Securing a Sustainable Future for Kelp Forests
Chapter 1. Ecology of kelp forests and their main threats

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Highlights

- Kelp forests are one of the most extensive coastal habitats in the world, covering 25 per cent of the world’s coastlines and 1.5–2 million km².
- These highly diverse ecosystems are created by a variety of large brown seaweed species, which thrive in cool high-energy environments and form forests with a dense canopy and shaded understory.
- Human activities have had a profound influence on kelp forests across their range, with increasingly negative impacts during the past 50 years.
- Climate change and warming temperatures are among the main threats facing kelp forests, and often interact with other pressures such as eutrophication, reduced water quality, overfishing, invasive species and kelp harvesting.

What are kelp forests?

Kelp do much the same underwater as trees in a forest do on land: they create three-dimensional structures that moderate their local environment, providing an abundant food source and a unique habitat for scores of associated organisms. Indeed, the forest analogy, and the role of kelp in creating habitat for marine organisms, has been recognized for centuries. Famously, Charles Darwin compared the giant kelp forests of South America to tropical rainforests, asserting that they support an equal number of species (Darwin 1839). Even if this is not strictly true, the biodiversity and productivity supported by kelp forests is truly remarkable (e.g. Teagle et al. 2017; Pessarrodona et al. 2021).

While there is no definitive definition of kelp (Bolton 2016), all kelp species have a common form consisting of three main parts: a blade or blades that take in sunlight and nutrients from the surrounding water, a stipe that supports the blade(s), and a holdfast which anchors the organism to the sea floor. Some kelp are rigid, held up by a stiff stipe, whereas others are highly flexible, either draping across the sea floor or being held upright or floating close to the surface by gas bladders. The majority of kelp species range in size from about half a metre to several metres, but a few species can grow to more than 30 m in length.

Many scientists use the term “kelp” to refer to brown seaweed (Ochrophyta) of the order Laminariales only, whereas others use it more broadly to also include some members of the orders Fucales, Tilipteridales and Desmarestiales (Fraser 2012; Wernberg and Filbee-Dexter 2019). Both uses are correct and have a long history. For example, the common name “bull kelp” can refer to Nereocystis luetkeana (Laminariales) in North America and to Durvillaea antarctica (Fucales) in New Zealand (Fraser 2012). While our definition of kelp forest (Box 1.1) is deliberately inclusive, here the focus is primarily on the Laminarian kelp as they, as a group, constitute the bulk of forest-forming species along most coastlines. There are just over 100 species of Laminarian kelp – around half of which are forest-forming either on their own or as part or multi-species canopies (Druehl 1970; Lane et al. 2006; Bolton 2010).

There is also no set definition of what constitutes a kelp forest. On land, where there are hundreds of definitions of specific types of forests, a “forest” is intuitively understood simply to be areas with lots of trees. Similarly, kelp forests are areas dominated by kelp that form a three-dimensional vegetated habitat with a canopy that either floats on the surface or is submerged with erect or draping canopies. Sometimes kelp forests are referred to as “kelp beds”. However, as this term has been used inconsistently across kelp species and canopy types, it may be best to simply use the term “kelp forests” because they all provide multilayered habitat similar to forests on land (Wernberg and Filbee-Dexter 2019).

Kelp forest structure and environment

There are three broad forms of kelp forests: surface canopies where the blades float on the surface held up by gas bladders (e.g. Macrocystis pyrifera, N. lutkeana, Ecklonia maxima), stipitate subsurface canopies where the blades are suspended in the water column, usually by a rigid stipe (e.g. Laminaria hyperborea, Lessonia trabeculata, E. cava) and prostrate canopies where the blades and flexible stipes are draped over the bottom (e.g. Saccharina latissima, E. radiata) (Figure 1.1). These forms (morphologies) are not always clearly distinct and intermediate forms also exist even within species due to different environmental conditions (e.g. Kennelly 1989). Some kelp forests are made up of a single species, but often several forest-forming species co-occur in mixed-species and multilayer canopies (Dayton et al. 1984; Maxell and Miller 1996; Connell and Irving 2008).
Box 1.1. Definition of kelp forests

Kelp forests can be defined as subtidal stands of large brown macroalgae that modify their physical environment to create distinct environmental conditions and habitat.

This definition recognizes that kelp constitute ecologically similar species from several phylogenetically distinct orders that usually spend a significant part of their life cycle fully submerged. These kelp species have a common structure, consisting of a holdfast, stipe(s) and blade(s) that create a canopy. It also recognizes that “forests” are emergent properties of kelp aggregations when these are extensive and dense enough to modify their biophysical environment and create a unique multilayered habitat.

