Rise of Turfs: A New Battlefront for Globally Declining Kelp Forests

KAREN FILBEE-DEXTER AND THOMAS WERNBERG

Kelp forests are structurally complex habitats, which provide valuable services along 25% of the world's coastlines. Globally, many kelp forests have disappeared and been replaced by turf algae over the last decade. Evidence that environmental conditions are becoming less favorable for kelps, combined with a lack of observed recovery, raises concern that these changes represent persistent regime shifts. Here, we show that human activities mediate turf transitions through geographically disparate abiotic (warming and eutrophication) and biotic (herbivory and epiphytism) drivers of kelp loss. Evidence suggests kelp forests are pushed beyond tipping points where new, stabilizing feedback systems (sedimentation, competition, and Allee effects) reinforce turf dominance. Although these new locks on the degraded ecosystems are strong, a mechanistic understanding of feedback systems and interactions between global and local drivers of kelp loss will expose which processes are easier to control. This should provide management solutions to curb the pervasive trend of the flattening of kelp forests globally.

Keywords: seaweeds, warming, eutrophication, habitat loss, regime shift

Kelp forests: Foundations of temperate reefs globally

The numbers of living creatures of all Orders whose existence intimately depends on kelp is wonderful ... I can only compare these great aquatic forests of the southern hemisphere with the terrestrial ones in the intertropical regions. Yet if in any country a forest was destroyed, I do not believe as many species of animals would perish as would here from the destruction of kelp.

—*Darwin 1839*

This passage from Charles Darwin's book *Voyages of the* Adventure *and* Beagle describes the awe of one of our greatest natural historians when he encountered the kelp forests off South America. His analogy of tropical rain forests clearly conveys both his profound amazement with the biological activity supported by kelp forests and an insight into the ecological role of kelps: They do underwater the same as trees do on land.

Kelp forests are extensive, underwater habitats dominated by large brown laminarian and fucalean seaweeds (Steneck and Johnson 2013). They grow best in cold, nutrient-rich water, in which they attain some of the highest rates of primary production of any natural ecosystem on Earth (Mann 1973), and some species can live up to 25 years (Steneck and Johnson 2013). Kelp forests dominate at temperate latitudes in both hemispheres, along approximately one-quarter of the world's coastlines (Steneck and Johnson 2013, Filbee-Dexter and Scheibling 2014).

As Darwin's observations clearly indicate, kelp forests support a plethora of associated species. Kelps are ecosystem engineers. They create complex biogenic habitats (Christie et al. 2009, Thomsen et al. 2010, Teagle et al. 2017), which influence the physical conditions, such as light, water flow, sedimentation, physical abrasion, and pH, in their surrounding environment (Eckman et al. 1989, Wernberg et al. 2005, Krause-Jensen et al. 2016). In addition to providing structural habitat (Teagle et al. 2017), the high productivity of kelp also provides an abundant food source for species such as fish, urchins, small crustaceans, and snails that graze directly on the attached kelps (Christie et al. 2009, O'Brien and Scheibling 2016). Other species filter feed on particulate organic material or prey on kelp-associated species (Norderhaug et al. 2005, Christie et al. 2009). Kelp forests also produce large quantities of detached *drift kelp*, which tumble across the seafloor or raft on the waters' surface, ending up in adjacent or distant habitats. As much as 80% of the local production ends up as drift, which can leave the kelp forest and support food webs in which autochthonous primary production is usually very low (Krumhansl and Scheibling 2012). Drift kelp is a primary source of food in many of these habitats and attracts a diverse community of detritivores and consumers, often substantially increasing secondary production (Bustamante et al. 1995, Krumhansl and Scheibling 2012). Through these trophic subsidies and by providing an important

transoceanic dispersal vector for kelp-rafting flora and fauna (Rothausler et al. 2012), drift kelp extend the ecological influence of kelp forests far beyond the locations where the kelps grow.

The intimate connection between kelp forests and humans

These ocean forests are crucially important not only to marine plants and animals but also to humans. *Homo sapiens* have exploited the rich resources provided by kelp forests for at least 10,000–70,000 years (e.g., Volman 1978, Jerardino and Navarro 2002, Balasse et al. 2005), but our intimate connection with kelp forests could be as old as humankind itself. Evidence suggests that early humans might have evolved along the rocky coasts of southern Africa as a consequence of a rich diet of marine organisms supported by highly productive kelp forests (Bustamante et al. 1995), including mussels and limpets, providing the omega-3 fatty acids and trace elements required for brain function and development (Compton 2011). Kelp forests have also played an important role in the biogeography of humans. About 16,000 years ago, early colonizers of the Americas followed a "kelp highway" along the Pacific Rim, sustained by the bounty provided by kelp forests (Erlandson et al. 2007).

Kelp forests also play an important role in the lives of modern humans by providing a broad range of ecosystem goods and services of great social, economic, and ecological value (figure 1; Vásquez et al. 2014, Bennett et al. 2016, Blamey and Bolton 2017). These goods and services arise as direct contributions from the kelp forests (e.g., kelp harvesting, commercial and recreational fishing, and tourism), as indirect contributions via the functions of the kelp forest (e.g., habitat provision, climate control, carbon sequestration, coastline protection, and nutrient filtering), or from the innate value of the kelp forest itself (e.g., its scientific or cultural importance and biodiversity). Although the economic value of these ecosystem services can be very difficult to establish, especially for indirect and nonuse services, it is estimated that kelp forests provide services worth US\$500,000–1,000,000 per kilometer of coastline (table 1). However, these figures are heavily dominated by direct-use services (e.g., Vásquez et al. 2014, Bennett et al. 2016), and the true value of kelp forests could be three to six times higher. Valuations of more broadly defined marine macrophyte communities, which better incorporate the indirect and nonuse values, place seagrass and seaweed beds as the third most productive systems globally, providing ecosystem services valued at US\$3,000,000 per kilometer (km) of coastline per year (assuming a 1-km-wide kelp forest at US\$30,000 per hectare per year; Costanza et al. 2014). Even this is most likely a considerable underestimation reflecting the lack of studies valuating services explicitly from kelp forests (Bennett et al. 2016). Recently, the value of coral reefs was increased more than 40 times previous estimates, mainly as a consequence of new studies valuating additional ecosystem services such as storm protection, erosion protection, and recreation (Costanza et al. 2014).

Kelp forests under siege

Human impacts on marine foundation species have accelerated over the past four to five decades. Globally, estuaries (Lotze et al. 2006), seagrass meadows (Orth et al. 2006, Waycott et al. 2009), and coral reefs (Pandolfi et al. 2003, Hughes et al. 2017) have been adversely affected. Kelp forests are no exception (Krumhansl et al. 2016). A recent global analysis revealed that 38% of the world's kelp forests have been in decline over the past five decades (Krumhansl et al. 2016), although interactions between local, regional, and global processes have produced complex responses in terms of the direction and ultimate drivers of kelp-forest change (Wernberg et al. 2011, Krumhansl et al. 2016).

