

Status and Trends for the World's Kelp Forests

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3.1 KELPS: OCEAN TREES

Kelp forests are extensive underwater habitats characterized by the presence of large seaweeds that form canopies over the seafloor. Kelps are typically competitively dominant and long-lived, with some species reaching tens of meters in height. They grow very fast and rapidly produce a vast amount of biomass (Krumhansl & Scheibling, 2012; Mann, 1973) and create a three-dimensional structure that alters their surrounding physical environment (Eckman, Duggins, & Sewell, 1989; Reed & Foster, 1984; Wernberg, Kendrick, & Toohey, 2005). As a consequence, kelp forests provide habitat, shelter, and food to a huge number of associated species (Teagle, Hawkins, Moore, & Smale, 2017). Kelp forests dominate along approximately one-quarter of the world's coastlines, in Arctic and temperate latitudes in both hemispheres (Krumhansl et al., 2016). Their diverse variety of habitat types (Fig. 3.1) delivers a broad range of valuable ecosystem services (e.g., Bennett et al., 2016).

Kelp forests show global declines and, like so many other marine ecosystems, they are under pressure from the direct and indirect effects of anthropogenic activities. These processes have been driving rapid changes in the distribution and abundance of many kelp forests globally over the past couple of decades, and in many instances declines in kelp forests threaten ecosystem services vital to human well-being (Filbee-Dexter & Scheibling, 2014b; Filbee-Dexter & Wernberg, 2018; Krumhansl et al., 2016; Steneck et al., 2002).

There is some debate about what constitutes 'kelp' (Fraser, 2012). Some reserve the term only for species of Laminariales whereas others use it more broadly to also include fucalean and other large seaweeds (Fraser, 2012). Here, we focus predominantly on subtidal laminarian kelps (Fig. 3.1) because these species constitute a well-defined group with respect to taxonomy, life cycles, ecology, distribution, and socioeconomic importance. However, 'kelp' is a non-taxonomic name and many other types of seaweeds provide similar functions (Bolton, 2016), with no imperative or precedence for limiting its use to the Laminariales per se (Fraser, 2012).

3.2 PHYLOGEOGRAPHY AND DISTRIBUTION

There are currently 112 species of laminarian kelp in 33 genera (Bolton, 2010). The group is believed to have evolved in the northern hemisphere around 100 million years ago and diversified into its current species around 25–30 million years ago (Silberfeld et al., 2010). Their point of origin is likely the cooler waters off northern Japan where the putative ancestors of the kelps occur today, and where the species diversity of the Laminariales is currently the highest (Fig. 3.2) (Bolton, 2010). Kelps subsequently crossed the equator, likely via 'stepping stones' of deep water in the tropics under the permanent thermocline (Graham, Kinlan, Druehl, Garske, & Banks, 2007). There have been at least four independent crossings of the equator; three from north to south and one from south to north (Bolton, 2010). There are still 2–3 times more species in the northern compared to the southern hemisphere.

Temperate rocky coastlines of western North and South America, South Africa, and parts of Tasmania are dominated by kelps that form floating canopies at the ocean's surface (Figs. 3.1 and 3.2; Table 3.1). Dense and diverse understories of prostrate kelps occur below floating canopies in many regions. The Arctic and temperate regions of the world are occupied by prostrate and stipitate kelp species (Fig. 3.2; Table 3.1), with some relatively large regions having very low species diversity (e.g., Beaufort Sea, southwestern Australia). There are no laminarian kelps in Antarctica.

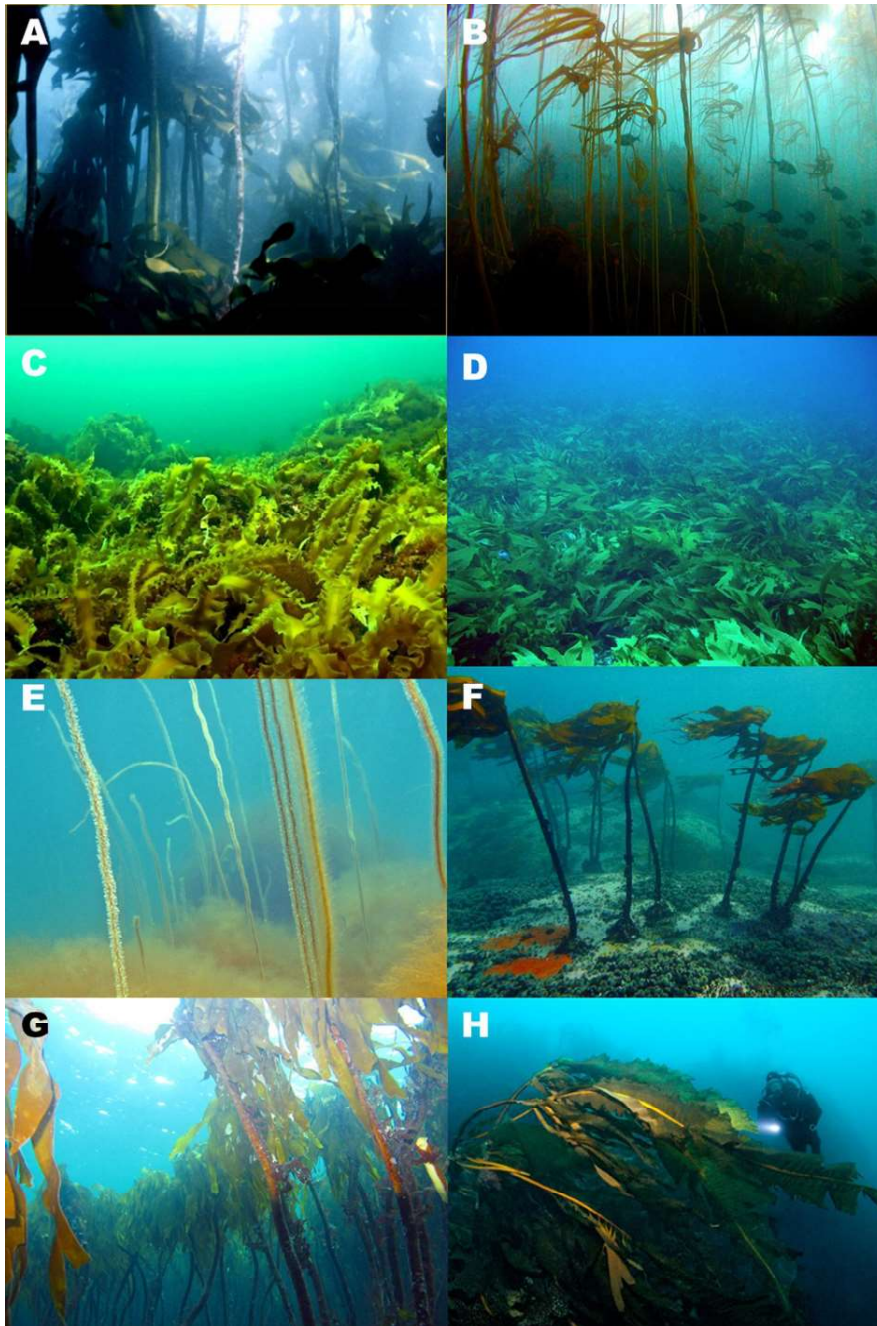


FIG. 3.1 Laminarian kelp forests are stands of large brown seaweeds that provide three-dimensional biogenic seascape structure. (A) *Ecklonia maxima*, South Africa (photo T. Wernberg), (B) *Saccharina latissima*, Atlantic Canada (photo R. E. Scheibling), (C) *Chorda filum*, Atlantic Canada (photo J. O'Brien), (D) *Nereocystis lutkaena*, Pacific Canada (photo J. Figurski), (E) *Alaria esculenta*, Greenland (photo Alamy), (F) *Laminaria hyperborea*, Norway (photo K. Filbee-Dexter), (G) *Ecklonia radiata*, Australia (photo T. Wernberg), and (H) *Laminaria pallida*, South Africa (photo T. Wernberg).

3.2.1 Growth Forms and Life Cycle

Kelps exhibit a great diversity of growth forms and life strategies. The kelp thallus consists of one or more flat blades (laminae) that originate from a stem-like structure (stipe), and the stipe is attached to a holdfast. Within this basic structure are many variations, including single cord-like thalli (Chordaceae), single stipes with single blades at the distal end of the stipe (Laminariaceae), which may be complete or digitate, single stipes with blades as 'wings' along the length of the stipe (Alariaceae), or multiple stipes with multiple blades (Lessoniaceae). Adding to this phylogenetic morphological variation, kelps also exhibit substantial phenotypic variation in size and habit.