Figure 1.1. Examples of kelp with (A) surface canopy (*Ecklonia maxima*, South Africa; photo credit: T. Wernberg), (B) stipitate canopy (*Laminaria hyperborea*, Norway; photo credit: K. Filbee-Dexter) and (C) prostrate canopy (*Saccharina latissima*, Canadian Arctic; photo credit: R. Scheibling)

Kelp are ecosystem engineers that modify their surrounding environment due to their large size, complex form, high density and the area they cover. They can reduce light penetration (Wernberg, Kendrick and Toohey 2005; Pedersen et al. 2014), dampen currents and waves (Mork 1996; Gaylord et al. 2007) and affect sedimentation (Eckman, Duggins and Sewell 1989; Wernberg, Kendrick and Toohey 2005) and the recruitment of marine organisms (Duggins, Eckman and Sewell 1990; Almanza et al. 2012). For example, the removal of kelp in both California and Australia resulted in a reduction in species richness of around 30 per cent (Graham 2004; Ling 2008). Kelp can reduce nutrients in the water column (Jackson 1997) and provide surface area on which epiphytic organisms can grow (e.g. Teagle et al. 2017). Kelp can also transfer carbon (via drift kelp, fragments and dissolved organic carbon) within kelp forests and to surrounding habitats (Bustamante, Branch and Eekhout 1995; Wernberg et al. 2006; Vilas et al. 2020). High rates of carbon fixation and export emphasize the potential for kelp carbon sequestration (Krause-Jensen and Duarte 2016).

Global distribution of kelp forests

Laminarian kelp likely originated in the cool waters around Japan about 100 million years ago and diversified into their current forms around 25–30 million years ago (Silberfeld et al. 2010). Complex morphologies (including branching patterns, gas bladders and other structures) evolved several times over the past 15–20 million years, highlighting the importance of morphological convergence in establishing modern upright, complex kelp forests (Starko et al. 2019). Despite evidence that they crossed the equator on four separate occasions, the evolutionary history of Laminarian kelp is still apparent today, as there are many more species in the northern hemisphere than in the southern hemisphere (Bolton 2010) (Figure 1.2), and very few species are found in both hemispheres. The most diverse region is the North Pacific, with over 40 species in Asia and nearly 40 species in North America (Lane et al. 2006).

Today, Laminarian kelp forests are found along around 25 to 30 per cent of the world’s coastlines. They are the largest marine biome in the world, covering 1.5–2 million km$^2$ which is 5–10 times more ocean area than coral reefs (Wernberg et al. 2019b; Starko, Wilkinson and Bringloe 2021) (Figure 1.2). Temperature is a strong driver of kelp biogeography. Given their evolutionary history, kelp are predominantly cool water species found at temperate, Arctic and sub-Antarctic latitudes. There are no Laminarian kelp in Antarctica (Lüning 1990). Kelp forests can also be found at tropical latitudes (e.g. Galapagos Islands) on deep seamounts in clear water where there is still enough light to sustain photosynthesis and upwelling provides low temperatures and high nutrient concentrations (Graham et al. 2007a).
Most kelp forests are subtidal and found from the water’s edge down to 15–25 m and in places with particularly clear water down to 40–60 m (Graham et al. 2007a; Marzinelli et al. 2015b; Ramos et al. 2016). However, several species of Laminarian kelp can be found in the intertidal zone, such as Postelsia palmaeformis in the North-East Pacific coast and L. spicata in the South-East Pacific coast (González et al. 2014). Kelp are also found depths in excess of 200 m (Žuljević et al. 2016).

Dominant and iconic kelp species

Most species of Laminarian kelp are relatively unknown and do not have common names in English. However, a few species are very well known for a variety of reasons. The genera Macrocystis, Ecklonia and Laminaria are probably the most widespread kelp, with species in both the northern and southern hemispheres (Bolton and Anderson 1994; Graham, Vásquez and Buschmann 2007b; Bartsch et al. 2008; Wernberg et al. 2019a). Giant kelp (M. pyrifera) is one of the most iconic kelp species in the world due its conspicuous floating canopy that forms tall, dense forests that support very diverse organisms (Graham, Vásquez and Buschmann 2007b). The species is distributed along the sub-Antarctic and the north-eastern Pacific coasts (Macaya and Zucarello 2010). Golden kelp, E. radiata, is the biological engine of the Great Southern Reef, where it forms extensive forests across thousands of kilometres of rocky reef along the south coast of Australia, in most places as the only Laminarian kelp (Bennett et al. 2016; Wernberg et al. 2019a). Bull kelp, N. luetkaena, is also largely distributed in the British Columbia coast, along the west coast of Canada (Schroeder et al. 2020).