Nevertheless, climate change has set Earth on a trajectory in which increasingly novel environments and biological interactions have the potential to alter or decouple many of the natural ecosystem drivers and feedback mechanisms maintaining otherwise highly resilient kelp forests. These changes can drive lasting transitions to new ecosystem states, which provide substantially different ecological services. Over the last decade, an emerging pattern has been that kelp forests increasingly are replaced by turfs, changing the reef seascape from a complex forest to a structurally simple mat of low-lying algae (e.g., Connell SD et al. 2008, Moy and Christie 2012, Filbee-Dexter et al. 2016, Wernberg et al. 2016a). These shifts to turfs represent widespread global loss in structural habitats and a new "battlefront" as kelp forests move away from traditional urchin-grazing (and overfishing) dynamics toward climate- and nutrient-driven replacement by turf algae.

The current downward trajectory of more than one-third of the world's kelp forests (Krumhansl et al. 2016) will cause major reductions in the quality and quantity of ecosystem services that these foundation species provide (e.g., loss of tourism, closures of recreational or commercial fisheries, and removal of carbon sink; cf. table 1). There is therefore a pressing need to understand the processes that are driving these regime shifts. Here, we provide an overview of the transformation of kelp forests to turf seascapes. We begin by reviewing the global literature on shifts from kelp forests to turf-dominated reefs. We map out the growing global extent of the problem and synthesize the available information on global and regional drivers and dynamics of these shifts, developing a generalized conceptual model of the interacting mechanisms. Finally, we examine in more detail the feedback mechanisms that prevent recovery of kelp forests. We suggest that efforts to reduce local anthropogenic impacts may be an effective strategy for curbing the degradation of kelp forests in many of these systems. However, a deeper, more mechanistic understanding of the drivers and the recovery potential of kelp forests following these shifts is
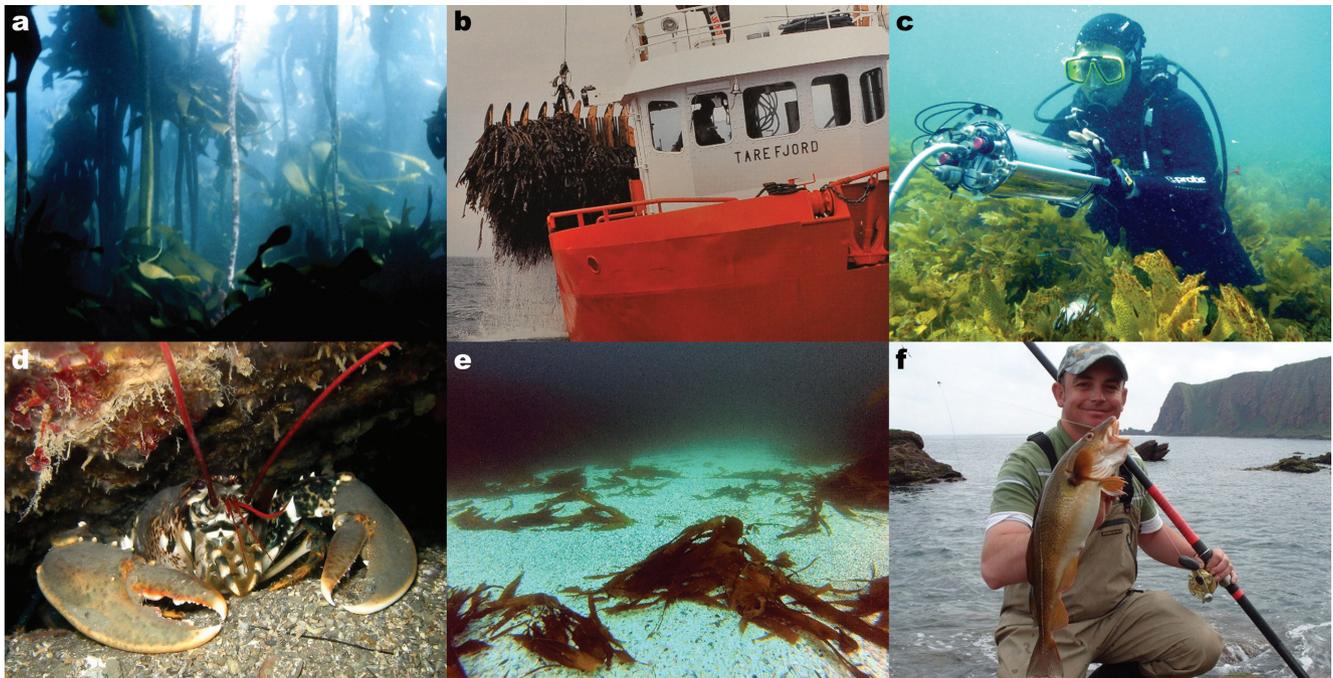
Figure 1. Kelp forests provide many ecological functions and ecosystem services. (a) A kelp forest (Ecklonia maxima) in South Africa. (b) A kelp trawler in Norway. (c) A scientific diver undertaking kelp research in Australia. (d) Commercially and recreationally important lobster (Homarus americanus) in a kelp forest in Canada. (e) Drift kelp (Laminaria hyperborea) accumulation on a sand bottom in Arctic Norway. (f) An angler with kelp cod (Gadus morhua) in the United Kingdom. Photographs: Thomas Wernberg (a, c, e), Kåre Foss (b), Karen Filbee-Dexter (d), Whitby Sea Anglers (f).

required to ensure cost-effective and successful management into the future.

The rise of turf algae

The term *turf algae* (or "turfs") covers a diverse group of macroalgae that superficially have similar morphologies and ecological traits, although there is no commonly accepted definition of turfs (Connell SD et al. 2014). Here, we consider *turfs* to be algae that provide little to no three-dimensional seascape structure compared with kelp and other canopy-forming macroalgae but that cover the bottom with a dense layer of fine filaments, branches, or plumes. Turf algae tend to be small, fast-growing, opportunistic species with high cover and turnover rates that can be highly stress tolerant compared with larger fleshy macroalgae (Airoldi 1998). They trap and accumulate sediment and modify the chemical environment (e.g., reducing oxygen or concentrating contaminants). Under this definition, coralline algae barrens, which have no filamentous algae, and *Sargassum* beds and *Codium* meadows of large erect macroalgae that provide standing three-dimensional structure do not qualify as turfs. Shifts to these low-structure, mat-like turfs represent an undesirable degradation of the ecosystem with associated losses of habitat, food, and productivity (Airoldi et al. 2007, Connell SD et al. 2014).

