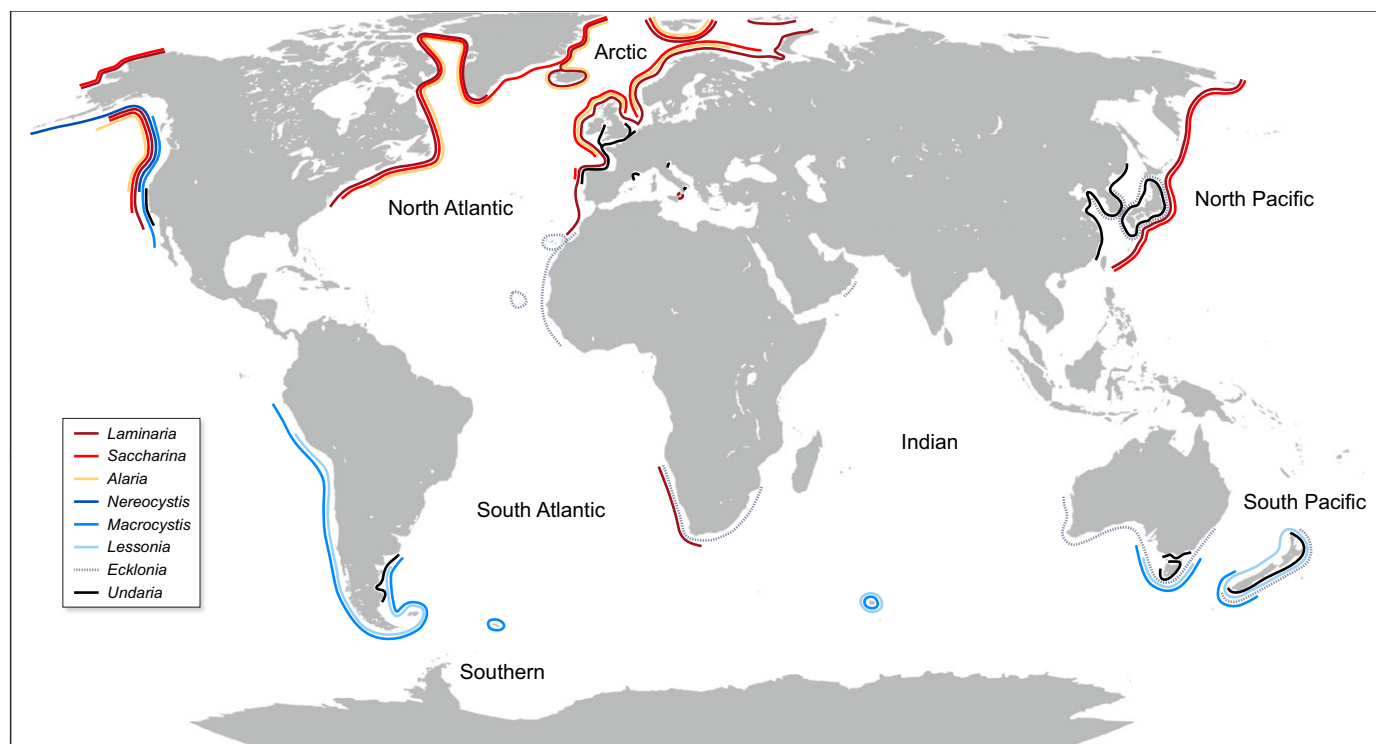
Kelp forests represent some of the most diverse and productive habitats on Earth, and provide a range of ecosystem goods and services on which human populations depend. As the distribution and ecophysiology of kelp species is strongly influenced by temperature, recent warming trends in many regions have 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 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 dorcampa* 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 & Wetthey, 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-Dalmau *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.