Some kelp have been used as food and medicine for more than 10,000 years (Dillehay et al. 2008) and are now well known as harvested or cultivated crops (see also section B of chapter 3). Lessonia species are the most harvested kelp in the world and are particularly important in Chile and Peru (Food and Agriculture Organization of the United Nations [FAO] 2021), whereas Laminaria species are extensively harvested in the European coast of the Atlantic, especially in Norway and France (Smale et al. 2013). In addition to the importance of kelp for food and the polysaccharide (sugar) industry, different kelp species have been used to obtain some bioactive compounds (e.g. phlorotannins), or to produce extracts for agronomical applications (e.g. fertilizer, see Buschmann et al. 2017). Finally, due to its high growth potential and high tissue-sugar content, there are different ongoing large-scale research and technological programmes for cultivating kelp for biofuel production, biomitigation of anthropogenic nitrogen inputs and carbon sequestration (e.g. Chopin and Tacon 2021; Naylor et al. 2021).

Kombu (S. japonica) and sugar kelp (S. latissima) have become some of the most cultivated kelp species globally (Naylor et al. 2021). Wakame (Undaria pinnatifida) is another well-known and widely cultivated kelp. Native to the cooler waters around the Republic of Korea, Japan and northern China, wakame is also known to be one of the most invasive seaweed species in the world and is now found in North and South America, Europe and Australia and New Zealand (Schaffelke and Hewitt 2007; South et al. 2017).
Figure 1.2. Distribution of common kelp groups around the world
Box 1.2. Kelp life cycle and abiotic requirements

Like plants on land, kelp require sunlight and carbon dioxide (CO₂) for photosynthesis and inorganic nutrients including nitrate, phosphate and several trace elements and vitamins, all of which are present in seawater. Kelp vary substantially in their capacity to store nutrients and energy. Some species (e.g. *S. latissima* and *L. solidungula*) can maintain growth under light- and nutrient-limiting conditions for weeks to months based on stores in their stipe (Dunton 1985), whereas other species (e.g. *M. pyrifera*) have a very low carbon and nutrient storage capacity and depend on a continuous supply of light and nutrients to sustain their growth (Graham, Vásquez and Buschmann 2007b). In addition, most kelp require a hard (rocky) bottom for attachment during development of both the gametophyte and sporophyte stage.

All Laminarian kelp have a life cycle with two distinct phases: a macroscopic sporophyte (the adult kelp) and a microscopic gametophyte (small life phase for sexual reproduction) (Figure 1.3). It is the sporophyte that makes up the kelp forest, but the full life cycle cannot be completed without the microscopic gametophyte, and these two life stages can have different environmental requirements and vulnerabilities. Non-Laminarian kelp, on the other hand, do not have an alternation of phases, but instead the gametes arise directly from the kelp and develop directly into a new adult.

Although all Laminarian kelp have the same basic life cycle (Figure 1.3), different species exhibit substantial variation in ecological strategies. Many species are perennial with a sporophyte that can live for anywhere between several years and more than a decade, whereas other species are annuals, where the entire life cycle lasts only a few months (Wernberg *et al.* 2019b). Some kelp show remarkable plasticity in population dynamics and can alternate between a perennial and annual strategy. For example, giant kelp (*M. pyrifera*) is usually perennial but in some populations in Chile the species is annual, relying on synchronous reproduction and microscopic stages that are able to survive for several months to connect successive time-separated generations (Buschmann *et al.* 2006).

Reproduction ranges from all year round in some species such as giant kelp (*M. pyrifera*) (Graham, Vásquez and Buschmann 2007b) to seasonally in other species such as cuvie (*L. hyperborea*) (Andersen *et al.* 2011), golden kelp (*E. radiata*) (Mohring *et al.* 2013b; Wernberg *et al.* 2019a) and bull kelp (*N. luetkeana*) (Schroeder *et al.* 2020), often determined by different environmental aspects. Specifically, blue light triggers the production of spores and day length controls the production of germ cells, sexual reproduction and sporophyte growth (Lüning and Dring 1975; Dring 1984). *L. solidungula* in the high Arctic can reproduce seasonally in the winter, in the absence of light (Dunton 1990). Spore production in some species is greatly influenced by changes in seawater temperature and nutrient availability, while spore production in others is not (Reed *et al.* 1997), emphasizing that the responses of different kelp are diverse, and it can be difficult to generalize.