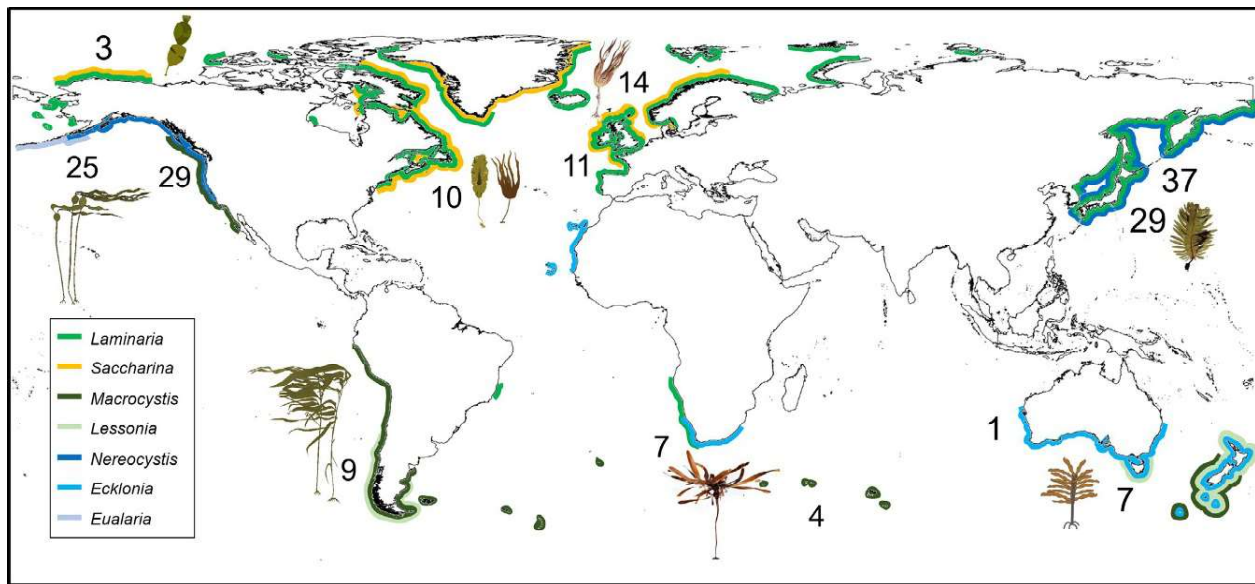


FIG. 3.2 Distribution of laminarian kelps globally. Colored lines and numbers indicate the main distribution of major kelp genera and numbers of kelp species, respectively. (After Bolton, J. (2010). *The biogeography of kelps (Laminariales, Phaeophyceae): a global analysis with new insights from recent advances in molecular phylogenetics*. Helgoland Marine Research, 64, 263–279; Steneck, R. S. & Johnson, C. R. (2013). *Kelp forests: dynamic patterns, processes and feedbacks*. In M. Bertness, B. Silliman, & J. Stachowicz (Eds.), *Marine community ecology* (pp. 315–336). Sinaur Associates Inc.; Filbee-Dexter, K. & Scheibling, R.E. (2014b). *Sea urchin barrens as alternative stable states of collapsed kelp ecosystems*. *Marine Ecology Progress Series*, 495, 1–25.)

Most habitat-forming species range in size from ca. 0.5 m to several meters (see Table 3.1). The largest kelps can attain lengths in excess of 30 m and achieve a biomass of 42 kg of fresh weight per individual. Some kelps have flexible stipes where the thallus drapes over the sea floor creating a sweeping prostrate canopy, while others have erect stipes that lift the thallus into the water column where it can form a dense canopy several meters above the sea floor (stipitate kelps). A few species have several blades and gas-filled bladders (pneumatocysts), which allow them to create a floating canopy on the sea surface.

Most species are perennial, but some are annuals. Perennial species can become relatively old, but intraspecific variations in longevity are large and usually depend on environmental conditions. For example, in Western Australia *Ecklonia radiata* rarely grows older than 5 years (Wernberg, 2005) but in New Zealand it reaches >10 years (Novaczek, 1981). Similarly, in Norway the average age of *Laminaria hyperborea* increases from 6 to 11 years with increasing latitude (Rinde & Sjøtun, 2005).

Laminarian kelp all have a heteromorphic diplohaplontic life cycle, and alternate between two generations: a microscopic haploid gametophyte generation and a diploid, macroscopic sporophyte generation that forms the kelp forests (Fig. 3.3). Reproduction starts with the formation of reproductive tissue (sporangia) in specialized reproductive blades (i.e., sporophylls; e.g., *Macrocystis pyrifera*, *Alaria esculenta*) or sori found on the blade of the sporophyte (e.g., *L. hyperborea*, *E. radiata*) where flagellated zoospores are formed. The zoospores are released, disperse, and settle to develop into male or female gametophytes, which subsequently produce gametes. The sperm leave the male gametophyte to fertilize the egg while still attached to the female gametophyte, which then develop into a juvenile sporophyte. Reproduction is often tightly cued to environmental conditions including light, nutrients, and water motion and most kelps show strong seasonality in reproduction (e.g., Bartsch, Vogt, Pehlke, & Hanelt, 2013; Mohring, Wernberg, Kendrick, & Rule, 2013).

3.2.2 Dispersal and Recruitment

Kelps disperse through motile zoospores, which are released from the adult sporophyte (Fig. 3.3) in very high density (e.g., a single individual of *Ecklonia maxima* in South Africa releases >30 billion zoospores per year, Joska & Bolton, 1987). Because the swimming speed of the zoospores is low it is often assumed that their dispersal capacity is also low (e.g., Santelices, 1990), but zoospores and recruits can be found hundreds of meters to several kilometers away from source populations (Fredriksen, Sjøtun, Lein, & Rueness, 1995; Reed, Laur, & Ebeling, 1988). Modeling indicates that up to 50% of the spores released by *M. pyrifera* can disperse >1 km, and, that a substantial fraction might disperse as far as 10 km (Gaylord, Reed, Raimondi, Washburn, & McLean, 2002). Dispersal range is mainly dictated by the zoospore release height,

TABLE 3.1 Examples of Species from the Major Kelp Genera, and Their Characteristics

Species	Main Distribution	Growth Form	Life Strategy	Biomass, Growth and Productivity	Associated Taxa	Ecology Notes	Example References
<i>Laminaria hyperborea</i>	NE Europe	Stipitate (1–2 m, single stipe with single-digitated blade)	Perennial	6–16 kg WW m ⁻²	Holdfast: 27–89 Stipe: 29–69 Blade: 34	Incredibly diverse associated community, harvested throughout W Europe	Christie et al. (2009)
<i>L. solidungula</i>	Arctic	Single blade with annual bands on single stipe. Individual kelps up to 25 m long. Prostrate canopy ~1 m.	Perennial	28 g DW m ⁻² yr ⁻¹		Only Arctic endemic kelp	Wilce and Dunton (2014)
<i>L. abyssalis</i>	Brazil	Prostrate 5–6 m long	Perennial	Max GR: 5.7% d ⁻¹ (in culture)		Deep tropical kelp	Yoneshigue-Valentin (1996)
<i>L. japonica</i>	W Pacific	Prostrate (single short stipe with single blade)	Perennial	33–34 kg WW m ⁻¹ yr ⁻¹		Extensively cultured in SE Asia (wakame)	Suzuki, Furuya, and Takeuchi (2006)
<i>Macrocystis pyrifera</i>	E Pacific, SE Australia, Southern Ocean	Floating (10–45 m length, (multiple stipe and multiple leaf-like blades)	Perennial	24–27 kg WW m ⁻² 2 kg DW m ⁻² yr ⁻¹	Holdfast: 21–114	‘Giant kelp’ that forms the tallest forests	Van Tussenbroek (1993)
<i>Lessonia trabeculata</i>	SE Pacific	Prostrate kelp with multiple branched thin blades	Perennial	9.5 kg DW m ⁻² yr ⁻¹ 4.6–5.8 kg DW m ⁻²		Harvested extensively in S America	Tala and Edding (2007)
<i>Eularia fistulosa</i>	NE Pacific	Multiple short 25 cm stipes with long floating blades. Max blade length 25 m	Annual	0.03–1.8 kg WW m ⁻²	Holdfast: 61	Dragon kelp	Stekoll, Deysler, and Hess (2007)
<i>Nereocystis leutkeana</i>	E Pacific	Floating (pneumatocysts) Max 30 m, single long stipe, multiple leaf-like blades	Annual	0.6–16 kg WW m ⁻²		Bull kelp	Stekoll et al. (2007)
<i>Ecklonia radiata</i>	Australasia	Stipitate/prostrate ~1 m, single stipe, multiple blades	Perennial	4–18 kg WW m ⁻² 21 kg WW m ⁻² yr ⁻¹	Holdfast: 25–351	Thermophile to 20 °C	Kirkman (1984)
<i>Ecklonia maxima</i>	South Africa	Floating (pneumatocysts) 8–15 m, single stipe, multiple lateral branches w blades	Perennial	0.3–10 kg DW m ⁻²	Holdfast: 97–775 g DW fauna	Sea bamboo	Velimirov et al. (1977)
<i>Saccharina latissima</i>	N Atlantic, Arctic	Prostrate (0.5–11 m, single stipe, single blade)	Perennial	2–5 kg WW m ⁻² 0.4–6 kg DW m ⁻² yr ⁻¹	Blade/stipe: 4 Holdfast: 13–25	Sugar kelp (farmed)	Mann (1972)
<i>Chorda filum</i>	N Atlantic	Floating (air cavities), 1–m, single long thin blade. Max length 6 m, 5 mm diameter	Annual	GR: 0.7 cm d ⁻¹			South and Burrows (1967)
<i>Agarum clathratum</i>	N Atlantic, Arctic	Prostrate (<1 m, single stipe, single perforated blade)	Perennial	GR: 0.018 mm d ⁻¹		Shade tolerant kelp, in understory or deep subtidal	Simonson et al. (2015)
<i>Undaria pinnatifida</i>	SE Asia (native), Pacific, E Atlantic, Southern Ocean	Prostrate, single convoluted blade	Annual	33 g DW m ⁻² yr ⁻¹	Blade: 17–24 Stipe: 7 Holdfast: 25–143	Top 100 invasive marine spp. globally	Gao et al. (2013), James et al. (2014)

Blank indicates no available information. Information on ecology, distribution and growth forms compiled from different sources. Most of the productivity (GR=growth rate) measures are taken from Krumhansl and Scheibling (2012) and associated taxa numbers are taken from Teagle et al. (2017).