The large-scale replacement of kelp forests with turf algae is a new phenomenon (figures 2 and 3). Another important

and extensively studied phenomenon of kelp loss is direct consumption by sea urchins, which can destructively graze erect macroalgae and trigger regime shifts to coralline algal-dominated "barrens" (Steneck et al. 2002, Filbee-Dexter and Scheibling 2014). Regime shifts from kelp forests to urchin barrens have been studied for decades on temperate rocky reefs worldwide (Filbee-Dexter and Scheibling 2014). These shifts are largely triggered by population explosions of sea urchins due to the removal of top predators, urchin-recruitment pulses, or altered environmental conditions (Steneck et al. 2002, Filbee-Dexter and Scheibling 2014). Following collapse to barrens, kelp forests can reestablish years or decades later, when sea urchin densities decline and grazing intensity is once again reduced to levels at which kelps can recruit and reestablish (Watson and Estes 2011, Filbee-Dexter and Scheibling 2014). In contrast, large-scale shifts from kelp forests to turfs have not shown recovery, but reefs have remained in a degraded turf state. It is unclear what is responsible for these new dynamics of persistent kelp loss. Potentially, human-driven environmental changes such as ocean warming or coastal eutrophication are favoring the growth and survival of turfs over kelps and decoupling the kelp loss and recovery processes from top-down control by urchins and/or their predators. Key questions now facing ecologists include: (a) what are the main drivers of shifts to turfs, (b) what feedback mechanisms are maintaining them, and how permanent are they, and (c) what strategies

Table 1. The estimated value of ecosystem goods and services from kelp forests around the world.

Region	Total value (US dollars per kilometer per year)	Key services evaluated (percentage of total value)	Main species	Reference
Northern Chile, Pacific Ocean[a]	811,000	Kelp fishing (76%) Commercial fisheries (15%) Scientific, biological, and climate value (9%)	*Lessonia* spp., *Macrocystis pyrifera*	Vásquez et al. 2013
Great Southern Reef, Australia, Indian Ocean and Southern Ocean[b]	914,000	Tourism (90%) Recreational and commercial fishing (10%)	*E. radiata*, various endemic fucoids	Bennett et al. 2016
South Africa, South Atlantic Ocean[c]	520,000	Commercial (incl. kelp), recreational, and illegal fishing (45%) Ecotourism (30%) Nutrient cycling and carbon sequestration (25%)	*Ecklonia maxima*	Blamey and Bolton 2017

[a]US$540 million, 666 km coastline
[b]AU$10 billion per year, 8100 km coastline, US$0.74
[c]5.2 billion South African rand per year, 700 km coastline, US$0.07

are available for moving forward toward solutions to the problem?

The global flattening of kelp forests

The shift from kelp forests to turfs has been increasingly documented along many temperate coasts globally. Early observations of these shifts were reported in the late 1990s and 2000s in localized areas of South Australia (Connell SD et al. 2008), the Baltic Sea and Skagerak (e.g., Middelboe and Sand-Jensen 2000, Eriksson et al. 2002), and Atlantic Canada (Filbee-Dexter et al. 2016). However, in the last decade, more widespread disappearance of kelp forests has been reported along hundreds of kilometers of coastline in Atlantic Canada (Filbee-Dexter et al. 2016), Europe (Moy and Christie 2012, Voerman et al. 2013), and Australia (table 2; figures 2 and 3; Wernberg et al. 2016a).

In the Indian Ocean, *Ecklonia radiata* kelp forests (figure 2a) collapsed along the coast of Western Australia during an extreme marine heatwave in the austral summer of 2010–2011, following four decades of background warming in this ocean-warming hotspot (Smale and Wernberg 2013, Wernberg et al. 2013, 2016a). Kelp forests were completely wiped out and replaced by turfs and *Sargassum* spp., along 100 km of coast at their range margin (figure 2b), where the cover of turfs increased from less than 10% to more than 80% in less than 2 years. The kelp forests to the north succumbed to acute thermal stress as temperature anomalies exceeded their physiological capacity (Smale and Wernberg 2013, Wernberg et al. 2016b) and thermal safety margins (Bennett et al. 2015a). At the same time, there was a substantial influx of tropical fish herbivores (figure 2c), resulting in a 400% increase in grazing rates to levels equivalent to healthy coral reefs. This increased herbivory facilitated the expansion of turfs while preventing the kelp from recovering (Bennett et al. 2015b). The tropical fishes also recruited farther south, beyond the acute catastrophic impacts of the heat wave. Here, they actively grazed the kelp

canopy, reducing its cover by almost 70% in less than 5 years at localized reefs (Zarco-Perello et al. 2017), paving the way for an equivalent expansion of turfs. In contrast, kelp forests in colder waters farther south did not experience similar canopy loss and proliferation of turfs even though temperature anomalies during the heatwave were similar (Wernberg et al. 2013, 2016a).

In the northeastern Atlantic Ocean, *Saccharina latissima* forests (figure 2d) have been replaced by filamentous turf algae (figure 2e) along the west and Skagerak coasts of Norway, where as much as 80% of the *S. latissima* populations have disappeared since 2002 (Moy and Christie 2012). This transformation appears to have been driven by a combination of warming sea temperatures over five decades; exceptionally warm summers in 1997, 2002, and 2006; and coastal eutrophication. However, other changes, such as increased siltation and invasive turf species, might also have been involved (Moy and Christie 2012). These environmental conditions favored rapidly growing filamentous algae, including kelp epiphytes that increased substantially in cover, presumably starving the kelps of light and nutrients (figure 2f; Andersen et al. 2011, Moy and Christie 2012). The effects have been most severe in shallow areas of protected fjords, where temperatures are higher and wave action insufficient to keep epiphytes from proliferating. However, turf-covered reefs have also been extending into cooler, exposed areas along the western coast (Hartvig Christie, Norwegian Institute for Water Research, Oslo, personal communication, 2 June 2017).