Dispersal and recruitment

Microscopic spores released from the adult kelp is the primary dispersal mechanism for kelp (Figure 1.3). Spores swim slowly but they can travel far with currents and waves, as evidenced by kelp recruits found hundreds of metres to several kilometres away from the nearest kelp forests (Reed, Laur and Ebeling 1988; Fredriksen *et al.* 1995). Dispersal range is mainly dictated by the spore release height, sinking rate and water motion. Up to 50 per cent of the spores released by giant kelp (*M. pyrifera*) can travel more than 1 km, and a substantial fraction might disperse as far as 10 km (Gaylord *et al.* 2002). Exceptional long-distance dispersal (hundreds or even thousands of kilometres) can occur through drifting or rafting of reproductively active dislodged individuals (Reed, Schroeter and Raimondi 2004).

Kelp recruitment (the addition of new adults to the kelp forest) is a complex process because of the two distinct life stages. For the sperm to be able to reach an egg, male and female gametophytes must settle within millimetres of one another (Reed 1990). Early life stage of kelp can persist in the kelp forest understorey for weeks to months (Hoffmann and Santelices 1991) and only start growing once stimulated by high light when the canopy is lost during storms or when harvested (Reed and Foster 1984; Santelices and Ojeda 1984; Christie, Fredriksen and Rinde 1998; Wernberg *et al.* 2020). Within weeks, dense kelp recruits emerge, with recruitment into the adult population taking anywhere from a few months to two or three years depending on the kelp species and local conditions (Reed 1990; Pedersen *et al.* 2012). Most recruits die within the first year, from predation, stress or self-thinning.
Figure 1.3. Life cycle of bull kelp (*Nereocystis luetkana*)

**Note:** All Laminarian kelp have a life cycle with two distinct phases: a macroscopic sporophyte (the adult kelp) and a microscopic gametophyte.

**Threats and stressors**

Human activities have had a profound influence on kelp forests, with increasingly negative impacts during the past 50 years (Dayton *et al.* 1998; Steneck *et al.* 2002; Krumhansl *et al.* 2016; Filbee-Dexter and Wernberg 2018). Many different processes are at play, operating at local to global scales and often causing a range of direct and indirect effects (Figure 1.4), leading to region-specific causes of kelp decline (Krumhansl *et al.* 2016). Many, but not all, of these threats are ultimately linked to, or compounded by, climate change and more often than not they interact in their effects (Box 1.2). These major threats include warming, marine heatwaves and other environmental extremes, ocean acidification, herbivory linked to overfishing of predators or range-shifting grazers, reduced water quality from increasing eutrophication, pollution, sedimentation and ocean darkening, harvesting and invasive species and diseases.
Note: Human activities have caused decline and loss of kelp forests globally and a transition to degraded habitats (right). Several drivers (red) have been responsible for these habitat transitions.

**Ocean warming, marine heatwaves and indirect effects of changing environmental conditions** are probably the most pervasive manifestations of global climate change in the oceans (Oliver et al. 2018) and a major threat to kelp forests globally. Warming ocean temperatures have been implicated either directly or indirectly, through their effects on other drivers, in almost all major impacts on kelp forests (Filbee-Dexter and Wernberg 2018; Wernberg et al. 2019b; Smale 2020).

The direct effects of warming are determined by the rate and magnitude of warming, species-specific responses, and the thermal history of the kelp forest. Most multicellular species have an optimal performance within a range of tolerable temperatures (Harley et al. 2012). Thus, how kelp responds directly to temperature increases will be dictated by how close ambient conditions are to their thermal optimum (Bennett et al. 2015a). For species occupying areas with low temperatures relative to their optimum, warming seawater may increase their growth and performance (Hargrave et al. 2017). Conversely, warming will have direct negative effects on kelp species occupying waters at or above their thermal optimum, as seen by the massive die-offs of kelp forests in Baja California at the southern end of its range (Arafeh-Dalmau et al. 2019; Edwards 2019). Short-term but high magnitude increases in temperature (i.e. heatwaves) that are above the thermal limit of kelp can lead to direct mortality (Wernberg et al. 2013), particularly if kelp already exist above their thermal optimum.

Direct negative effects on kelp caused by water temperatures being above their thermal optimum for prolonged periods include reductions in growth rate, damage to kelp tissue, decreased resilience to disturbance, reduced reproduction and ultimately death (Bartsch et al. 2013; Simonson, Metaxas and Scheibling 2015; Alsuwaiyan et al. 2021). Cellular damage arising from warm temperatures can reduce kelp tissue strength and extensibility, and decrease the ability of kelp to withstand wave forces (Simonson, Metaxas and Scheibling 2015). Rising temperatures can also impact kelp reproduction, fertilization and the survival of early life stages (Bartsch et al. 2013; Mohring et al. 2013a). Although the impacts on these early life stages are less well understood compared to adults, they are likely very important in the population’s overall response to environmental changes (Schiel and Foster 2006; Harley et al. 2012).