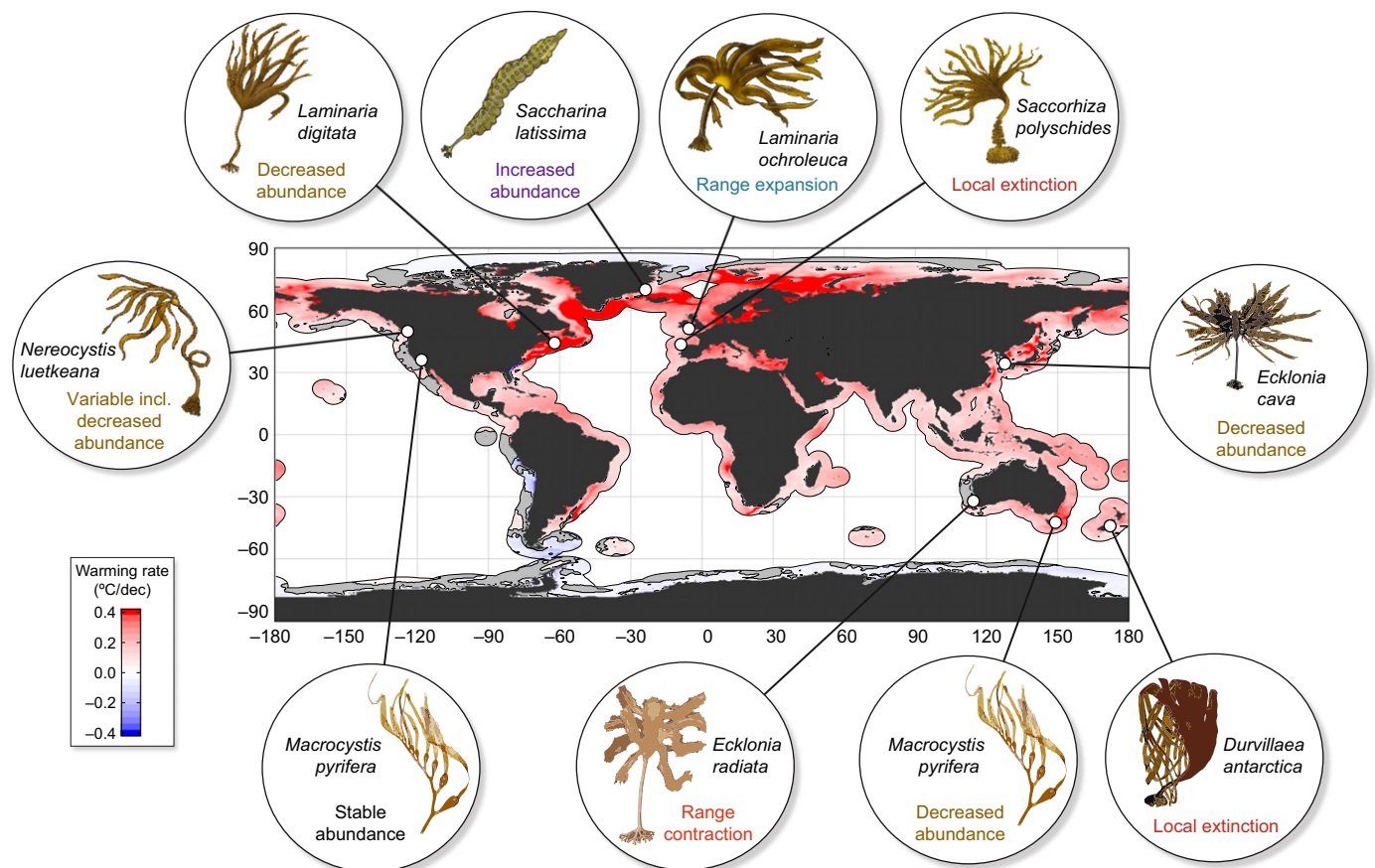
Ocean	Region	Species	Response	Reference
Atlantic	Norway (65–68°N)	<i>Laminaria hyperborea</i>	Increased abundance	Rinde <i>et al.</i> (2014)
	Norway (58–43°N)	<i>Saccharina latissima</i>	Decreased abundance	Moy & Christie (2012)
	Ireland (54°N)	<i>Alaria esculenta</i>	Decreased abundance	Simkanin <i>et 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)
	Nova Scotia (45°N)	<i>L. digitata</i> , <i>S. latissima</i> , <i>Agarum</i> <i>clathratum</i>	Decreased abundances	Filbee-Dexter <i>et al.</i> (2016)
Pacific	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).

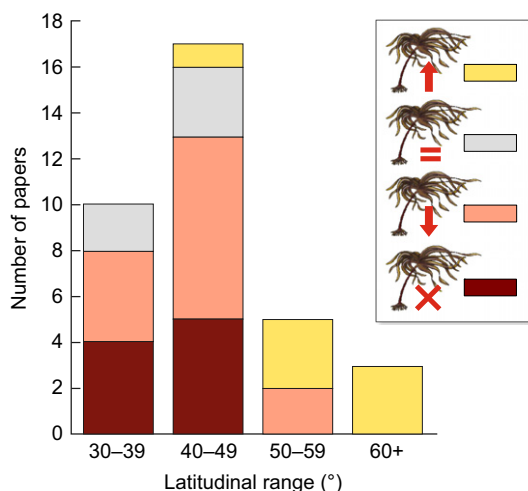
## VII. Polar Oceans

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.