In the western Atlantic Ocean, in Nova Scotia, Canada, *Laminaria digitata* and *S. latissima* forests (figure 2g) have disappeared along the central Atlantic coast, with average canopy-cover losses of 89% compared with baseline measures from 1982 (Filbee-Dexter et al. 2016). These declines were gradual, beginning in the early 1990s, and reductions in kelp were associated with an increase in turf-forming algae and two invasive algal species, *Fucus serratus* and *Codium*
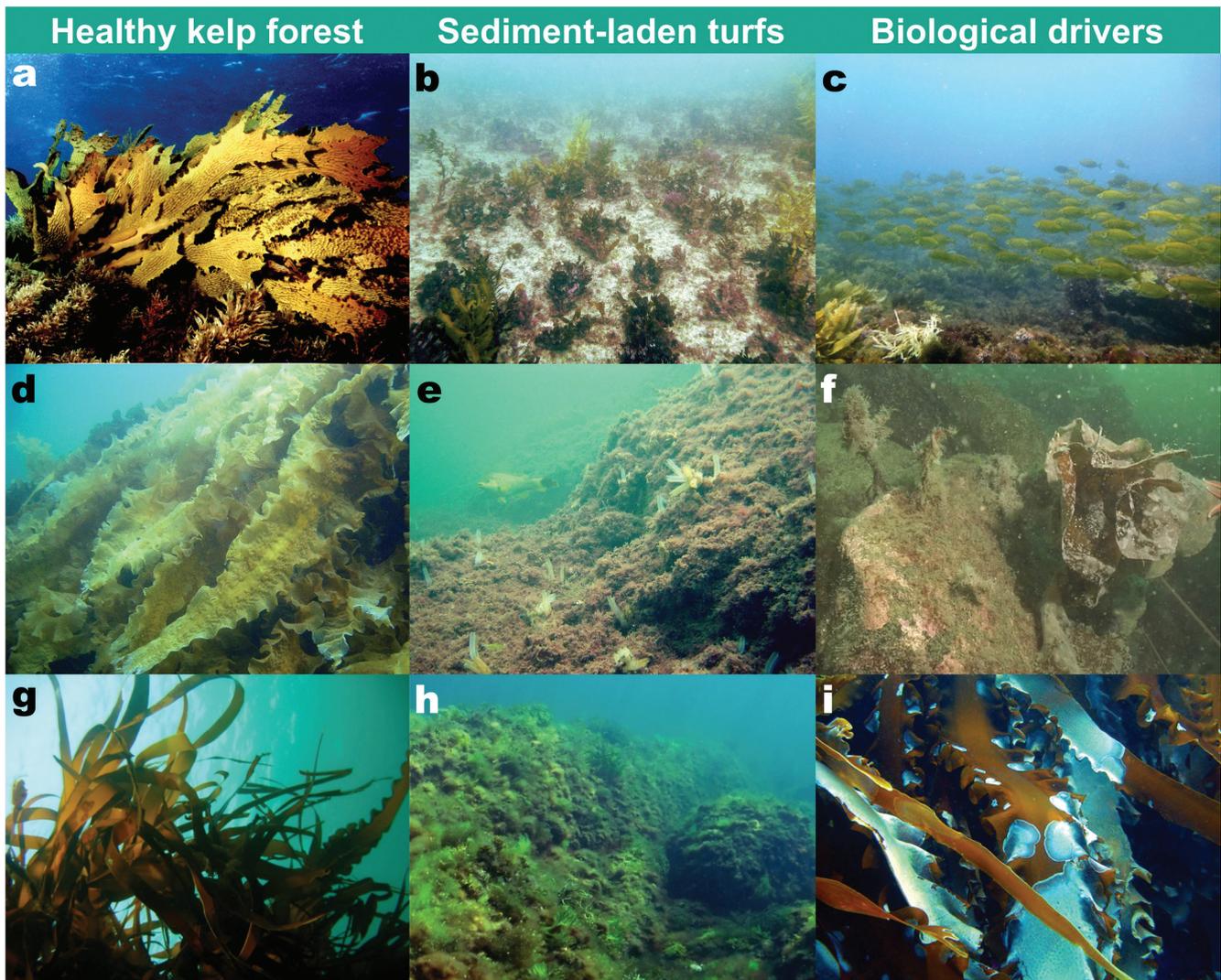
Figure 2. Kelp forests have undergone regime shifts from lush, structurally complex forests to highly simplified, sediment-laden turf reefs. Examples include the disappearance of forests of Ecklonia radiata *from Western Australia (top panel),* Saccharina latissima *from southwestern Norway (middle panel), and* Laminaria digitata *and S. latissima from Atlantic Canada (bottom panel). The photographs show healthy kelp forests (a, d, g), sediment-laden turf reefs (b, e, h) and biological drivers: (c) tropical herbivores (*Siganus fuscescens*) cropping kelp recruits, (f) epiphytes smothering kelps, and (i) the invasive bryozoan (*Membranipora membranacea*) encrusting and weakening kelp fronds. Photographs: Thomas Wernberg (a, b, c), Hartvig Christie (d, e, f), Karen Filbee-Dexter (g), and Robert Scheibling (i, h).*

fragile subspecies *fragile* (figure 2h). This region is a global-warming hotspot, and the declines in kelp were largely driven by the indirect effects of warming temperatures that increased the recruitment and growth of the invasive bryozoan *Membranipora membranacea* (figure 2i; Saunders et al. 2010, Krumhansl et al. 2014). *M. membranacea* encrusts kelp fronds, leading to higher breakage and mortality during periods of wave action (Krumhansl et al. 2011). Stronger storms, the increased intensity of mesograzing, and the direct physiological effects of warm temperatures also played a role in eroding the resilience of the kelp forest (Filbee-Dexter and Scheibling 2012, Krumhansl et al. 2014, O'Brien et al. 2015). Shifts to turfs have been most dramatic

in protected bays where water temperatures are warmer, and kelp forests are still found in cooler, more exposed parts of the coast. Similarly, 300–600 km to the southwest in the Gulf of Maine, United States, shifts to filamentous and corticated red algae occurred during the mid-1990s to mid-2000s (Steneck et al. 2013). Currently, turfs are abundant along sheltered and southern reefs (Steneck et al. 2013), and in some areas, kelp forests have been entirely replaced by invasive red turf algae (Dijkstra et al. 2017).

Most other places that have experienced transitions from macroalgal forests to turfs (table 2) have followed the same general pattern that emerges from the three examples described above (cf. figure 4). For one, many of these
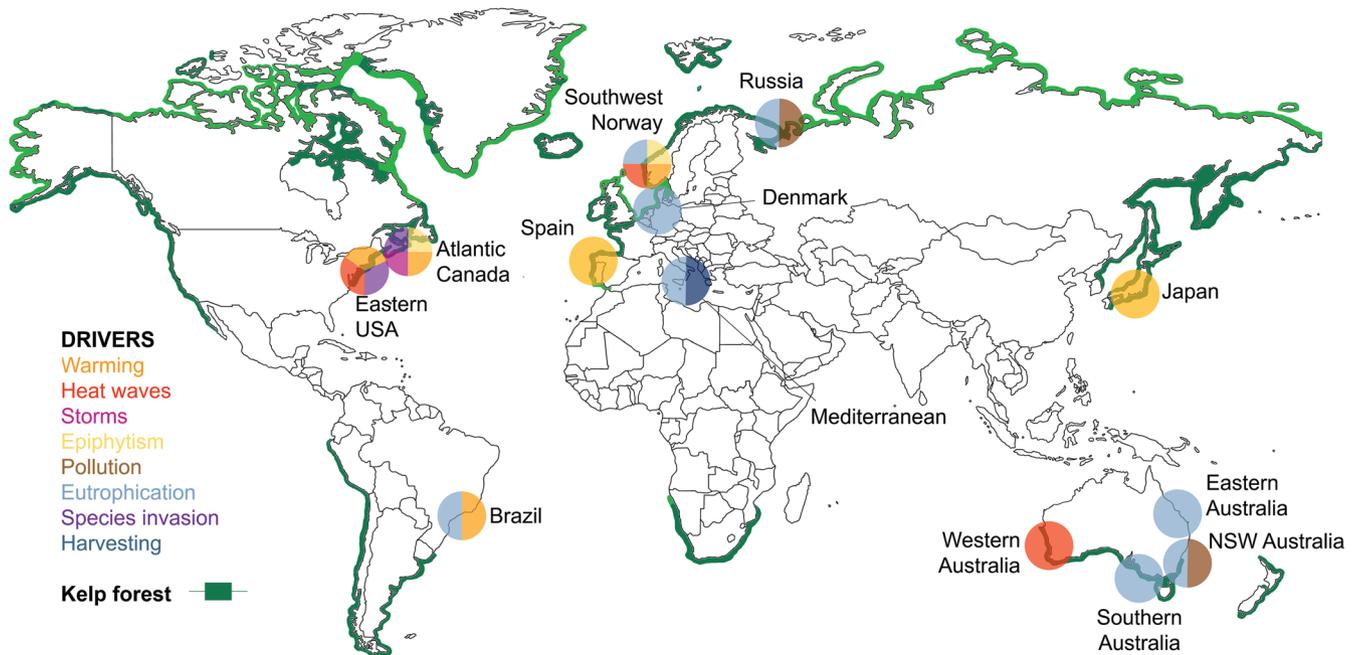
Figure 3. A global map showing the locations of shifts from habitat-forming macroalgae to turfs (circles) overlaid on the approximate distribution of global kelp forests (green; light green unknown but inferred from habitat requirements; Filbee-Dexter and Scheibling 2014). The slice colors of circles indicate different drivers implicated in the shift. See table 2 for further details.