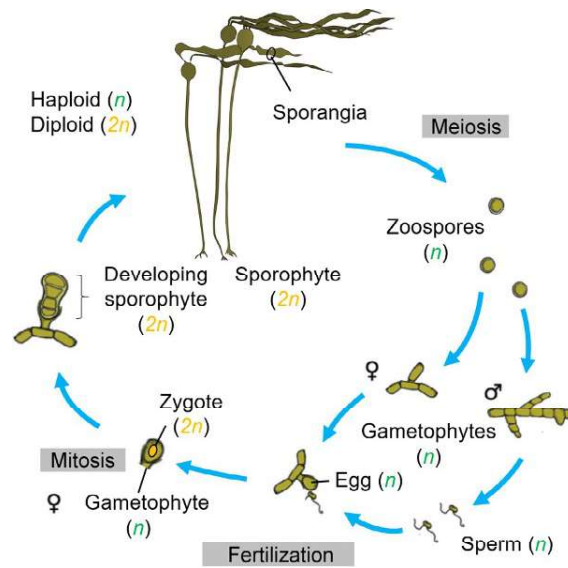


FIG. 3.3 The laminarian kelp life cycle involves alternation between two life stages: a haploid gametophyte and a diploid sporophyte. Spores settle and grow into male and female gametophytes. Eggs are fertilized while attached to the mother gametophyte by motile sperm. Only the grown sporophyte is macroscopic.

sinking rate, and by water motion. Exceptional long-distance dispersal (100–1000s km) can occur with drifting or rafting of reproductively active dislodged individuals (Reed, Schroeter, & Raimondi, 2004).

Recruitment involves multiple microscopic stages (i.e., gametophytes and juvenile sporophytes; Fig. 3.3). Because the sperm has to find an egg, male and female gametophytes must settle in close proximity at densities of ca. 1 mm^{-2} in order to secure fertilization (Reed, 1990). Gametophytes and microscopic sporophytes can persist in the kelp forest understory for weeks to months, where they serve as a ‘seedbank’ (Hoffmann & Santelices, 1991). Microscopic sporophytes start growing once stimulated by high light (Reed & Foster, 1984), such as when the canopy is lost during storms or when harvested. Within a few weeks, kelp recruits 5–10 cm in length emerge in high densities (e.g., up to 70 recruits m^{-2} in Norwegian *L. hyperborea* forests (Pedersen, Nejrup, Fredriksen, Christie, & Norderhaug, 2012). Recruitment into the adult population takes anywhere from a few months to 2–3 years depending on the species and local conditions (Pedersen et al., 2012; Reed, 1990). Most juvenile plants succumb to predation, stress, or self-thinning within the first year, but some individuals can remain viable for years without growing (Sjötun, Christie, & Helge Fosså, 2006) until space and light become available.

3.2.3 Environmental Requirements

Temperature is the most important factor controlling the range distributions of kelps (Lüning, 1990). Kelps are predominantly found in cold temperate and polar waters. Optimum temperatures for growth range from 5 to 10 °C in arctic *L. solundgula* to 15–20 °C in amphiequatorial species such as *Laminaria ochroleuca* and *Laminaria abyssalis*, while the upper lethal temperatures for the same species range from 16 °C to 23–24 °C, respectively (Wiencke, Bartsch, Bischoff, Peters, & Breeman, 1994). Gametophytes are less susceptible to heat stress than sporophytes and can survive temperatures 3–4 °C higher. However, the upper temperature limit for gametogenesis is typically 5–6 °C lower than the upper lethal limit for the sporophytes, so reproduction may be negatively affected by increasing temperature before survival of sporophytes is affected (e.g., Bartsch et al., 2013).

The realized niche occupied by kelps varies across locations, and depends on light, waves, suitable substrates, and nutrient availability (Steneck et al., 2002). Most species occur on hard substrates such as bedrock, boulders, cobbles, or biogenic structures (e.g., mussels or shells). Kelps typically extend to depths of 30–40 m, and the lower limit of kelp forests is mainly determined by the availability of light, as well as by the presence of grazers (e.g., urchins) and suitable substrate. In the Arctic, kelps tend to occur shallower because daylight hours are more limited throughout the year (as little as 5 m depth, Wulff et al., 2009), whereas in regions where light penetration is high kelps can reach up to 200 m depth (Žuljević et al., 2016).

In general, kelps thrive best in turbulent waters. In areas with low water motion, the diffusive boundary layer along the blade limits the capacity of kelps to acquire inorganic carbon and dissolved nutrients and eliminate waste products, which may reduce photosynthesis and growth (Hurd, 2000). Water motion also strongly influences kelp morphology, with

numerous adaptations in holdfast, stipe, and blade characteristics that enable them to withstand high-flow environments (Denny, Gaylord, & Cowen, 1997; Fowler-Walker, Wernberg, & Connell, 2006). However, in extremely high-flow environments drag can become too high for kelps to survive (e.g., Thomsen, Wernberg, & Kendrick, 2004).

Similar to other algae, kelps require nutrients for growth, so low nutrient levels can limit kelp growth and productivity in some regions (Graham, Kinlan, et al., 2007; Johnson et al., 2011). Some kelps can take advantage of high nutrient availability (often in winter) by taking up excess nutrients and storing them for use during subsequent periods of low nutrient availability (e.g., Henley & Dunton, 1997). Upwelling can stimulate the growth and biomass of kelps (Graham, Kinlan, et al., 2007; Velimirov, Field, Griffiths, & Zoutendyk, 1977). Eastern boundary upwelling zones experience the strongest rates of upwelling, and thus support some of the highest rates of kelp primary production globally. These include the south-east Pacific Humboldt, California, and Benguela coasts (Field et al., 1980; Graham, Vasquez, & Buschmann, 2007; Thiel et al., 2007). Within regions, local variation in kelp biomass, productivity, and ecological dynamics can be correlated with upwelling intensity (Pérez-Matus, Carrasco, Gelcich, Fernandez, & Wieters, 2017; Rothman, Mattio, Anderson, & Bolton, 2017). Localized upwelling can also create conditions that support kelps in the deep, nutrient-rich regions in the tropics. For example, deep-water kelps (*Eisenia galapagensis*) were recently discovered at 30–60 m depth off the Galapagos (Graham, Kinlan, et al., 2007), even though this region is normally outside of the environmental niche for kelps due to low nutrients and high temperatures.

3.2.4 Seasonal Dynamics of Production

Kelps are among the most productive primary producers on the planet. Net primary production of kelps globally ranges from ~30 to 2500 g DW m⁻² yr⁻¹, amounting to an average of ~500 g C m⁻² yr⁻¹ (Krumhansl & Scheibling, 2012; Mann, 1973). The only other ecosystems that rival this rate of productivity are tropical rain forests (average = 2200 g DW m⁻² yr⁻¹) and wetlands (2000 g DW m⁻² yr⁻¹) (Mann, 1973). While overall, kelps contribute relatively little to total global productivity and carbon storage because they occupy a small proportion of the Earth's surface, they substantially increase overall productivity in coastal zones (Duggin, Simenstad, & Estes, 1989).

The biomass increases occur through the initiation and elongation of blades and stipes. The location of meristematic tissue is one of the distinguishing features between kelp families; in the Laminariaceae, growth occurs at the stipe–blade junction whereas growth also occurs along the edge of the stipe in the Alariaceae. Further, in the Lessoniaceae, the primary meristem splits to form series of small blades (Bolton, 2010). New tissues produced at the meristem push older tissues towards the blade's distal end, where they erode off as small particulates or fragments (Mann, 1972; Tala & Edding, 2007). It is estimated that total blade biomass can turn over 1–5 times per year for species in the genera *Laminaria* and *Saccharina* (Mann, 1972). For kelps with multiple stipes that have blades along their lateral extent (aka fronds), frond initiation occurs at the holdfast. Fronds lengthen at the apical meristem, which produces new blade, stipe, and pneumatocyst tissue at the distal tip of the frond. Biomass dynamics for populations of the canopy kelp species *M. pyrifera* are more strongly influenced by frond initiation and loss rates than dynamics of blade growth and whole plant loss (Reed, Rassweiler, & Arkema, 2008). It is estimated that *M. pyrifera* replaces its entire biomass 6–7 times per year (Reed et al., 2008). For all kelps, growth of a blade or frond ceases when meristematic tissue is lost following blade or frond breakage.