## Acknowledgements

I thank various members of the international kelp ecology community for offering valuable information on current research and for insightful discussions over the past 12 years. Rui Seabra, Fernando Lima and Jack Sewell assisted with Fig. 2, and Nadia Frontier assisted with the literature search.

## ORCID

Dan A. Smale  <https://orcid.org/0000-0003-4157-541X>

## References

- Arafeh-Dalmau N, Montaña-Moctezuma G, Martínez JA, Beas-Luna R, Schoeman DS, Torres-Moye G. 2019. Extreme marine heatwaves alter kelp forest community near its equatorward distribution limit. *Frontiers in Marine Science* 6: 499.
- Assis J, Araújo MB, Serrão EA. 2018. Projected climate changes threaten ancient refugia of kelp forests in the North Atlantic. *Global Change Biology* 24: e55–e66.
- Assis J, Castilho Coelho N, Alberto F, Valero M, Raimondi P, Reed D, Alvares Serrão E. 2013. High and distinct range-edge genetic diversity despite local bottlenecks. *PLoS ONE* 8: e68646.
- Bartsch I, Paar M, Fredriksen S, Schwanitz M, Daniel C, Hop H, Wiencke C. 2016. Changes in kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996–1998 and 2012–2014 reflect Arctic warming. *Polar Biology* 39: 2021–2036.
- Bennett S, Wernberg T, Arackal Joy B, de Bettignies T, Campbell AH. 2015a. Central and rear-edge populations can be equally vulnerable to warming. *Nature Communications* 6: 10280.
- Bennett S, Wernberg T, Harvey ES, Santana-Garçon J, Saunders BJ. 2015b. Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecology Letters* 18: 714–723.
- Bolton JJ, Anderson RJ, Smit AJ, Rothman MD. 2012. South African kelp moving eastwards: the discovery of *Ecklonia maxima* (Osbeck) Papenfuss at De Hoop Nature Reserve on the south coast of South Africa. *African Journal of Marine Science* 34: 147–151.
- Bonsell C, Dunton KH. 2018. Long-term patterns of benthic irradiance and kelp production in the central Beaufort sea reveal implications of warming for Arctic inner shelves. *Progress in Oceanography* 162: 160–170.
- Breeman AM. 1990. Expected effects of changing seawater temperatures on the geographic distribution of seaweed species. In: Beukema JJ, Wolf WJ, Brouns JJWM, eds. *Expected effects of climate change on marine coastal ecosystems*. Dordrecht, the Netherlands: Springer, 69–76.
- Campbell AH, Harder T, Nielsen S, Kjelleberg S, Steinberg PD. 2011. Climate change and disease: bleaching of a chemically defended seaweed. *Global Change Biology* 17: 2958–2970.
- Carnell PE, Keough MJ. 2019. Reconstructing historical marine populations reveals major decline of a kelp forest ecosystem in Australia. *Estuaries and Coasts* 42: 765–778.
- Casado-Amezúa P, Araújo R, Bárbara I, Bermejo R, Borja Á, Díez I, Fernández C, Gorostiaga JM, Guinda X, Hernández I *et al.* 2019. Distributional shifts of canopy-forming seaweeds from the Atlantic coast of Southern Europe. *Biodiversity and Conservation* 28: 1151–1172.