habitats are under pressure from the direct effects of abiotic drivers because of warming or nutrient pollution. This pressure can be either lethal, causing kelp mortality, or sublethal, causing reduced performance and increasing vulnerability to other drivers (Wernberg et al. 2010). Often, abiotic drivers also lead to changes in other biological components of the ecosystem, which in turn can have indirect negative effects on the kelp. Examples of these biotic drivers include increased grazing intensity from herbivores in southwestern Europe and Mediterranean Sea (Vergés et al. 2014, Franco et al. 2015) and competition from invasive red algae in the Gulf of Maine (figure 4; Dijkstra et al. 2017).

Multiple drivers trigger collapse to turfs

Observations, experiments, and correlational studies throughout the global range of kelp forests suggest that a suite of stressors and environmental changes can lead to kelp loss and shifts to turfs (Strain et al. 2014). Often several processes are at play at the same time, making it hard to identify the more important drivers of loss of kelp (figure 3). These drivers can be system specific and include gradual changes such as background warming, eutrophication, pollution, and invasive species, as well as abrupt processes such as storms, heat waves, and harvesting (figure 4; table 2).

There is strong evidence that warming, in particular, has played an important role in most shifts to turfs documented in the last decade (table 2). Ultimately, kelps are cool-water organisms and, toward the warmer ends of their

distribution, warming will reduce their growth, weaken their tissue, and negatively affect how they deal with other perturbations such as grazing, epiphytism, or mechanical damage (Wernberg et al. 2010, Simonson et al. 2015). Consequently, most of the collapsed kelp forests have been located in warming hotspots or near the edges of their distribution, where they likely are less resilient to additional perturbations (e.g., *L. digitata* in France and Denmark, Raybaud et al. 2013; *S. latissima* in Gulf of Maine and Atlantic Canada, Merzouk and Johnson 2011; and *E. radiata* in Australia, Wernberg et al. 2010, Wernberg et al. 2016a). In contrast, in the center and cooler ends of their species' distributions, kelp forests in some regions have experienced significant discrete warming events without collapsing (e.g., Wernberg et al. 2013, Krause-Jensen and Duarte 2014, Araújo et al. 2016, Reed et al. 2016). Canopy-removal experiments in Western Australia prior to the collapse of northern kelp forests showed substantially faster canopy recovery at cooler southern locations compared with warmer northern locations, where turf algae increased in cover before the canopies could recover (Wernberg et al. 2010). Further indirect evidence for the importance of elevated temperatures comes from observational "space-for-time" studies of warming along geographic temperature gradients, where low kelp and high turf cover are more prevalent in warmer regions compared with colder regions (Wernberg et al. 2010, Tuya et al. 2012, Filbee-Dexter et al. 2014). However, in almost all shifts to turf algae, significant kelp loss occurred before

Table 2. The drivers, dominant species, durations of shift, and descriptions of shifts to turfs documented throughout ranges of kelp forests and other canopy-forming macroalgae.

Possible drivers	Region	Description	Macroalgal species	Time period	Source
Asia					
Gradual warming	Western Pacific, Japan	Kelp loss and shift in algal community (increased tropical *Sargassum* spp.).[a] Herbivorous fish suppress recovery.	*Ecklonia* spp. and canopy-forming temperate *Sargassum* spp.	1970s–2010; decline: 1990s	Tanaka et al. 2012
Australia					
Eutrophication	Southern Ocean, Australia	Shift to turfs along 70 km. Trapped sediment prevented recruitment.	*Ecklonia radiata*	1968–1973[b], 1990s–2007; decline: late 1990s	Connell SD et al. 2008, Gorgula and Connell 2004, Gorman et al. 2009
Heat wave	Indian Ocean, Australia	Shift to turfs along 100 km. Tropical herbivorous fish suppress recovery.	*E. radiata*	2000s–2012; decline: post-2011	Bennett et al. 2015, Wernberg et al. 2013, 2016a
Pollution, eutrophication	South Pacific Ocean, Australia (New South Wales)	Historic loss of canopy-forming fucoid and increase in turfs. Loss associated with proximity to urban areas.	*Phyllospora comosa*	1940s[b]–2007; decline: pre-1980s	Coleman et al. 2008
Possibly eutrophication	South Pacific Ocean, Australia (East coast)	Loss of canopy-forming algae and increase in turfs.	*Sargassum* spp.	1960s–present	Phillips and Blackshaw 2011
Europe					
Eutrophication, harvest	Baltic Sea, Germany	Shift to turfs. Reinforced by hard substrate loss due to stone harvesting.	*Fucus* spp	1950s, 1987–1988; decline: pre-1987	Vogt and Schramm 1991
Eutrophication, pollution	Mediterranean Sea, Italy	Shift to turfs. Loss associated with proximity to urban areas.	*Cystoseira* spp.	Decline: post-1999	Benedetti-Cecchi et al. 2001
Warming, epiphytism, eutrophication	NEA, Western and Southern Norway	Shift to turfs and ephemeral algae. Drivers may vary between western and southern coasts.	*S. latissima*	1990–2010; decline: 2002	Andersen et al. 2011, Moy and Christie 2012,
Gradual warming, heat waves	NEA, Spain	Decline and replacement by turfs.	*L. hyperborea, Laminaria aculeata*	1990s–2010; decline: 2007	Voerman et al. 2013
Eutrophication	Denmark	Shift to turfs and green algae.	*Fucus* spp.	1950–1951, 1999; decline: pre-1999	Middelboe and Sand-Jensen 2000
Eutrophication	Skagerak (NEA/Baltic), Sweden and Denmark	Shift to turfs. Nutrient rise due to either human inputs or increased inflow of Baltic Sea and Kattegat water.	*S. latissima* (and other large brown macroalgae)	1941, 1998; decline: pre-1998	Eriksson et al. 2002
Eutrophication, pollution	Barents Sea, Russia (Kola Bay)	Shift to red algae *Phyllophora truncata.*	*S. latissima, A. esculenta*	1960s–2009; decline: post-1994	Golikov and Scarlato 1972, Malavenda et al. 2012
North America					
Gradual warming, epiphytism, species invasions, storm activity	NWA, North America	Shift to turfs along 110 km. Mesograzers reduce kelp recruitment and recovery.	*L. digitata, S. latissima*	1960–2016; decline: post-1990s	Filbee-Dexter et al. 2016
Possible link with gradual warming, heatwave, species invasion	NWA, United States of America (Gulf of Maine)	Shift to filamentous and corticated red algae, including the invasive alga *Dasysiphonia japonica.*	*S. latissima*	1977–2015; decline: 1990s and 2000s	Steneck et al. 2013, Dijkstra et al. 2017
South America					
Possibly eutrophication, warming	Sãu Sebastião region, Brazil	Replacement by turfs.	*Sargassum* spp.	1980s–2016	Daniel Gorman, Departamento de Oceanografia Física, Química e Geologico, University of São Paulo, São Paulo personal communication, 3 May 2017