For kelp species with a single blade (typically prostrate kelps), standing biomass throughout the year is mainly determined by seasonal changes in blade elongation and erosion, as well as the dislodgement of whole kelp thalli. Growth rate typically peaks in late winter and spring and declines in summer and autumn (de Bettignies et al., 2014; Reed et al., 2008). Kelps with multiple fronds show similar seasonal variation in growth rates compared to single-blade species, but seasonal dynamics of productivity (g m⁻² d⁻¹) are more strongly influenced by biomass dynamics than growth (e.g., thallus growth and loss, dislodgement, Reed et al., 2008). For example, net primary productivity in *M. pyrifera* is more strongly influenced by wave-induced frond loss and kelp dislodgement than individual growth rate (Reed et al., 2008) because it is more susceptible to dislodgement by waves than kelps with smaller growth forms, due to higher drag in the water column (Miller, Reed, & Brzezinski, 2011). As a result, the biomass of *M. pyrifera* (g m⁻² d⁻¹) is highest in summer following relatively calm periods, and lowest in winter when wave and storm activity peaks (Reed et al., 2008). For annual kelp species, such as *Nereocystis luetkeana*, individuals are removed during storms in late fall and early winter, leaving very little to no standing biomass during winter months.

Peak productivity in arctic, subarctic, and temperate kelp ecosystems occurs in late winter and early spring, when nutrient levels are high and water temperatures are low (de Bettignies, Wernberg, Lavery, Vanderklift, & Mohring, 2013; Graham, Vasquez, & Buschmann, 2007; Krumhansl & Scheibling, 2011a; Tala & Edding, 2007). In the Arctic, peak productivity takes place in darkness based on stored nutrients (Henley & Dunton, 1997; Wilce & Dunton, 2014) but in other systems it depends on nutrient availability and high light (Graham, Vasquez, & Buschmann, 2007). In these regions, productivity

decreases in late summer and fall when waters warm and nutrient concentrations decrease. Erosion rates typically increase during this time due to declining tissue quality caused by these environmental conditions, as well as increased grazing activity and fouling of other organisms (Andersen, Steen, Christie, Fredriksen, & Moy, 2011; Krumhansl & Scheibling, 2011b; Simonson, Metaxas, & Scheibling, 2015). Damaged kelp tissues are more susceptible to breakage by wave forces, leading to the defoliation of kelp canopies during fall and winter storms (de Bettignies, Thomsen, & Wernberg, 2012; Krumhansl, Lee, & Scheibling, 2011).

3.2.5 Foundation Species for Diverse Communities

The high productivity of kelp (see Table 3.1) provides an abundant food source for herbivores such as fish, urchins, small crustaceans, and snails that graze directly on the attached kelps (Christie, Norderhaug, & Fredriksen, 2009; Teagle et al., 2017). As a result, kelps support diverse and productive communities (Teagle et al., 2017). Still, grazing losses on live kelp are typically low and an average of about 80% of the annual production enters the food web as detached kelp detritus (Krumhansl & Scheibling, 2012) (Fig. 3.4) that may end up in adjacent or distant habitats such as beaches (Bustamante et al., Graham, Vasquez, & Buschmann, 2007), shallow temperate reefs with no kelps (Vanderklift & Wernberg, 2008), deep coastal areas (Filbee-Dexter & Scheibling, 2014a), or deep sea canyons (Vetter & Dayton, 1998), where they can shape the diversity and abundance patterns of species and fuel high secondary productivity (Krumhansl & Scheibling, 2012). Although most research has focused on impact of kelp on benthic fauna, small detached kelp particles are also used by planktonic larvae (Feehan, Grauman-Boss, Strathmann, Dethier, & Duggins, 2017) and suspension feeders (Renaud, Løkken, Jørgensen, Berge, & Johnson, 2015).

Kelps are also foundation species that modify the local environment (Fig. 3.4) (Teagle et al., 2017; Thomsen et al., 2010). Many kelps form dense canopies which, due to their size and growth form, influence physical conditions including

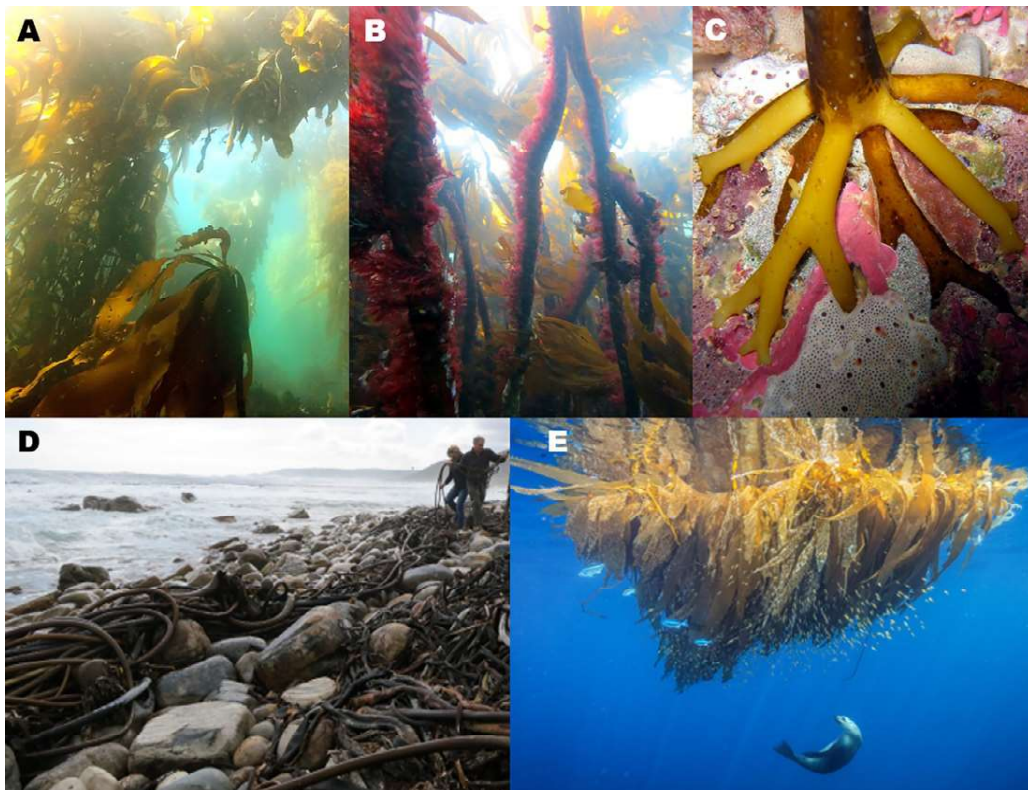


FIG. 3.4 Kelps form complex biogenic habitats that support a highly diverse and productive associated flora and fauna. (A) Canopy of *Macrocystis pyrifera*, California (photo: xxx**), (B) *Laminaria hyperborea* stipes with red seaweed epiphytes, Norway (photo T. Wernberg), and (C) an *Ecklonia radiata* holdfast, Western Australia (photo T. Wernberg). (D) Most kelp ends up as detritus (shore-cast *E. maxima* in South Africa (photo: T. Wernberg, D) and deep sea environments. (E) Rafts of floating kelp also serve as a trans-oceanic dispersal vector for marine flora and fauna (photo Brian Skerry, National Geographic Creative).

light, water flow, sedimentation, physical abrasion, and pH in their surrounding environment (Eckman et al., 1989; Krause-Jensen et al., 2016; Wernberg et al., 2005). They can reduce the amount of light reaching the seafloor to 10% or less of that reaching the top of the canopy (Pedersen, Nejrup, Pedersen, & Fredriksen, 2014; Reed & Foster, 1984; Wernberg et al., 2005). This ‘ecosystem engineering’ may negatively affect some species, but also create a unique habitat for sub-canopy species (Wernberg et al., 2005). Kelp canopies slow water movement and trap particulate organic matter and larvae, which enhances settlement by a diverse community of detritivores and filter feeders (Arkema, Reed, & Schroeter, 2009).

The physical structure of kelps attracts a multitude of species that use their structure for protection from predators or physical stress (Christie et al., 2009; Teagle et al., 2017). Epiphytes on kelp stipes also further increase the structural complexity (Christie et al., 2009; Thomsen et al., 2010), and many early life stages of fishes use the kelp forest as a nursery (Levin, 1994). Numerous predators rely on these kelp-associated species (Estes, Smith, & Palmisano, 1978). Finally, floating rafts of kelps can drift across the open ocean and provide an important trans-oceanic dispersal structures for various flora and fauna (Rothausler, Gutow, & Thiel, 2012).

As a consequence, the associated community of marine mammals, fish, invertebrates, epiphytes, and other algae is extremely diverse. Over 10 phyla have been recorded in kelp forests (Steneck et al., 2002) and a single *L. hyperborea* kelp individual can host >100 different species (Table 3.1) at densities up to 1 million per m² (Christie et al., 2009).

3.2.6 Ecosystem Services and Values

Kelps provide a wide range of ecosystem goods and services of great social, economic, and ecological value. Broadly, these ecosystem services fall into three categories: those of direct, indirect, and intrinsic value (Table 3.2).

The socioeconomic importance of kelp goes back for at least 10,000–70,000 years (e.g., Erlandson et al., 2007; Volman, 1978). Today, kelps are used in the production of fertilizers and feed for agriculture and aquaculture (Correa et al., 2016), food and pharmaceuticals (Vea & Ask, 2011), and biofuels (Hafting et al., 2015). The biomass of cultivated kelp (mostly *Saccharina japonica* and *Undaria pinnatifida*) has doubled over the last decade, to >8 million tons in 2014 with an annual value of ~US \$1.4 billion, and is now one of the fastest growing aquaculture industries in the west (Kim, Yarish, Hwang, Park, & Kim, 2017). Wide-scale commercial harvest of kelps along coasts in Asia, Africa, Europe, and South and North America has occurred in the last four decades (e.g., Buschmann et al., 2014; Kain & Dawes, 1987). Most recently, there has been an emerging economic interest in seaweeds as a new bio-marine industry and a “super food” (Buschmann et al., 2014; Correa et al., 2016).