Changing environmental conditions can also affect kelp indirectly by influencing biotic interactions that weaken their competitive advantage. For example, warming stimulates the growth of turf algae which competes with kelp for light and space (Straub et al. 2019). Small grazers such as snails eat kelp faster at higher temperatures (Simonson, Metaxas and Scheibling 2015), which can lead to high loss of blades in the forest canopy (Krumhansl, Lauzon-Guay and Scheibling 2014). Similarly, warming temperatures enhance rates of kelp overgrowth by encrusting species and also cause tissue weakening and canopy defoliation (Andersen et al. 2011; Krumhansl and Scheibling 2011). Climate changes can also alter distribution, densities or behaviour of herbivorous (grazing) sea urchins and fish, which can in turn increase rates of grazing and heavily influence the extent and abundance of kelp (Filbee-Dexter and Scheibling 2014; Vergés et al. 2014a).

In terms of other environmental stressors, the increasing frequency of extreme storms has increased the dispersal range of the keystone species through rafting, such as southern bull kelp (D. antarctica), potentially causing an establishment of non-native taxa in Antarctica (Fraser et al. 2018). Changes to upwelling regimes, for example as a consequence of increasingly severe El Niño events or incursions of warm nutrient-poor currents, can cause collapse of kelp forests due to combined temperature and nutrient stress (Johnson et al. 2011).

Ocean acidification refers to the decreasing alkalinity of the oceans as they absorb carbon dioxide. These changes in the chemical balance of seawater are generally predicted to pose a serious threat to marine life (Kroeker et al. 2013). Ocean acidification is, however, unlikely to affect kelp forests directly, as studies have found minimal effects on kelp reproduction, biomass, photosynthesis and survival (Leal et al. 2017; Provost et al. 2017; Fernández et al. 2021). Nevertheless, ocean acidification could have indirect negative effects through increasing the virulence of diseases (Qiu et al. 2019) or increasing the competitive strength of filamentous turf algae (Connell et al. 2013). Specifically, ocean acidification stimulates growth of turf algae due to carbonate enrichment, at the same time as the lower pH impairs turf consumers (gastropods and urchins), and these effects may be further strengthened by increasing temperatures and marine heatwaves (Connell and Russell 2010; Provost et al. 2017; Straub et al. 2019).

One major question in relation to the effects of ocean acidification on kelp forests revolves around their capacity to regulate and buffer ocean pH in their immediate surroundings through photosynthesis (Krause-Jensen et al. 2016), creating a local ocean acidification refuge for themselves and associated species. Recently, it was suggested that this refuge effect would impose limitations on the size of sea urchin barrens, as sea urchin activity would be negatively affected due to low pH far from kelp forests (Ling et al. 2020).

Grazing (herbivory) is generally low in healthy kelp forests (Christie and Norderhaug 2017) but it can have devastating effects when grazers increase in abundance. Population explosions of kelp grazers have occurred on all continents except Antarctica, as a consequence of hunting and overfishing of grazer predators (Steneck et al. 2002) or climate-driven range expansion of grazers from warmer latitudes (Vergés et al. 2014a). For example, in Alaska hunting of sea otters led to increased sea urchins, a main prey of sea otters, and these sea urchins overgrazed hundreds of kilometres of kelp forests (Estes and Palmsano 1974). Destructive grazing of kelp has been recorded among many different kinds of herbivores including sea urchins, fish, crustaceans and snails (see, for example, Estes and Steinberg 1988; Vásquez and Buschmann 1997; Byrnes et al. 2006; Filbee-Dexter and Scheibling 2014; Vergés et al. 2014a; Zarco-Perello et al. 2017; Norderhaug et al. 2021).

Hunting and overfishing of sea urchin predators including sea otters (North American Pacific, Estes and Palmisano 1974), ground fish (Northern Europe, Norderhaug et al. 2021) and lobsters (Australia, Ling et al. 2009a) have been implicated in sea urchin outbreaks and the subsequent formation of sea urchin barrens. Barrens are areas of reef devoid of habitat-forming seaweed that can extend over thousands of kilometres of coastline or occur in small patches (tens to hundreds of metres) within a kelp forest. They are less productive, provide reduced habitat and support less biodiversity compared to kelp forests. Transitions from kelp forest to barrens often occur as regime shifts and can be abrupt transformations of the ecosystem. These shifts are triggered by large increases in the densities of sea urchins, which overcome feedbacks such as kelp whiplash, abundant drift kelp and high predation within the forests that usually keep sea urchins from grazing destructively. The barren state can be difficult to recover from and can exist for decades in some regions, even if the original drivers of high sea urchin densities are relaxed (Filbee-Dexter and Scheibling 2014; Ling et al. 2015).