[a]The changes in understory following kelp loss are not reported.
[b]Anecdotal or observational evidence of the occurrence of macroalgal reefs.
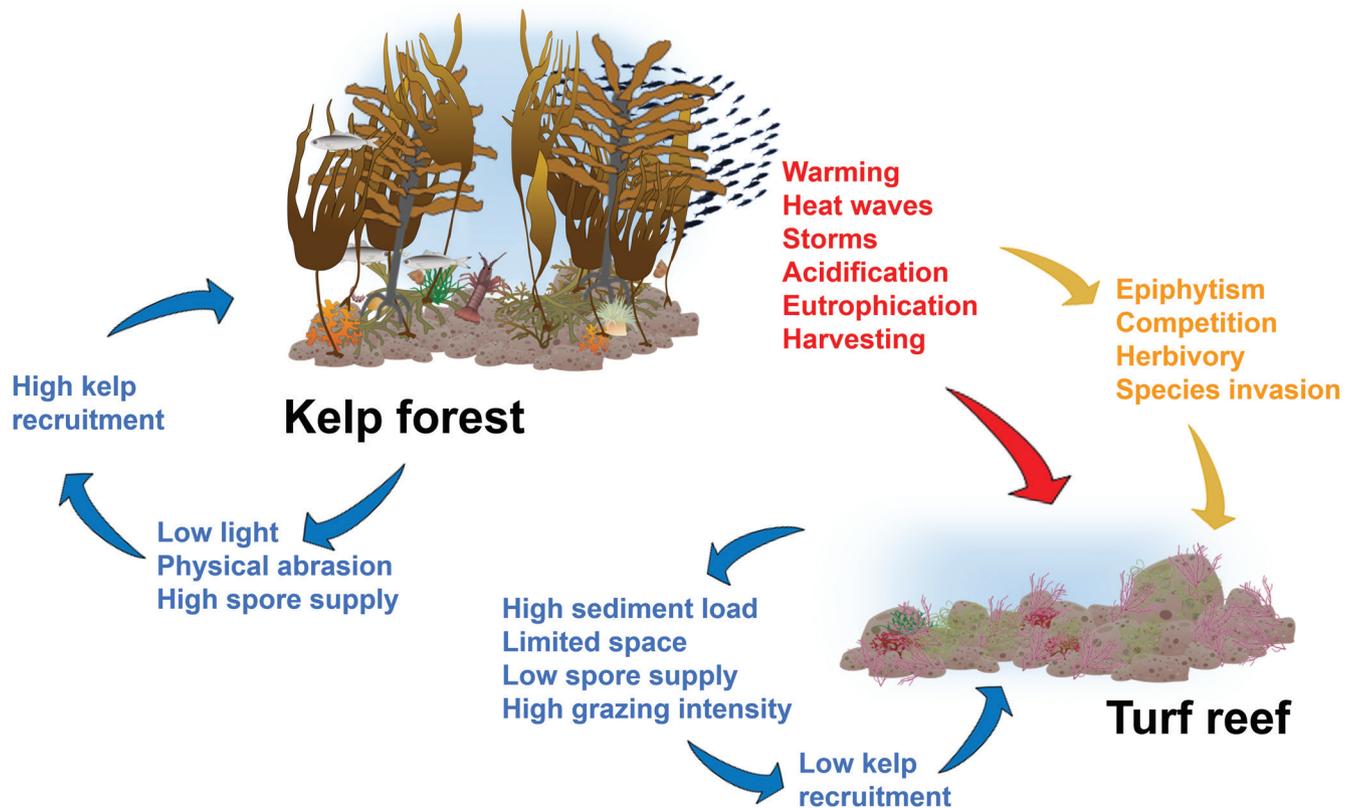
Figure 4. A schematic overview of the direct (red) and indirect (orange) drivers and feedback mechanisms (blue) implicated in regime shifts from kelp forests to turf algae globally (table 2). The arrows indicate the positive effect of these drivers on kelp loss and replacement by turfs, as well as the positive feedback mechanisms on either the kelp or turf state.

temperature thresholds for mortality were passed, suggesting that widespread kelp mortality is not due to the direct effects of warming but is instead triggered by the cumulative effects of multiple stressors, extreme events, or altered biotic interactions that are often indirectly caused by increased temperatures.

In contrast to gradual warming, in which canopy cover is reduced over longer timescales (years to decades; Filbee-Dexter et al. 2016), heat waves that exceed the physiological tolerance limits of kelp can cause shift to turfs over relatively short timescales (weeks to months; Wernberg et al. 2013). The most dramatic example of this was the marine heat wave in Western Australia mentioned above (Wernberg et al. 2013, 2016a). Periods of exceptionally warm temperatures have also been implicated in shifts to turfs in Nova Scotia (Filbee-Dexter et al. 2016) and Norway (Moy and Christie 2012), both of which experienced higher-than-normal summer temperatures 2 to 3 years preceding the greatest loss of kelp cover. A similar pattern of kelp loss occurred along the coast of northern California when influx of extremely warm waters in 2014 and 2015 caused a dramatic 93% reduction of *Nereocystis luetkeana* kelp forests (Catton et al. 2016). However, unlike Norway, Australia, or Nova Scotia, the kelp forest in northern California shifted to sea urchin barrens because of concurrent booms in purple sea urchin (*Strongylocentrotus purpuratus*) populations that overgrazed

the reefs (Catton et al. 2016). In contrast, in Southern California, substantial warming from 2013 to 2015 did not cause kelps to disappear, although their abundance was among the lowest ever recorded following this heat wave (Reed et al. 2016). Across these cases, it is clear that both periods of extreme warming and/or gradual increases in temperature are having increasingly severe direct or indirect effects on the reproduction, growth, and survival of kelps (Airoldi and Beck 2007, Wernberg et al. 2010, Filbee-Dexter et al. 2016).