- Connell SD, Russell BD, Turner DJ, Shepherd SA, Kildea T, Miller D, Airoldi L, Cheshire A. 2008. Recovering a lost baseline: missing kelp forests from a metropolitan coast. *Marine Ecology Progress Series* 360: 63–72.
- Diez I, Muguerza N, Santolaria U, Ganzedo U, Gorostiaga JM. 2012. Seaweed assemblage changes in the eastern Cantabrian Sea and their potential relationship to climate change. *Estuarine, Coastal and Shelf Science* 99: 108–120.
- Feehan CJ, Grace SP, Narvaez CA. 2019. Ecological feedbacks stabilize a turf-dominated ecosystem at the southern extent of kelp forests in the Northwest Atlantic. *Scientific Reports* 9: 7078.
- Fernandez C. 2011. The retreat of large brown seaweeds on the north coast of Spain: the case of *Sacchariza polyschides*. *European Journal of Phycology* 46: 352–360.
- Filbee-Dexter K, Feehan CJ, Scheibling RE. 2016. Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. *Marine Ecology Progress Series* 543: 141–152.
- Filbee-Dexter K, Wernberg T. 2018. Rise of turfs: a new battlefield for globally declining kelp forests. *BioScience* 68: 64–76.
- Filbee-Dexter K, Wernberg T, Fredriksen S, Norderhaug KM, Pedersen MF. 2019. Arctic kelp forests: diversity, resilience and future. *Global and Planetary Change* 172: 1–14.
- Frölicher TL, Fischer EM, Gruber N. 2018. Marine heatwaves under global warming. *Nature* 560: 360–364.
- Harley CDG, Anderson KM, Demes KW, Jorve JP, Kordas RL, Coyle TA, Graham MH. 2012. Effects of climate change on global seaweed communities. *Journal of Phycology* 48: 1064–1078.
- Hobday AJ, Alexander LV, Perkins SE, Smale DA, Straub SC, Oliver EC, Benthuyens J, Burrows MT, Donat MG, Feng M *et al.* 2016. A hierarchical approach to defining marine heatwaves. *Progress in Oceanography* 141: 227–238.
- IPCC. 2013. The physical science basis. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM, eds. *Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change*. Cambridge, UK: Cambridge University Press.
- Johnson CR, Banks SC, Barrett NS, Cazassus F, Dunstan PK, Edgar GJ, Frusher SD, Gardner C, Haddon M, Helidoniotis F *et al.* 2011. Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental Marine Biology and Ecology* 400: 17–32.
- King NG, McKeown NJ, Smale DA, Moore PJ. 2018. The importance of phenotypic plasticity and local adaptation in driving intraspecific variability in thermal niches of marine macrophytes. *Ecography* 41: 1469–1484.
- King NG, McKeown NJ, Smale DA, Wilcockson DC, Hoelters L, Groves EA, Stamp T, Moore PJ. 2019. Evidence for different thermal ecotypes in range centre and trailing edge kelp populations. *Journal of Experimental Marine Biology and Ecology* 514–515: 10–17.
- Kirihara S, Nakamura T, Kon N, Fujita D, Notoya M. 2006. Recent fluctuations in distribution and biomass of cold and warm temperature species of Laminariales algae at Cape Ohma, Northern Honshu, Japan. *Journal of Applied Phycology* 18: 521–527.
- Kordas RL, Harley CDG, O'Connor MI. 2011. Community ecology in a warming world: the influence of temperature on interspecific interactions in marine systems. *Journal of Experimental Marine Biology and Ecology* 400: 218–226.
- Krause-Jensen D, Duarte CM. 2014. Expansion of vegetated coastal ecosystems in the future Arctic. *Frontiers in Marine Science* 1: 77.
- Krause-Jensen D, Marbà N, Olesen B, Sejr MK, Christensen PB, Rodrigues J, Renaud PE, Balsby TJS, Rysgaard S. 2012. Seasonal sea ice cover as principal driver of spatial and temporal variation in depth extension and annual production of kelp in Greenland. *Global Change Biology* 18: 2981–2994.
- Krumhansl KA, Okamoto DK, Rassweiler A, Novak M, Bolton JJ, Cavanaugh KC, Connell SD, Johnson CR, Konar B, Ling SD *et al.* 2016. Global patterns of kelp forest change over the past half-century. *Proceedings of the National Academy of Sciences, USA* 113: 13785–13790.
- Kumagai NH, García Molinos J, Yamano H, Takao S, Fujii M, Yamanaka Y. 2018. Ocean currents and herbivory drive macroalgae-to-coral community shift under climate warming. *Proceedings of the National Academy of Sciences, USA* 115: 8990–8995.
- Li Y, Han W, Zhang L. 2017. Enhanced decadal warming of the southeast Indian Ocean during the recent global surface warming slowdown. *Geophysical Research Letters* 44: 9876–9884.