Kelp forests generally have a positive influence on coastal fisheries (Bertocci, Araújo, Oliveira, & Sousa-Pinto, 2015), and support highly productive and valuable fisheries and tourism industries in some regions (Table 3.2), which make a substantial contribution to local communities. For example, up to 15% of the total economic activity within several regions of Australia is derived from fishing and tourism in kelp forests along the Great Southern Reef (Bennett et al., 2016). Other ecosystem services are much more difficult to quantify and value. Some kelp forests support highly unique biodiversity (e.g., Bennett et al., 2016) or have intrinsic, social, and cultural value for society through the oral histories and traditions of coastal peoples (Erlandson et al., 2007; Turner, 2000). Kelp remains a traditional food for some communities (e.g., Inuit and Sami in the high Arctic, fishing communities in Scandinavia and Japan). Fascinatingly, kelps may have played a role in the early history and biogeography of humans. Evidence suggests that coastal habitats along southern Africa provided an important source of marine food rich in omega-3 fatty acids and trace elements required for evolution and development of brain function in early humans (Compton, 2011). Early colonizers of the Americas are thought to have followed the ‘kelp highway,’ sustained by resources provided by kelp forests along the Pacific rim (Erlandson et al., 2007).

TABLE 3.2 Ecosystem Services from Kelp Forests. Valuations in 1000s of USD per year per km of Coastline from Chile, Southern Australia, and South Africa

Direct	Indirect	Intrinsic
Kelp harvesting (\$616) Commercial and recreational fishing (\$91–234) Tourism (\$156–823)	Habitat provision Primary production Climate control (\$73 ^a) Carbon storage and nutrient filtering (\$130) Coastline protection	Oral histories and traditions of coastal peoples Scientific value (\$73 ^a) Biodiversity (\$73 ^a)

^aValuation is total provided by climate control, scientific value, and biodiversity.

From Filbee-Dexter, K. & Wernberg, T. (2018). Rise of turfs: a new battle front of globally declining kelp forests. *Bioscience*, in press.

While the total economic value of ecosystem services from kelp forests can be very difficult to establish, preliminary estimates value kelp forests around 500,000–1,000,000 USD per year per kilometer of coastline (Filbee-Dexter & Wernberg, 2018). These values are most likely substantial under-estimates because they are based almost exclusively on direct values, and do not include indirect or intrinsic value.

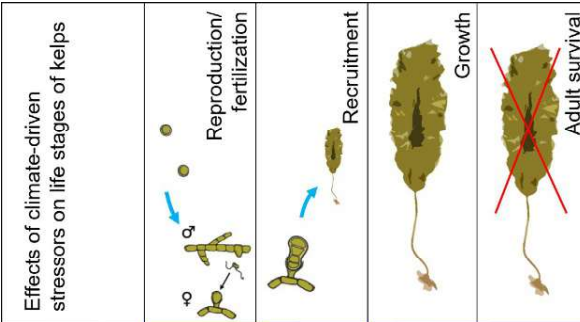
3.3 THREATS FACING GLOBAL KELP FORESTS

Kelp forests have been degraded by anthropogenic activity during the last century, and have been most heavily altered over the last two decades (Filbee-Dexter & Wernberg, 2018; Krumhansl et al., 2016; Steneck et al., 2002). Trajectories of change have been system-specific, reflecting a high degree of local variability in the drivers of change and response by kelps (Krumhansl et al., 2016). Multiple interacting stressors operating at local to global scales are at play in all regions, and include ocean warming, heat waves, storms, changes in the distribution and abundance of kelp consumers, and other human activities such as overfishing, harvesting, eutrophication, and pollution.

3.3.1 Ocean Warming and Heatwaves

Warming sea temperatures have direct and indirect impacts on kelp performance. Direct impacts are determined by the relationship between the rate and magnitude of warming, species-specific responses, and the thermal history of a kelp population. Most multicellular species display a hump-shaped thermal performance curve, with optimal performance under temperature conditions that are intermediate within the range of temperatures they can withstand (Harley et al., 2012). Thus, the direct response by kelps to increases in temperature will be dictated by how close conditions are to their thermal optimum. For species occupying areas with low temperatures relative to their optimum, warming seawater may increase growth and performance (Hargrave, Foggo, Pessarrodona, & Smale, 2017). Conversely, warming will have direct negative impacts on kelp species occupying waters at or above their thermal optimum. Short-term but high magnitude increases in temperature (i.e., heat waves), that are above the thermal limit of kelps, can lead to direct mortality (Wernberg et al., 2013), particularly if kelps are already existing above their thermal optimum (Wernberg et al., 2010).

Direct negative impacts to kelps caused by prolonged periods with water temperatures above their thermal optimum include reductions in growth rate, damage to kelp tissue, decreased resilience to disturbance, reduced reproduction and, ultimately, mortality (Fig. 3.5) (Bartsch et al., 2013; Simonson et al., 2015). Cellular damage arising from warm temperatures can reduce kelp tissue strength and extensibility, and decrease the ability of kelps to withstand wave forces (Simonson et al., 2015). Rising temperatures can also impact kelp reproduction, fertilization, and the survival of gametophytes (Bartsch et al., 2013; Mohring, Kendrick, Wernberg, Rule, & Vanderklift, 2013). Although the impacts on these microscopic life stages are less well understood compared to adults, they are likely very important in the overall population response to environmental changes (Harley et al., 2012; Schiel & Foster, 2006).



Effects of climate-driven stressors on life stages of kelps	Reproduction/ fertilization	Recruitment	Growth	Adult survival
↑°C (Tropics)	-	-	-	-
↑°C (Arctic)	0	+	+	0
↑ CO ₂	0	?	+	?
↑ Storms	?	?	?	-

FIG. 3.5 Effects of increased temperature, acidification, and increased storm intensity on different parts of the life cycle of kelps. Orange is negative effect, blue is positive effect, yellow is neutral effect, and gray is unknown. Tropics and Arctic represents effects of increased temperatures along the warmer edges of kelp range, and the cooler margins in polar regions, respectively.

Changing environmental conditions can also indirectly affect kelp by influencing biotic interactions that weaken kelp blades and increase loss. Mesograzers create partial or full-thickness perforations on kelp blades, which become weak points when blades are under stress by wave action (de Bettignies et al., 2012; Krumhansl & Scheibling, 2011a). Mesograzers (e.g., the snail *Lacuna vincta*) increase their grazing intensity at higher temperatures (Simonson et al., 2015), which combined with direct reductions in kelp tissue quality in warmer waters can lead to high rates of canopy defoliation (Krumhansl, Lauzon-Guay, & Scheibling, 2014). Further, grazing rates on individual kelps intensify at lower kelp population densities, enhancing rates of kelp canopy loss at higher water temperatures (O'Brien, Scheibling, & Krumhansl, 2015). Similarly, warming temperatures enhance rates of kelp overgrowth by encrusting bryozoan species, which also cause tissue weakening and canopy defoliation (Andersen et al., 2011; Krumhansl & Scheibling, 2011a). Climate changes can also alter distribution, densities, or behavior of herbivorous sea urchins and fish, the grazing action of which can heavily influence the abundance and distribution of kelps (Filbee-Dexter & Scheibling, 2014b; Vergés et al., 2014).

3.3.2 Other Climate-Driven Stressors

While warming is the most pervasive climate-related stressor, climate change is also associated with changes in the frequency and intensity of storms, as well as ocean acidification. Strong storms increase breakage or cause the dislodgement and removal of entire individuals or stands of kelp (de Bettignies et al., 2013; Ebeling, Laur, & Rowley, 1985; Filbee-Dexter & Scheibling, 2012). The effects of storms on kelps are magnified by temperature- or grazer-induced damage to kelp tissues (Krumhansl & Scheibling, 2011a). The direct impacts of acidification on kelps are not fully understood (Fig. 3.5). Some studies show that acidification has little to no impact on kelp reproduction and survival (Leal, Hurd, Fernández, & Roleda, 2017) whereas others have suggested some actively growing kelps could be stimulated as they can be carbon limited in nearshore environments (Swanson & Fox, 2007). There is evidence, however, that acidification impacts the competitive interactions between filamentous turf algae and kelps, and can lead to competitive dominance by turfs (Connell, Kroeker, Fabricius, Kline, & Russell, 2013). Climate-driven sea ice loss currently occurring in the high Arctic (areal loss of 3.5%–4.5% per decade) increases light availability for kelp growth. This, combined with increasing temperatures, may lead to the northward expansion of arctic kelps (Muller, Laepple, Bartsch, & Wiencke, 2009), and an increase in the depth range and productivity of these habitats (Krause-Jensen & Duarte, 2014). However, warm temperatures that lead to high freshwater run-off may increase the turbidity of coastal waters, leading to reductions in both kelp growth and the success of microscopic life stages (Traiger & Konar, 2011).