Climate-driven range expansion of warm-water herbivores, which are particularly prevalent at the warm-range margins of kelp forests, has led to increased herbivory and loss of kelp forests in many regions around the world (Vergés et al. 2014a). In eastern Australia, sea urchins have expanded progressively further south into Tasmania in recent decades,
leading to widespread formation of urchin barrens (Ling et al. 2009a; Ling et al. 2009b). Also in Australia, tropical fish have extended down the east and west coasts, resulting in the loss of between 60 and 100 per cent of kelp canopies in some areas (Bennett et al. 2015b; Vergés et al. 2016; Zarco-Perello et al. 2017). Similar observations have been made in Japan (Haraguchi et al. 2009; Nakamura et al. 2013) and the Mediterranean Sea (Vergés et al. 2014b).

In addition to sea urchins and fish, many invertebrates such as small crustaceans and snails also consume kelp. These small grazers may not have a substantial direct grazing effect on kelp (Hereward et al. 2018), but they can increase kelp mortality and erosion by creating perforations and weak points on blades and stipes, which break when kelp blades are under stress from wave action and currents (Haggitt and Babcock 2003; de Bettignies, Thomsen and Wernberg 2012). Further, when kelp abundance declines, grazers concentrate on the fewer remaining kelp, enhancing rates of kelp canopy loss at higher water temperatures (O’Brien, Scheibling and Krumhansl 2015).

**Eutrophication, pollution and sedimentation** are prominent symptoms of urbanization, human waste and food production (Airoldi 2003; Gorman, Russell and Connell 2009; Duarte 2014). The associated reduction in water quality poses a significant threat to kelp forests in nearshore areas with high human population densities and intense agriculture or aquaculture. Eutrophication darkens the water column and can stimulate phytoplankton and fast-growing opportunistic seaweed species, including some epiphytic species that grow directly on kelp (Pedersen and Borum 1997). Epiphytes may increase the drag on blades and cover kelp tissue, which may impede light conditions (even further) and affect the uptake of nutrients and inorganic carbon (Andersen et al. 2011). High nutrient availability may also prevent kelp recruitment by stimulating the biomass and sediment accumulation of fast-growing, mat-forming turf algae that can cover the substrate (Airoldi 2003; Gorman and Connell 2009; Pessarrodona et al. 2021). Acute eutrophication and sedimentation have been shown to quickly impact kelp forests negatively, however the negative effects were transient and kelp forests recovered quickly as soon as the stressors abated (Shaffer and Parks 1994; Tegner et al. 1995). In contrast, persistent sedimentation can affect microscopic stages and sexual reproduction performance (Muth et al. 2017), with increased sediments and nutrients as a result of expanding human populations, urbanization and soil erosion having an insidious effects on kelp forests and having been implicated with habitat degradation and the loss of habitat-forming seaweed species all over the world, including in California (Foster and Schiel 2010), Norway (Moy and Christie 2012), Australia (Coleman et al. 2008; Connell et al. 2008) and Brazil (Gorman et al. 2020).

**Harvesting** of kelp for materials, food and fodder is probably one of the oldest direct human influences on kelp forests (Turner 2000; Erlandson et al. 2007, see also section B-4 of chapter 3), and has been recognized as having a negative impact on kelp in some regions (Krumhansl et al. 2016). Intense or prolonged harvesting can alter the structure and functioning of kelp forests (O’Connor and Anderson 2010; Geange 2014), but as many kelp forests lack baseline data for the resource, it is difficult to track the industry’s impacts (Bennion et al. 2018). In Chile, kelp fishers now use specialized harvesting equipment, resulting in intensive removal of kelp (L. berteroana and L. trabeculata). High harvesting intensity leads to increased kelp density but reduced kelp size (holdfast diameter, number of stipes, total length) and age. In some areas, kelp do not recover within the seven-year fallow period. An increase in sea urchin barrens has been reported in heavily harvested areas in northern Chile, but no quantitative data exist.

In Norway, *L. hyperborea* is harvested on an industrial scale using small trawls (Figure 1.5A) that tear the kelp from the sea floor and leave 3 m wide tracks (Figure 1.5B). These trawl tracks have reduced ecological function and biodiversity (Steen et al. 2016), with substantial effects on seaweed biomass and fish communities (including on invertebrate and fish diversity, and the abundance of juvenile and small fish), which may in turn affect seabirds foraging in kelp forests (Lorentsen, Sjøtun and Grémillet 2010; Norderhaug et al. 2020). It can take four years for kelp biomass to return to pre-harvest levels, but at least six years for associated communities to recover (Steen, Norderhaug and Moy 2020).