In addition to warming, increasing carbon dioxide concentrations in the future could exacerbate the effects of rising temperatures. Although there are limited observations of changes caused by ocean acidification, experimental evidence suggests that turfs could outcompete and dominate over kelps and other habitat-forming macrophytes under acidified conditions. The underlying mechanisms appear to include both the stimulated growth of the turfs because of carbon enrichment (Connell SD and Russell 2010) and an inability of herbivores to compensate by higher growth rates (Mertens et al. 2015).

Biological stressors also play a role in driving loss of kelp and proliferation of turfs. In the north Atlantic, rising temperatures increase the recruitment and growth of epiphytes, which coat the kelp blades in encrusting colonies (Saunders et al. 2010, Andersen et al. 2011). Extensive overgrowth

by these epiphytes reduces the strength of the kelp tissue, increasing breakage and canopy loss during storms (Filbee-Dexter and Scheibling 2012) and contributing to shifts to turfs (Krumhansl et al. 2011, 2014). Grazing by fish and invertebrates can also contribute to kelp loss through direct consumption (Vergés et al. 2014, Zarco-Perello et al. 2017), by increasing fragmentation and breakage (Krumhansl et al. 2011), or by reducing the supply of kelp propagules through the targeted consumption of reproductive tissue (e.g., *Lacuna vincta*; O'Brien and Scheibling 2016). In addition to favoring the growth of turfs, altered environmental conditions can increase the growth or reproduction of invasive species. During shifts to turfs in Nova Scotia (Canada), the Gulf of Maine (United States), and Japan, invasive algae also increased in abundance and appear to have prevented the recovery of native kelps through competition for light and space and by reducing the availability of kelp propagules over successive seasons.

An important human-driven change that can promote the growth of turfs over canopy-forming species is eutrophication. Eutrophication reduces light penetration in coastal waters and can favor the persistence of turf algae (Gorman et al. 2009), which have high growth rates (Airoldi 1998) and rapid nutrient-uptake rates compared with larger, canopy-forming algae (Pedersen and Borum 1997). In the northern Mediterranean Sea, Sweden, Denmark, and South Australia, the disappearance of canopy kelps and other macroalgae was largely attributed to increases in coastal nutrients and sediment loading (table 2). Similar dynamics have been documented in Kola Bay, Russia, and New South Wales, Australia, but in these regions, the impacts were further compounded by sewage and urban pollution, favoring turf algae (table 2).

Feedback mechanisms providing resilience to turfs

Kelps are usually considered the competitively dominant species on rocky reefs. They grow quickly, have a high recruitment potential, are often long lived and form dense canopies that change the local environment to favor kelp recruitment (figure 4). They prevent the growth of most other algae through shading (Reed and Foster 1984, Wernberg et al. 2005) or mechanical abrasion (Toohey et al. 2004, Russell 2007). A closed kelp canopy limits the growth of delicate, filamentous algae, and only robust and more shade-tolerant algae (e.g., articulated corallines and corticated macroalgae) are able to survive in the understory. For example, both light and sediment levels under the kelp *E. radiata* decline sharply with increasing kelp density (Wernberg et al. 2005), and these changes have been experimentally linked to the reduced biomass of turfs (Russell 2007). At the same time, kelps produce a large propagule supply, and the reduced water flow within their canopies ensures the retention of the propagules (Eckman et al. 1989, Steneck et al. 2002), which maintains high spore density and therefore high recruitment potential within the forests.

Once kelps are lost, many of the feedback processes reinforcing their dominance are also lost, and as turf algae start to proliferate, new feedback processes are established (figure 4). Turf algae can prevent the establishment and survival of early-life-stage kelps in two ways. First, turf algae are able to quickly overgrow and monopolize primary substrate, limiting the availability of the suitable hard substratum required for kelp-spore settlement (Airoldi 1998, 2003, Gorgula and Connell 2004, Connell SD and Russell 2010). Second, sediment accumulation by turfs (e.g., Isaeus et al. 2004, Filbee-Dexter et al. 2016) reduces the rates of germination and survival of kelp and canopy-forming macroalgae recruits (Reed 1990, Isaeus et al. 2004, Gorman and Connell 2009). Even juveniles that manage to recruit onto mats of turf are more susceptible to dislodgement because of weak attachment (John O'Brien, Department of Biology, Dalhousie University, Halifax, personal communication, 2 June 2017).

Allee effects (declines in individual fitness at low population density) on declining kelp populations may also stabilize the turf state. Decreased sporophyte density makes it easier for herbivores to access the kelps and concentrates grazing on fewer remaining plants (e.g., Hoey and Bellwood 2011, Franco et al. 2015, O'Brien and Scheibling 2016), directly and indirectly accelerating kelp loss. Sparse kelp forests experience lower fertilization rates because reproductive sporophytes are rare and farther apart, resulting in a reduction in kelp propagules (Reed 1990, O'Brien and Scheibling 2016). This is compounded by the short dispersal range of kelp spores (typically 1–10 meters; Gaylord et al. 2012), which limits the extent of population recovery. Experimental work in *Macrocystis pyrifera* forests suggests that threshold densities of spore settlement (1 spore per square millimeter) must be achieved for successful fertilization and recruitment of kelps (Reed 1990). Extensive or prolonged kelp loss will reduce propagule supply and could lower spore density below these thresholds, further reinforcing the dominance of turfs. The competitive effects of turf-forming algae on canopy species are generally limited to early life stages, but there are some cases in which species of turf algae proliferate dramatically under high nutrient conditions and appear to smother adult kelps (Andersen et al. 2011).

Is a collapse to turfs a regime shift?

Considerable research has focused on whether degraded reefs could be considered "alternative stable states" of healthy kelp forest ecosystems (Connell JH and Sousa 1983, Petraitis and Dudgeon 2004, Filbee-Dexter and Scheibling 2014). A defining characteristic of regime shifts between alternative stable states is *hysteresis*, in which the initial tipping point to a new state occurs at a critical threshold of environmental or biological stress that is greater than the threshold required to recover the system (Connell JH and Sousa 1983, Petraitis and Dudgeon 2004). For example, if the input of nutrients was the driver of a shift to turfs, hysteresis implies that in order to recover kelp forests, nutrient

concentrations would need to be reduced much below the threshold nutrient concentration that triggered the initial shift to turfs. The feedback mechanisms that prevent kelp from reestablishing on turfs suggest that these transitions likely exhibit hysteresis. This has important implications for conservation because management options may be severely limited if strong feedback mechanisms are locking the system into the degraded state (Folke et al. 2004).