3.3.3 Fishing and Kelp Harvesting

The grazing activity of sea urchins causes persistent losses of kelp over large areas of coastline. As a result, sea urchins play a significant role in determining the distribution of kelps globally (Filbee-Dexter & Scheibling, 2014b; Steneck et al., 2002). Urchin densities can be controlled by predators such as cod, sea otters, crabs, and lobsters. Many of these predator species are of high commercial importance, which has led to their decline over the past several centuries (Estes et al., 1978; Leleu, Remy-Zephir, Grace, & Costello, 2012; Ling, Johnson, Frusher, & Ridgway, 2009). Losses of key sea urchin predators can dramatically increase sea urchin populations, which then destructively graze kelp beds (See Regime Shift section below). In some cases, increasing seawater temperatures can interact with the effects of predator removal to induce kelp loss (Catton, Rogers-Bennett, & Amrhein, 2016; Ling et al., 2009).

While harvest of seaweed has been practiced among indigenous communities for millennia (Erlandson et al., 2007; Turner, 2000), new markets for seaweed products have recently increased the demand for commercial harvest (Buschmann et al., 2014; Correa et al., 2016). As a result, kelps are currently harvested in most temperate regions (Buschmann et al., 2014). Its impacts are largely dictated by harvest method and intensity. For most kelp species, harvest has a minimal impact if only a portion of the biomass is removed (Borraz-Chavez, Edwards, & Vásquez, 2012; Krumhansl, Bergman, & Salomon, 2017; Levitt, Anderson, Boothroyd, & Kemp, 2002), leaving meristematic tissue intact and enabling kelp regrowth. Conversely, kelp mortality occurs if the entire blade of single-bladed kelps is removed, or if all fronds are harvested from kelps with multiple stipes (Borraz-Chavez et al., 2012). For some species, however, even partial removal can cause reductions in reproductive output, which can have long-term implications for population dynamics (Geange, 2014; O'Brien & Scheibling, 2016). The impacts of harvest on kelp performance can also be more severe if harvest occurs during seasonal periods of low growth (Gao, Endo, Yamana, Taniguchi, & Agatsuma, 2013), or if the kelps are stressed by high water temperatures (Krumhansl et al., 2017). Poor kelp harvest management can lead to kelp losses on regional scales (Vásquez, 2008), but harvest is generally sustainable if well regulated.

3.3.4 Pollution and Eutrophication

Pollution leading to eutrophication is an important human-driven threat to kelp forests in nearshore areas. Eutrophication increases light attenuation in the water column and can stimulate phytoplankton and fast-growing filamentous and sheet-like opportunistic macroalgae, including some epiphytic species (Airoldi, 2003; Pedersen & Borum, 1997). Epiphytes may increase the drag on blades and cover kelp tissue, which may impede light conditions (even further) and impact the uptake of nutrients and inorganic carbon (Andersen et al., 2011). High nutrient availability may also prevent recruitment of kelp by stimulating the biomass of fast-growing, mat-forming algae that can cover the substrate (Airoldi, 2003; Gorman & Connell, 2009).

3.4 TRAJECTORIES OF KELP FORESTS GLOBALLY

Stressors on kelps have increased in number and severity over the past half century and are threatening many kelp forest ecosystems globally. The impacts of these changes can be highly variable, with some regions experiencing persistent collapse of kelp forest over the long term, and others experiencing little to no change, altered communities, or even increases.

3.4.1 Regime Shifts and Alternative States of Kelp Forests

In some cases, stressors causing kelp loss over short or long timescales can favor sudden, persistent shifts to alternative community states (Fig. 3.6). These 'regime shifts' to alternative states occur when kelp forests are pushed past a critical threshold and reorganize into new configurations maintained by stabilizing feedbacks that resist further change or recovery (Scheffer, Carpenter, Foley, Folke, & Walker, 2001). The two most commonly observed and well-studied alternative states in kelp forest ecosystems are sea urchin barrens (Filbee-Dexter & Scheibling, 2014b) and turf reefs (Filbee-Dexter & Wernberg, 2018) (Fig. 3.6).

Urchin barrens are devoid of fleshy and filamentous algae and are primarily covered by encrusting coralline algae of low nutritional value. They are created when a change in sea urchin abundance or behavior triggers destructive grazing of attached kelps (see previous section). Their spatial extent can range from 1000s of km of coastline to small open clearings (100s of m in extent) within a kelp bed (Filbee-Dexter & Scheibling, 2014b). Shifts between kelp beds and barrens can be relatively abrupt. Once threshold urchin densities are achieved, destructively grazing sea urchins have unlimited, high-quality food and high fertilization rates, creating positive feedback mechanisms that accelerate the formation of barrens (Lauzon-Guay & Scheibling, 2007). When standing kelp is gone, several key feedback mechanisms stabilize the barrens' state. Encrusting coralline algae induces sea urchin settlement, which increases recruitment on barrens. Food-limited sea

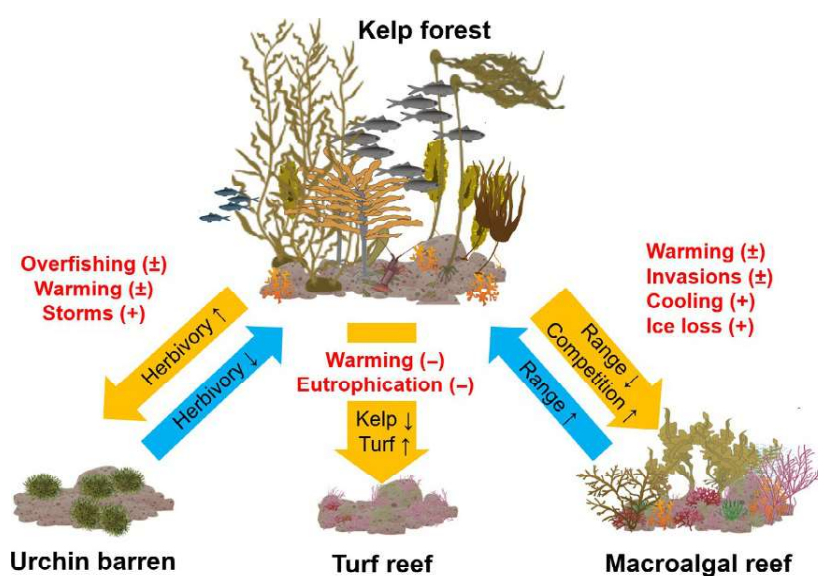


FIG. 3.6 Replacement of kelp forests by three alternative ecosystem states: urchin barrens, turf reefs, and macroalgal reefs. Prominent drivers are red, with + drivers pushing the system toward a decline of kelp, - drivers leading to an increase kelp, and ± drivers varying in their effect across different regions. Arrows show mechanisms of kelp loss and kelp recovery.

urchins constantly scour the barrens and prevent the recruitment and reestablishment of kelps. Loss of kelp canopy also removes habitat for urchin predators, reduces physical abrasion (which can interfere with urchin feeding, [Velimirov & Griffiths, 1979](#)), and removes a supply of kelp propagules, further lowering recruitment ([Filbee-Dexter & Scheibling, 2014b](#)). Shifts between kelp forests and barrens can be cyclical, with reefs flipping between barrens and kelp forests over year to decade-long periods ([Steneck et al., 2002](#)).

The alternative ‘turf’ state comprises rocky reefs covered by small, often finely branched filamentous or foliose low-lying algae ([Filbee-Dexter & Wernberg, 2018](#)). Turf algae tend to be stress tolerant compared to kelps, and have high cover and turnover rates. Once kelps are lost, turfs can quickly monopolize primary substrate and modify the chemical environment by reducing oxygen or concentrating contaminants. Their dense network of filament traps and accumulates high loads of sediment ([Gorgula & Connell, 2004](#)), which limits kelp settlement and reduces germination and survival of recruits ([Devinny & Vorse, 1978](#); [Gorman & Connell, 2009](#)). As for the barren state, Allee effects such as increased grazing or reduced spore supply may further stabilize the turf state ([O'Brien & Scheibling, 2016](#)), but in contrast to shifts to the barren state, there have been no observations of turfs shifting back to kelps ([Filbee-Dexter & Wernberg, 2018](#)).

When kelps are lost, other macroalgal species can expand and/or increase in abundance either from competitive release or when new environmental changes favor their growth and reproduction over kelps. These macroalgae include understory species that are usually suppressed by competition with canopy kelps, or species that have invaded or expanded into the range of kelp. For example, invasive *Codium fragile* subspecies *fragile* and numerous red algae have increased in abundance and replaced native kelps in Atlantic Canada and eastern USA ([Filbee-Dexter & Wernberg, 2018](#)). Canopy-forming *Sargassum* spp. expanded into declining *Ecklonia cava* forests in Japan ([Tanaka, Taino, Haraguchi, Prendergast, & Hiraoka, 2012](#)). Increased cover of invasive *Sargassum muticum* coincided with declines in *Laminaria digitata*, *L. hyperborea*, and *Saccharina latissima* in Spain, France, and in Denmark ([Cosson, 1999](#); [Stæhr, Pedersen, Thomsen, Wernberg, & Krause-Jensen, 2000](#); [Viejo, 1997](#)).