In contrast, harvesting kelp (*E. maxima*) in South Africa by cropping the floating canopy above the main meristem (point of growth) resulted in minimal effects on the understory flora and fauna communities. Within a year, kelp biomass and associated communities were indistinguishable between harvested and control plots (Levitt et al. 2002).
**Figure 1.5.** A. Wild harvesting of cuvie (*Laminaria hyperborea*) in Norway using a trawl (photo credit: H. Steen). B. A single surviving kelp standing in a trawl track (photo credit: J. Thormar)

**Figure 1.6.** Global wild harvesting of different kelp species

**Invasive species and disease** are emergent threats to kelp forests. Invasive species are predominantly associated with competition for space and light or overgrowth. For example, the decline of sugar kelp (*S. latissima*) in the North-West Atlantic is due in part to pre-emption of space by expansive covers of invasive turf algae (Dijkstra *et al.* 2017; Feehan, Grace and Narvaez 2019). Also in the North-West Atlantic, the large green alga dead man’s fingers (*Codium fragile*) expanded rapidly where kelp forests declined (Mathieson *et al.* 2003) and expanding populations of the invasive brown alga japweed (*Sargassum muticum*) have been associated with declines in sugar kelp in Denmark (Staehr *et al.* 2000) and fingerkelp (*L. digitata*) in France (Cosson 1999). In the United Kingdom of Great Britain and Northern Ireland (UK), experiments showed that competition from the invasive kelp *U. pinnatifida* suppressed growth and recruitment of native sugar kelp, fingerkelp and *Saccorhiza polyschides* (Epstein, Fogg and Smale 2019). Fouling by invasive
invertebrates can also have a negative effect on kelp forests. For example, in the North-West Atlantic, kelp blades covered by the bryozoan *Membranipora membranacea* decreased reproductive output and growth and increased mortality, leading to a defoliation of kelp forests there (Saunders and Metaxas 2008).

In many cases, the effects of invasive species on kelp have been mediated or compounded by increased ocean temperatures and/or physical disturbances. Although there is both experimental and observational evidence that marine invasive species negatively affect seaweed abundances (including kelp) (Thomsen et al. 2009), questions remain as to the extent to which invasive species are drivers or passengers of declines in kelp forests and where and when this occurs (Didham et al. 2005).

Diseases can cause kelp die-off (e.g. Cole and Babcock 1996). Wild kelp species are heavily colonized by prokaryotes (Marzinelli et al. 2015a; Florez et al. 2017), viruses (Beattie et al. 2018) and eukaryotes including fungi and oomycetes (Li et al. 2010) as well as parasitic microscopic filamentous algae (Potin 2012) and invertebrates (Wahl and Mark 1999). In New Zealand, die-off of golden kelp (*E. radiata*), the dominant seaweed forest in the region (Wernberg et al. 2019a), was attributed to a combination of environmental stress and viral infections (Cole and Babcock 1996; Easton, Lewis and Pearson 1997), leading to the loss of pigmentation and bleaching (Beattie et al. 2018). In Europe, oomycete (water moulds) infections of wild kelp populations of cuvie (*L. hyperborea*), fingerkelp (*L. digitata*) and sugar kelp (*S. latissima*) produced a severe effect on kelp growth and survivorship (Eggert, Peters and Küpper 2010). Endophytic infections by a filamentous brown alga have been found in galls affecting natural populations of *L. nigrescens* (Thomas et al. 2009). At this point in time, reports of major pathogen outbreaks in kelp forests remain rare. However, increasing pollution and climate change (warming in particular) are likely to increase pathogen virulence (Campbell et al. 2012; Qiu et al. 2019).

“Multiple stressors” refers to the combined effects of several stressors (such as those listed above) at the same time. The coastal zone is a focal point for human activities, where broad changes in environmental conditions are superimposed on other stressors such as pollution, coastal development, fisheries, invasive species and aquaculture. These other stressors, which are increasing with rising human population density, can have compounding effects on kelp forests. Interactions among multiple stressors can be complex (Strain et al. 2014) and in some cases can create abrupt and large declines in kelp forests. For example, overfishing of large predators can make kelp forests vulnerable to climate-driven threats such as range shifts of grazing sea urchins or marine heatwaves (Rogers-Bennet and Catton 2019). Warming and marine heatwaves can make kelp forests more vulnerable to additional stressors (Wernberg et al. 2010) and reduce kelp genetic diversity and adaptive capacity through directional selection or selective mortality, which can lower their resilience to other stressors such as pollution. Eutrophication and warming events can interact to drive increased kelp mortality due to the combined effects of reduced light and increased temperature stress. However, increased nutrients can help establish introduced kelp species such as wakame when storms create bare openings in the kelp canopy and in some regions, physiological studies on kelp show that nutrient availability can result in a higher tolerance to impacts of climate change (Fernández et al. 2021). Low salinity and turbidity in areas with run-off or melting ice can interact with temperature shifts to alter kelp forest extent and structure.