- Lima FP, Ribeiro PA, Queiroz N, Hawkins SJ, Santos AM. 2007. Do distributional shifts of northern and southern species of algae match the warming pattern? *Global Change Biology* 13: 2592–2604.
- Lima FP, Wetthey DS. 2012. Three decades of high-resolution coastal sea surface temperatures reveal more than warming. *Nature Communications* 3: 704.
- Ling SD. 2008. Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. *Oecologia* 156: 883–894.
- Ling SD, Scheibling RE, Rassweiler A, Johnson CR, Shears N, Connell SD, Salomon AK, Norderhaug KM, Pérez-Matus A, Hernández JC *et al.* 2015. Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 370: 20130269.
- Martínez B, Radford B, Thomsen MS, Connell SD, Carreño F, Bradshaw CJA, Fordham DA, Russell BD, Gurgel CFD, Wernberg T. 2018. Distribution models predict large contractions of habitat-forming seaweeds in response to ocean warming. *Diversity and Distributions* 24: 1350–1366.
- Merzouk A, Johnson LE. 2011. Kelp distribution in the northwest Atlantic Ocean under a changing climate. *Journal of Experimental Marine Biology and Ecology* 400: 90–98.
- Moy FE, Christie H. 2012. Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along the south and west coast of Norway. *Marine Biology Research* 8: 309–321.
- Oliver E, Donat MG, Burrows MT, Moore PJ, Smale DA, Alexander LV, Benthuyens JA, Feng M, Sen Gupta A, Hobday AJ *et al.* 2018. Longer and more frequent marine heatwaves over the past century. *Nature Communications* 9: 1324.
- Pessarrodona A, Foggo A, Smale DA. 2019. Can ecosystem functioning be maintained despite climate-driven shifts in species composition? Insights from novel marine forests. *Journal of Ecology* 107: 91–104.
- Pessarrodona A, Moore PJ, Sayer MDJ, Smale DA. 2018. Carbon assimilation and transfer through kelp forests in the NE Atlantic is diminished under a warmer ocean climate. *Global Change Biology* 24: 4386–4398.
- Pfister CA, Berry HD, Mumford T. 2018. The dynamics of kelp forests in the Northeast Pacific Ocean and the relationship with environmental drivers. *Journal of Ecology* 106: 1520–1533.
- Piñeiro-Corbeira C, Barreiro R, Cremades J. 2016. Decadal changes in the distribution of common intertidal seaweeds in Galicia (NW Iberia). *Marine Environmental Research* 113: 106–115.
- Pinsky ML, Eikeset AM, McCauley DJ, Payne JL, Sunday JM. 2019. Greater vulnerability to warming of marine versus terrestrial ectotherms. *Nature* 569: 108–111.
- Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K, Bruno JF, Buckley LB, Burrows MT *et al.* 2013. Global imprint of climate change on marine life. *Nature Climate Change* 3: 919–925.
- Pörtner HO, Farrell AP. 2008. Physiology and climate change. *Science* 322: 690–692.
- Reed D, Washburn L, Rassweiler A, Miller R, Bell T, Harrer S. 2016. Extreme warming challenges sentinel status of kelp forests as indicators of climate change. *Nature Communications* 7: 13757.
- Rinde E, Christie H, Fagerli CW, Bekkby T, Gundersen H, Norderhaug KM, Hjermand Ø. 2014. The influence of physical factors on kelp and sea urchin distribution in previously and still grazed areas in the NE Atlantic. *PLoS ONE* 9: e100222.
- Scheibling RE, Gagnon P. 2009. Temperature-mediated outbreak dynamics of the invasive bryozoan *Membranipora membranacea* in Nova Scotian kelp beds. *Marine Ecology Progress Series* 390: 1–13.
- Schoenrock KM, O'Callaghan T, O'Callaghan R, Krueger-Hadfield SA. 2019. First record of *Laminaria ochroleuca* Bachelot de la Pylaie in Ireland in Béal an Mhuirthead, county Mayo. *Marine Biodiversity Records* 12: 9.
- Seabra R, Varela R, Santos AM, Gómez-Gesteira M, Meneghesso C, Wetthey DS, Lima FP. 2019. Reduced nearshore warming associated with Eastern Boundary Upwelling Systems. *Frontiers in Marine Science* 6: 104.
- Simkanin C, Power AM, Myers A, McGrath D, Southward A, Mieszkowska N, Leaper R, O'Riordan R. 2005. Using historical data to detect temporal changes in the abundances of intertidal species on Irish shores. *Journal of the Marine Biological Association of the United Kingdom* 85: 1329–1340.
- Smale DA, Burrows MT, Moore PJ, O'Connor N, Hawkins SJ. 2013. Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecology and Evolution* 3: 4016–4038.
- Smale DA, Wernberg T. 2013. Extreme climatic event drives range contraction of a habitat-forming species. *Proceedings of the Royal Society B: Biological Sciences* 280: 20122829.