However, in many shifts to turfs, unprecedented and rapid changes in environmental conditions are driving collapse to new and more degraded reefs (Wernberg et al. 2011 Araújo et al. 2016, Filbee-Dexter et al. 2016, Krumhansl et al. 2016). As a result, turf reefs generally do not persist under similar environmental conditions as the initial kelp forests and the marine environments are unlikely to return to these prior conditions. This differs from regime shifts to urchin barrens, which are often driven by loss of urchin predators (fish or sea otters) without accompanying environmental change and can recover the previous kelp state when these predators rebound (Watson and Estes 2011, Filbee-Dexter and Scheibling 2014). This does not mean that barrens are necessarily easier to recover than turfs (e.g., Marzloff et al. 2015), but it does influence how we apply classical ecological theory to understand these shifts. We suggest that, in the context of current environmental change scenarios, it makes little difference to the consequences for ecological and human communities if the impoverished turf state persists indefinitely as a true alternative stable state under constant environmental conditions (Petraitis and Dudgeon 2004). What matters is that the key drivers of kelp loss are likely to intensify under these scenarios, that these transformations involve feedback mechanisms that are difficult to reverse, and that the consequences will be serious on timescales relevant to humans.

Insights for future research

On a global scale, it is clear that local biogeographic and oceanographic conditions play a role in increasing vulnerability or buffering perturbations, allowing some kelp forests to persist—or even expand (Bolton et al. 2012)—in the face of changing environmental conditions (Wernberg et al. 2013, Reed et al. 2016). It is striking that kelp-to-turf transformations have not been documented along the west coast of North or South America or in southern Africa. In these regions, kelp forests exist predominantly within upwelling zones where temperatures remain cool and/or within temperature ranges well inside their physiological capacity (Steneck et al. 2002). Insights into the mechanisms that enable kelp to thrive in these areas will be crucial when predicting the impacts of future environmental change on kelp forests globally. It is also important to note that threats to kelp forests are not limited to replacement by turfs. Changes in dominant kelp species, commercial kelp harvesting, pollution, and increases in kelp pathogens are also affecting the structure and function of these ecosystems (Steneck and Johnson 2013, Krumhansl et al. 2016). Ongoing shifts from kelp forests to urchin barrens are occurring in Tasmania,

western Canada, northern California, and Alaska (Filbee-Dexter and Scheibling 2014, Catton et al. 2016), suggesting that turfs only establish dominance when kelp is lost under certain conditions (e.g., low urchin abundances). Currently, the mechanisms that drive a kelp forest toward either a turf or barrens state are not clear but remain important to explore.

On a more localized scale, patches of kelp forests remain within some larger regions that have predominately shifted to turfs. For example, cooler, wave-exposed headlands off the coast of Nova Scotia (Filbee-Dexter et al. 2016) and Maine (Steneck et al. 2013) and exposed shoals at the entrance to fjords in western Norway (Moy and Christie 2009) support relatively intact kelp forests compared with nearby regions that have shifted to turfs. An interesting question moving forward is how these spatially fragmented or restricted kelp forests contribute to ecological function compared with more extensive forests. In addition, these refuge habitats may be crucial for supplying spores for kelp recruitment on reefs with high turf cover. Understanding why these areas do not collapse may provide insight on how to build the resilience of kelp forests to prevent future shifts.

The phenomenon of the replacement of kelp forest by turfs is part of a global trend toward the increased dominance of turf algae in many marine ecosystems, including coral reefs, seagrass meadows, and rocky intertidal platforms. Although shifts in these marine ecosystems represent a similar loss of habitat complexity and these ecosystems provide comparably valuable ecological goods and services, far more attention and research has been given to loss of coral reefs compared with loss of kelp forests and seagrass beds (Waycott et al. 2009, Bennett et al. 2016). For example, relative to the value of the kelp forest ecosystems in Australia and South Africa, public funding of research into understanding these ecosystems and the threats they are facing is disproportionally low (Bennett et al. 2016, Blamey and Bolton 2017). This highlights the need to quantify the value of kelp forests and increase public awareness of the threats they face.

Conclusions

Solutions require understanding synergies between local and global drivers. Informed management strategies can either focus on increasing the resilience of intact kelp forests by relaxing the drivers of shifts to turfs or manipulating turf assemblages to promote recovery of kelp following collapse. Our current understanding of the key drivers of these transformations is largely based on correlative links between declines in kelp abundance and changes in various abiotic or biotic conditions. A crucial next step is to develop a stronger causal and mechanistic understanding of what drives these shifts and their reinforcing feedback mechanisms. This will involve verifying the importance of individual drivers and interactions experimentally or examining impacts along spatial gradients or ranges of environmental conditions. In regions with multiple stressors, reducing local anthropogenic

pressure may be an effective strategy for restoring kelp forests (Wernberg et al. 2011, Strain et al. 2014). For example, in Sydney Harbour, crayweed forests (*Phyllospora comosa*) were successfully restored by transplanting healthy, fertile adult plants onto turfs after improvements in sewage treatment increased water quality in this area (Campbell et al. 2014). In order to restore kelp forests that have already shifted to turfs, it is important to know the strength (or presence) of feedback processes maintaining the degraded turf state. The relative importance and strength of these will likely vary across systems and will strongly influence the success of restoration initiatives. Specifically, research aimed at understanding the competitive interactions limiting kelp regeneration at early life stages and the establishment potential of kelp on turf reefs across a range of spore densities, patch sizes, or levels of initial juvenile recruitment would enable us to identify the threshold levels of kelp abundance necessary for recovery.

However, on relevant timescales for managers, it is not possible to control the regional or global drivers (such as warming or storm events) that are driving shifts to turfs in many kelp forest ecosystems. Perhaps the most alarming aspect of this new turf phenomenon is the dearth of examples of natural recovery of kelp forests. Although this could be due to the recent nature of these transitions, the direction of ongoing environmental changes away from conditions that favor kelp, combined with signs of hysteresis in the turf state, suggests we are witnessing the early stages of a pervasive trend of flattening temperate reefs as a result of climate change and other increasing human stressors. We have a narrowing window of opportunity to identify the processes that impart resistance and stability in kelp forests or drive these shifts to turfs, and this information is essential to solutions to restore, recover, or prevent further degradation.

Acknowledgments

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Karen Filbee-Dexter (kfilbeedexter@gmail.com) is a postdoctoral researcher at the Norwegian Institute for Water Research, in Oslo, Norway. She studies regime-shift dynamics in kelp-forest ecosystems under changing environmental conditions. Thomas Wernberg (thomas.wernberg@uwa.edu.au) is a biologist at the University of Western Australia, in Perth, Australia. He studies the impact of climate change and humans on the stability of marine ecosystems. KFD and TW jointly conceived, designed, analyzed, and wrote the manuscript.