**Knowledge gaps and priority areas for future research**

Key knowledge gaps concerning the ecology of kelp forests range from small-scale issues associated with their microscopic life stages to broad-scale biogeographic questions around their distribution and abundance in many bioregions. At the smallest scale, the ecology of the microscopic gametophyte stage is poorly known, especially under field conditions. At the species and population scale, important questions remain as to how performance and sensitivity to stress vary within and across kelp forests (Muth et al. 2019). This includes the adaptive capacity of many kelp species to resist or respond to increased stress across all stages of their life cycle.

It is also unclear how population connectivity and dispersal can drive genetic diversity and thereby influence the adaptation and resilience of natural kelp forests. Most of the predictions for the future state of kelp forests consider only gradual change in ocean temperature as a main driver of change. However, in reality virtually all kelp forests exist in multi-stressor seascapes. Understanding and predicting the combined effects of multiple future stressors is essential for informed management of these ecosystems. Extreme events including marine heatwaves, storms and outbreaks of grazers are increasing, while coastal populations are expanding, which is leading to increased pollution, eutrophication, sedimentation, coastal darkening, invasive species and activities such as fish and seaweed farming. As we move into the Anthropocene, the coastal zone is increasingly facing multiple human pressures, from our need to expand food production, coastal infrastructure and agriculture to ocean warming and climate-driven changes.
### Table 1.1. Dominant kelp species and their main threats in different regions around the world

<table>
<thead>
<tr>
<th>Region</th>
<th>Dominant kelp species</th>
<th>Main threats</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arctic</td>
<td><em>Alaria</em> spp., <em>Saccharina latissima</em>, <em>Agarum clathratum</em>, <em>Laminaria digitata</em>,</td>
<td>Arctic kelp forests may expand as sea ice retreats, with temperate species replacing endemic seaweed species. Sedimentation, turbidity and glacial melt cause kelp loss in some areas.</td>
<td>Filbee-Dexter <em>et al</em>. 2019; Krause-Jensen <em>et al</em>. 2020</td>
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<td></td>
<td><em>L. solidungula</em>, <em>Hedophyllum nigripes</em></td>
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<td>NW Atlantic</td>
<td><em>L. digitata</em>, <em>S. latissima</em>, <em>A. clathratum</em></td>
<td>Warming, marine heatwaves, invasive species, overfishing</td>
<td>Filbee-Dexter, Feehan and Scheibling 2016; Feehan, Grace and Narvaez 2019; Steneck <em>et al</em>. 2013</td>
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<td>NE Atlantic</td>
<td><em>L. hyperborea</em>, <em>S. latissima</em>, <em>Alaria esculenta</em> and <em>L. digitata</em> (in the north) and <em>L. ochroleuca</em> and <em>Saccorhiza polychides</em> (in the south)</td>
<td>Warming, marine heatwaves, eutrophication, herbivory by urchins, overfishing</td>
<td>Smale <em>et al</em>. 2013; Filbee-Dexter <em>et al</em>. 2020; Norderhaug <em>et al</em>. 2021</td>
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<td></td>
<td><em>Macroystis pyriforma</em> (Baja)</td>
<td><em>Macroystis</em>: El Niño–Southern Oscillation</td>
<td></td>
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<tr>
<td>NE Pacific</td>
<td>Bull kelp, giant kelp</td>
<td>Warming, overfishing</td>
<td>Schroeder <em>et al</em>. 2020</td>
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<tr>
<td>Southern Africa</td>
<td><em>Ecklonia maxima</em>, <em>L. pallida</em>, <em>E. radiata</em></td>
<td><em>E. maxima</em>: harvesting</td>
<td>Bolton <em>et al</em>. 2012; Rothman pers. comm.</td>
</tr>
<tr>
<td>Oceania</td>
<td><em>E. radiata</em>, <em>M. pyriforma</em> (around Tasmania and southern New Zealand). Diverse assemblages of subtidal fucoids</td>
<td>Warming, marine heatwaves, eutrophication, sedimentation, tropical fish, urchins</td>
<td>Wernberg <em>et al</em>. 2019a</td>
</tr>
</tbody>
</table>
Chapter 1 references