- Smale DA, Wernberg T, Oliver ECJ, Thomsen M, Harvey BP, Straub SC, Burrows MT, Alexander LV, Benthuyssen JA, Donat MG *et al.* 2019. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature Climate Change* 9: 306–312.
- Smale DA, Wernberg T, Yunnice ALE, Vance T. 2015. The rise of *Laminaria ochroleuca* in the Western English Channel (UK) and preliminary comparisons with its competitor and assemblage dominant *Laminaria hyperborea*. *Marine Ecology* 36: 1033–1044.
- Starko S, Bailey LA, Creviston E, James KA, Warren A, Brophy MK, Danasel A, Fass MP, Townsend JA, Neufeld CJ. 2019. Environmental heterogeneity mediates scale-dependent declines in kelp diversity on intertidal rocky shores. *PLoS ONE* 14: e0213191.
- Steneck RS, Johnson CR. 2013. Kelp forests: dynamic patterns, processes and feedbacks. In: Bertness MD, Silliman B, Stachowicz J, eds. *Marine community ecology*. Sunderland, MA, USA: Sinauer, 315–336.
- Straub SC, Thomsen MS, Wernberg T. 2016. The dynamic biogeography of the anthropocene: the speed of recent range shifts in seaweeds. In: Hu Z-M, Fraser C, eds. *Seaweed phylogeography: adaptation and evolution of seaweeds under environmental change*. Dordrecht, the Netherlands: Springer Netherlands, 63–93.
- Sunday JM, Bates AE, Dulvy NK. 2012. Thermal tolerance and the global redistribution of animals. *Nature Climate Change* 2: 686–690.
- Sunday JM, Pecl GT, Frusher S, Hobday AJ, Hill NA, Holbrook NJ, Edgar GJ, Stuart-Smith RD, Barrett NS, Wernberg T *et al.* 2015. Species traits and climate velocity explain geographic range shifts in an ocean warming hotspot. *Ecology Letters* 18: 944–953.
- Tanaka K, Taino S, Haraguchi H, Prendergast G, Hiraoka M. 2012. Warming off southwestern Japan linked to distributional shifts of subtidal canopy-forming seaweeds. *Ecology and Evolution* 2: 2854–2865.
- Teagle H, Hawkins SJ, Moore PJ, Smale DA. 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and Ecology* 492: 81–98.
- Teagle H, Smale DA. 2018. Climate-driven substitution of habitat-forming species leads to reduced biodiversity within a temperate marine community. *Diversity and Distributions* 24: 1367–1380.
- Thomsen MS, Mondardini L, Alestra T, Gerrity S, Tait L, South PM, Lilley SA, Schiel DR. 2019. Local extinction of Bull Kelp (*Durvillaea* spp.) due to a marine heatwave. *Frontiers in Marine Science* 6: 1–10.
- Vergés A, Doropoulos C, Malcolm HA, Skye M, Garcia-Pizá M, Marzinelli EM, Campbell AH, Ballesteros E, Hoey AS, Vila-Concejo A *et al.* 2016. Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proceedings of the National Academy of Sciences, USA* 113: 13791–13796.
- Vergés A, Steinberg PD, Hay ME, Poore AGB, Campbell AH, Ballesteros E, Heck KL, Booth DJ, Coleman MA, Feary DA *et al.* 2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society B: Biological Sciences* 281: 20140846.
- Voerman SE, Llera E, Rico JM. 2013. Climate driven changes in subtidal kelp forest communities in NW Spain. *Marine Environmental Research* 90: 119–127.
- Wernberg T, Bennett S, Babcock RC, de Bettignies T, Cure K, Depczynski M, Dufois F, Fromont J, Fulton CJ, Hovey RK *et al.* 2016. Climate driven regime shift of a temperate marine ecosystem. *Science* 353: 169–172.
- Wernberg T, Krumhansl K, Filbee-Dexter K, Pedersen MF. 2019. Chapter 3 – Status and trends for the world's kelp forests. In: Sheppard C, ed. *World seas: an environmental evaluation*, 2<sup>nd</sup> edn. Cambridge, MA, USA: Academic Press, 57–78.
- Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettignies T, Bennett S, Rousseaux CS. 2013. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change* 3: 78–82.
- Wernberg T, Thomsen MS, Tuya F, Kendrick GA, Staehr PA, Toohey BD. 2010. Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. *Ecology Letters* 13: 685–694.
- Wiens JJ. 2016. Climate-related local extinctions are already widespread among plant and animal species. *PLoS Biology* 14: e2001104.
- Witman JD, Lamb RW. 2018. Persistent differences between coastal and offshore kelp forest communities in a warming Gulf of Maine. *PLoS ONE* 13: e0189388.

## 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.

Please note: Wiley Blackwell are not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.