3.4.2 Global Trajectories

Threats to kelp forest ecosystems have increased in number and severity over the past half century, leading to a global decline of kelp abundances of ~2% per year ([Krumhansl et al., 2016](#)). Trajectories of change vary considerable across regions, however, both in terms of magnitude and direction. Declines have been observed in 38% of the regions for which there are sufficient data for analysis, and increases have occurred in 27% of regions ([Krumhansl et al., 2016](#)). The remaining regions show no detectable change over this time period ([Krumhansl et al., 2016](#)). This pattern of highly variable trajectories across regions reflects, in part, spatial differences in the presence, magnitude, and effect of various drivers of change. Coherent patterns of change across regions could indicate that a single driver of kelp forest dynamics dominates globally, or that the resilience of kelps to multiple drivers is being eroded worldwide. The fact that signals of change differ both in direction and magnitude across regions indicates that local and regional factors play an important role in mediating the response of kelp forests to global climate change, and that some kelp forests remain resilient in the face of ocean warming ([Wernberg et al., 2013](#)), though widespread losses in regions with the longest monitoring programs suggest that resilience may be declining globally.

3.4.3 Short-Term Records of Kelp Change

Kelp forest biomass tends to be highly variable over seasonal and interannual timescales due to their tendency to respond quickly to changes in environmental conditions (e.g., [Dayton & Tegner, 1984](#); [Henley & Dunton, 1997](#); [Wernberg & Goldberg, 2008](#)). When looking at short timescales (<20 years), the occurrence of regional declines is nearly as common as the occurrence of regional increases in kelp globally ([Fig. 3.7](#)) ([Krumhansl et al., 2016](#)). High magnitude but relatively short-duration declines have been observed in regions such as Tasmania, Western Australia, Chile, and the Aleutian Islands, USA. In some of these cases, rapid declines reflect recent losses due to climate-related disturbance events ([Wernberg et al., 2013](#)). For example, a marine heatwave in Western Australia in the austral summer of 2010/11, following four decades of gradual warming, caused extensive kelp loss ([Wernberg et al., 2013, 2016](#)). This loss has persisted because regional warming has allowed herbivorous tropical fish to expand into the temperate reefs. These fish graze on kelp recruits and prevent the kelp forests from reestablishing ([Bennett, Wernberg, Harvey, Santana-Garcon, & Saunders, 2015](#); [Zarco-Perello, Wernberg, Langlois, & Vanderklift, 2017](#)). Declines over short time periods have also been noted in response to the rapid intensification of human activities (e.g., kelp harvest in Chile) ([Vásquez, 2008](#)), and will likely persist as long as these activities are not properly managed.

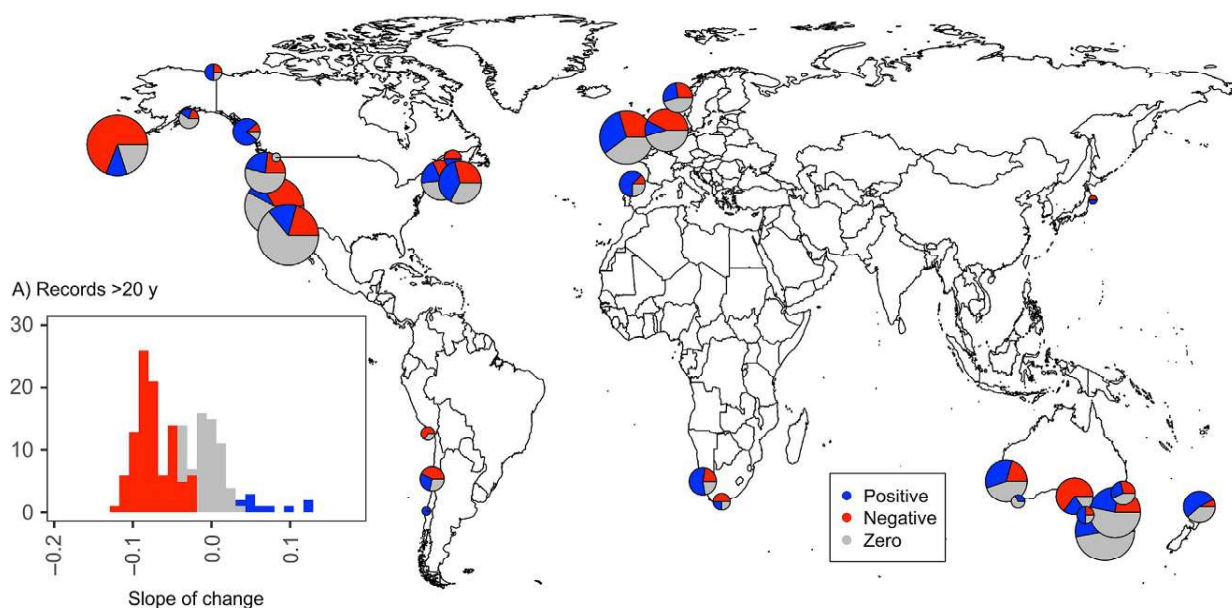


FIG. 3.7 Trajectory of change in records of kelp abundance globally. Size of the pie chart represents number of records. Inset (A) summarizes changes for a subset of records that span >20 years. (Adapted from Krumhansl, K. A., Okamoto, D. K., Rassweiler, A., Novak, M., Bolton, J. J., Cavanaugh, K. C., et al., (2016). *Global patterns of kelp forest change over the past half-century*. *Proceedings of the National Academy of Sciences*, 113, 13785–13790.)

3.4.4 Long-Term Records of Kelp Change

Where kelp forests have been monitored for 20–50 years, declines are observed more commonly than increases, indicating that global losses reflect temporally persistent shifts in some regions (Fig. 3.7). Declines over longer timescales have been observed in Nova Scotia, the Gulf of Maine, North-Central California, Norway, Ireland, and South Australia, where some of the longest available time series of kelp abundances exist. In these cases, losses have occurred mainly in response to persistent shifts in environmental conditions. Along the west and Skagerak coasts of Norway, loss of kelp forests appears to have been partly driven by warming sea temperatures over five decades and by exceptionally warm summers in 1997, 2002, and 2006 (Moy & Christie, 2012). The effects of climate change may be exacerbated by local stressors such as invasive species and seawater pollution. For example, kelp declines in Atlantic Canada in the last 2 decades have largely been driven by indirect effects of warming temperatures, which increased recruitment and growth of an invasive bryozoan, damaging fronds, and increasing breakage and mortality (Krumhansl et al., 2011). In the northern Mediterranean Sea, Sweden, Denmark, southern Norway, and South Australia, the disappearance of canopy kelps was largely attributed to increases in coastal nutrients and sediment loading (Filbee-Dexter & Wernberg, 2018). In industrial regions in Kola Bay (Russia) and New South Wales (Australia), sewage and urban pollution led to localized declines in kelps and other habitat-forming seaweeds (Filbee-Dexter & Wernberg, 2018).

3.4.5 Kelp Trajectories Within Different Regions

In some regions, dramatic kelp loss has occurred in the last decade. Shifts from kelp forest to turfs along 10 s to 100 s of km of coastline in Atlantic Canada (Filbee-Dexter, Feehan, & Scheibling, 2016), Europe (Araújo et al., 2016), and Australia (Connell et al., 2008; Wernberg et al., 2016) have occurred. In Tasmania, the southern intrusion of the East Australian Current has expanded the range of sea urchins, driving the loss of kelp forests (Johnson et al., 2011). In Northern California, high sea temperatures from the ‘warm blob’ caused both the extensive mortality of kelps and triggered a population boom of purple sea urchins, which overgrazed 100 s of km of coast (Catton et al., 2016).

In many regions, however, kelp forests have remained relatively stable or have increased. In some cases, a lack of change reflects insufficient data to detect such change (e.g., Merzouk & Johnson, 2011), but in other cases, kelp forest persistence reflects effective ecosystem management, a high degree of kelp forest resilience, a minimal presence of stressors, and/or climate impacts that favor kelp abundance or suppress competitors and consumers. For example, increases in kelp abundances along Vancouver Island, British Columbia, have occurred in response to the recovery of sea otters through

harvest restrictions (Watson & Estes, 2011), and kelps have rebounded in Southern California following improved wastewater management practices (Foster & Schiel, 2010). In some cases, climatic shifts may benefit kelps, particularly when change is characterized by regional cooling (e.g., south coast of South Africa, Bolton, Anderson, Smit, & Rothman, 2012), or where regional kelp populations include warm-adapted species that may be favored under warming climate regimes (Smale, Wernberg, Yunnice, & Vance, 2015). In Norway, warming sea temperatures are causing sea urchin recruitment failure and increased *L. hyperborea* abundance along the west coast (Fagerli, Norderhaug, & Christie, 2013). Some kelp populations may have the capacity to adapt to change, or may be less vulnerable to climatic disturbances because they experience relatively warm and/or variable conditions naturally.

3.4.6 Gaps in Our Understanding, Data Limitations and Biases

The most comprehensive global analysis of kelp forest change to date (Krumhansl et al., 2016) was only able to obtain data from, and describe trajectories of change in, about 33% of regions inhabited by kelp forests worldwide. Thus, our global picture of kelp forest change is severely limited, and biased by those temperate regions for which there is the most data. For example, in cases where abundant data are only available for recent years, patterns of change over the last decade may obscure long-term trends evident in alternative data sources or through anecdotal evidence (e.g., kelp increase in South Africa, Bolton et al., 2012; variable change in Greenland, Krause-Jensen et al., 2012; kelp declines in southern Europe, Voerman, Llera, & Rico, 2013; Atlantic Canada, Filbee-Dexter et al., 2016; and Western Australia, Wernberg et al., 2016). What is striking is the noticeable lack of data from Arctic regions; worldwide, the only consistent monitoring of arctic kelps is occurring in Alaska, USA, and Svalbard, Norway (Bartsch et al., 2016; Wilce & Dunton, 2014).

Our capacity to detect change in global kelp forests is also complicated by the fact that few records of kelp abundance date back to earlier than the 1990s. Most kelp forest monitoring programs were initiated after SCUBA technologies became widely adopted in the 1980s, but have been inconsistent through time due to the nature of short-duration funding cycles and a lack of interest in basic ecological monitoring. Ultimately, our capacity to detect and mediate further kelp forest losses worldwide will be dependent on the extent of resources put towards monitoring, particularly in those regions for which monitoring programs have been absent or inconsistent over the past century.

3.5 THE FUTURE OF KELP FORESTS

Kelp forests are highly dynamic ecosystems that respond strongly to variation and change in their surrounding biological, physical, and chemical environment. As a consequence, many kelp forests have changed in distribution, extent, composition, and function in response to climate change, reduced water quality, harvesting, and fishing over the past fifty years (Filbee-Dexter & Wernberg, 2018; Krumhansl et al., 2016; Steneck et al., 2002). These changes are expected to continue and likely accelerate in the future, as the climate continues to change and human activities intensify. While there is strong consensus on the general drivers and direction of change, substantial uncertainty remains regarding rates of change, the combined effects of multiple interacting stressors (e.g., Strain, Thomson, Micheli, Mancuso, & Airoidi, 2014; Wernberg, Smale, & Thomsen, 2012), and the role of regional factors (climate, currents, geomorphology, human population pressure, etc.) in mediating these effects (Krumhansl et al., 2016; Wernberg et al., 2011).

3.5.1 Projected Changes in Kelp Distribution

A steadily growing number of increasingly sophisticated habitat suitability models forecast substantial changes in the distribution of kelp forests by the end of this century. In Australia, for example, projections to 2100 for 15 prominent species of kelps and canopy-forming temperate seaweeds projected an average loss of 62% (range: 27%–100%) of their current distributions under the conservative RCP 2.6 emission scenario (Martinez et al., 2018). Under the intermediate RCP 6.0 scenario, *M. pyrifera* was predicted to go extinct in Australia and *E. radiata* to lose 71% and become compressed onto the south coast (Martinez et al., 2018). Similarly, eight North Atlantic kelp species were projected to lose 50% (range: 0–100) of their distribution in regions at their warm range margins by 2100 under RCP 2.6 and several local extinctions under RCP 8.5 (Assis, Araújo, & Serrão, 2018). At the same time, the models also show range expansions at the cool margins for three of the eight species including *S. latissima* expanding into the Arctic and *L. ochroleuca* expanding into southern Europe (Assis et al., 2018). In some cases, the kelps may establish new kelp forests (e.g., when ice sheets melt, Krause-Jensen & Duarte, 2014) and in other cases they expand into existing kelp forests such as seen in southern Europe where *L. ochroleuca* slowly has been replacing *L. hyperborea* over recent decades (Smale et al., 2015). In Japan, models suggest *E. cava* will be able to cope with increasing temperatures under RCP 2.6 but could be impacted by range-shifting herbivores (Takao,

Kumagai, Yamano, Fujii, & Yamanaka, 2015), as it has been seen in Australia under moderate temperature increase (Vergés et al., 2016; Zarco-Perello et al., 2017). Under RCP 8.5, however, the kelps would also be directly affected by the warmer temperatures and contract their distribution by 85% (Takao et al., 2015). Increasing temperatures may also facilitate the establishment of invasive kelps in new regions, such as has been seen with *Undaria pinnatifida* in northern New Zealand (James, Middleton, Middleton, & Shears, 2014).

3.5.2 Management Options, Building Resilience, and Solutions for Recovery

Some forms of management have been effective in restoring kelp forests. Early strategies involved controlling population outbreaks of sea urchins in order to reduce grazing intensity and increase kelp cover. For example, the establishment of marine reserves in New Zealand increased lobster and predatory fish populations, resulting in substantial recovery of kelp in the MPA compared to unregulated areas (Leleu et al., 2012). Direct removal of urchins by commercial harvest lowered sea urchin densities and restored kelp forests in Maine and California, USA. More drastic examples of urchin removal to recover kelp forests include researchers 'quick liming' sea urchins in northern Norway (Sunset, Strand, & Moy, 2010) and Nova Scotia (Bernstein & Welsford, 1982), and divers culling urchins on barrens in Australia (Sanderson, Ling, Dominguez, & Johnson, 2016) and California (Wilson & North, 1983). However, the effectiveness of this 'top down control' strategy can be severely limited (Sanderson et al., 2016). In Tasmania, a large-scale experimental introduction of hundreds of spiny lobsters into sea urchin barrens reduced sea urchin densities, but resulted in little to no recovery of kelp (Johnson et al., 2007).

Other strategies to restore kelp forests focus on bottom-up controls of kelp abundance, by reducing nutrients or pollution. More active solutions proposed to increase the resilience of vulnerable kelp forests includes active restoration methods (Fig. 3.8). Seeding of kelps may assist recovery in areas with extensive kelp loss where source populations of kelps are missing (e.g., regions where source kelps have disappeared such as Western Australia). Increasing the biomass of kelp by transplanting adults has been explored on small scales in the Gulf of St. Lawrence, Canada, Australia, California, USA, Japan, and northern Norway, with mixed results (e.g., Deysher, Dean, Grove, & Jahn, 2002; Wilson & North, 1983).

The potential for species to adapt genetically to handle changing environmental conditions depends on the amount of standing genetic variation in the population and the rate that new genetic changes are incorporated into populations (Somero, 2010). For example, in cases where kelps cannot expand their distribution quickly enough to cope with changing



FIG. 3.8 Examples of kelp forest restoration. (A) Divers suppressing purple sea urchins to restore kelp forests in California (Tom Boyd, Santa Monica Bay), (B) ongoing project in northern Norway transplanting adult kelps onto sea urchin barrens in order to recover kelp forest state (Camilla With Fagerli, NIVA), and (C) artificial square kelp forests created by pushing rocks from a barge (D) onto sand bottom in San Clemente, California (<https://www.ocregister.com/2011/07/07/family-science-night-to-spotlight-giant-kelp-forest/>).

environmental conditions, assisted migration could accelerate range expansion and enhance local adaptation (Hewitt et al., 2011). Similarly, by identifying resistant genotypes in kelps that perform well under stressful conditions, it may be possible to breed resilience into vulnerable populations or promote recovery of degraded ecosystems by introducing better adapted individuals or genes into natural communities, with the hope their traits become intermixed and incorporated into wild populations. The implementation of these measures over traditional conservation strategies has created intense debate in the last decade (McLachlan, Hellmann, & Schwartz, 2007). These strategies are contentious, but will likely be more strongly explored and considered in the future.

There is a growing consensus that recovering past ecological communities will be difficult in light of persistent changes in environmental conditions (Hobbs, 2007). Kelp forests are no exception and it may not be possible to manage kelp loss resulting from climate change. Warming oceans, increased storm severity, or altered ocean currents may be mitigated to some extent by maintaining high biodiversity and species richness within vulnerable ecosystems, or by reducing local impacts such as pollution or harvest (Brown, Saunders, Possingham, & Richardson, 2013). However, in many cases the future impacts of climate change on kelp forests greatly exceed the management capacities of coastal areas and these changes are going to happen regardless of what we do now. Adapting to new or altered temperate reef communities, and better understanding how these changes will impact the services they provide, may be the best option for coastal managers.

3.6 CONCLUSION

Kelp forests are highly dynamic ecosystems and many are now changing in response to human activities at local, regional, and global scales. Observed and predicted changes include range contractions and habitat loss (Filbee-Dexter et al., 2016; Tanaka et al., 2012; Wernberg et al., 2016), range expansions with colonization of new habitat or species replacements (Bolton et al., 2012; Smale et al., 2015), and increasing establishment of invasive kelps (James et al., 2014). At the same time, similar changes occur in a variety of species that compete with, or consume, kelps (Stæhr et al., 2000; Vergés et al., 2014), adding to the complexity of net effects on the kelp forests. The ecological consequences include habitat loss (Wernberg et al., 2016), loss of important detrital resource subsidies (Krumhansl et al., 2014), reduced temporal stability of the forest structure (South et al., 2015), as well as the creation of novel communities (e.g., tropical herbivores on temperate reefs) (Vergés et al., 2014). Another possible consequence is a loss of genetic diversity in the kelp forests, which may in turn reduce their resilience to further change (Wernberg et al., 2018). These changes will likely have significant impacts on marine biodiversity and ecosystem functioning because kelps are foundation species for hundreds if not thousands of habitat-associated plants and animals, many of which are socioeconomically important (Bennett et al., 2016; Blamey & Bolton, 2017; Vásquez et al., 2014).

Unlike other threatened marine ecosystems, kelps do have a remarkable ability to regrow full canopies within short time spans (years) and there are examples of wide-scale kelp forest recovery occurring in the past. Although the diversity of responses to biological, chemical, and physical change both between species within regions and between regions within species makes it virtually impossible to generalize predictions about the future of kelp forests, it seems almost certain that many kelp forests a few decades from now will differ substantially from what they are today.

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