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1 **Rise of Turfs: A New Battle Front for Globally Declining**

2 **Kelp Forests**

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15

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23 **Abstract**

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 Globally, many kelp forests have disappeared and been replaced by turf algae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

36

37 **Key words:** Seaweeds, warming, eutrophication, habitat loss, regime shift

38 **Kelp forests –foundations of temperate reefs globally**

39 *“The numbers of living creatures of all Orders whose existence intimately depends*
40 *on kelp is wonderful ... I can only compare these great aquatic forests of the southern*
41 *hemisphere with the terrestrial ones in the intertropical regions. Yet if in any country*
42 *a forest was destroyed, I do not believe as many species of animals would perish as*
43 *would here from the destruction of kelp”* (Darwin, 1839).

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

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

55 As Darwin’s observations clearly indicate, kelp forests support a plethora of associated
56 species. Kelps are ecosystem engineers. They create complex biogenic habitats (Christie et al.
57 2009, Thomsen et al. 2010, Teagle et al. 2017), which influence the physical conditions, such as
58 light, water flow, sedimentation, physical abrasion, and pH in their surrounding environment
59 (Eckman et al. 1989, Wernberg et al. 2005, Krause-Jensen et al. 2016). In addition to providing
60 structural habitat (Teagle et al. 2017), the high productivity of kelp also provides an abundant
61 food source for species such as fish, urchins, small crustaceans and snails that graze directly on
62 the attached kelps (Christie et al. 2009, O’Brien and Scheibling 2016). Other species filter feed
63 on particulate organic material or prey on kelp associated species (Norderhaug et al. 2005,

64 Christie et al. 2009). Kelp forests also produce large quantities of detached ‘drift’ kelp which
65 tumble across the seafloor or raft on the waters’ surface, ending up in adjacent or distant habitats.
66 As much as 80% of the local production ends up as drift which can leave the kelp forest and
67 support food webs where autochthonous primary production is usually very low (Krumhansl and
68 Scheibling 2012). Drift kelp is a primary source of food in many of these habitats and attracts a
69 diverse community of detritivores and consumers, often substantially increasing secondary
70 production (Bustamante et al. 1995, Krumhansl and Scheibling 2012). Through these trophic
71 subsidies, and by providing an important trans-oceanic dispersal vector for kelp-rafting flora and
72 fauna (Rothausler et al. 2012), drift kelp extend the ecological influence of kelp forests far
73 beyond the locations where the kelps grow.

74

75 **The intimate connection between kelp forests and humans**

76 These ocean forests are not only critically important to marine plants and animals, but also to
77 humans. *Homo sapiens* have exploited the rich resources provided by kelp forests for at least
78 10,000 – 70,000 years (e.g., Volman 1978, Jerardino and Navarro 2002, Balasse et al. 2005), but
79 our intimate connection with kelp forests could be as old humankind itself. Evidence suggests
80 that early humans might have evolved along the rocky coasts of southern Africa, as a
81 consequence of a rich diet of marine organisms, supported by highly productive kelp forests
82 (Bustamante et al. 1995), including mussels and limpets providing the omega-3 fatty acids and
83 trace elements required for brain function and development (Compton 2011). Kelp forests have
84 also played an important role in the biogeography of humans. About 16,000 yrs ago early
85 colonizers of the Americas followed a ‘kelp highway’ along the Pacific rim, sustained by the
86 bounty provided by kelp forests (Erlandson et al. 2007).

87 Kelp forests also play an important role in the lives of modern humans, through providing
88 a broad range of ecosystem goods and services of great social, economic and ecological value
89 (Vásquez et al. 2014, Bennett et al. 2016, Blamey and Bolton *in press*; Fig. 1). These goods and

90 services arise as direct contributions from the kelp forests (e.g., kelp harvesting, commercial and
91 recreational fishing and tourism), as indirect contributions via the functions of the kelp forest
92 (e.g., habitat provision, climate control, carbon sequestration, coastline protection and nutrient
93 filtering) or from the innate value of the kelp forest itself (e.g., its scientific or cultural importance
94 and biodiversity). While the economic value of these ecosystem services can be very difficult to
95 establish, especially for indirect and non-use services, it is estimated that kelp forests provide
96 services worth 500,000 – 1,000,000 USD per kilometer of coastline (Table 1). However, these
97 figures are heavily dominated by direct-use services (e.g., Vásquez et al. 2014, Bennett et al.
98 2016) and the true value of kelp forests could be 3 – 6 times higher. Valuations of more broadly
99 defined marine macrophyte communities, which better incorporate the indirect and non-use
100 values, place seagrass and seaweed beds as the third most productive systems globally, providing
101 ecosystem services valued at 3,000,000 USD per km coastline per yr (assuming a 1 km wide
102 kelp forests at 30,000 USD per hectare per yr; Costanza et al. 2014). Even this is most likely a
103 considerable under-estimation reflecting the lack of studies valuating services explicitly from
104 kelp forests (Bennett et al. 2016). Recently, the value of coral reefs was increased more than 40
105 times previous estimates, mainly as a consequence of new studies valuating additional ecosystem
106 services such as storm protection, erosion protection and recreation (Costanza et al. 2014).

107

108 **Kelp forests under siege**

109 Human impacts on marine foundation species have accelerated over the past 4 – 5 decades.
110 Globally, estuaries (Lotze et al. 2006), seagrass meadows (Orth et al. 2006, Waycott et al. 2009)
111 and coral reefs (Pandolfi et al. 2003, Hughes et al. 2017) have been adversely affected. Kelp
112 forests are no exception (Krumhansl et al. 2016). A recent global analysis found that 38% of the
113 world's kelp forests have been in decline over the past five decades (Krumhansl et al. 2016),
114 although interactions between local, regional and global processes have produced complex

115 responses in terms of direction and ultimate drivers of kelp forest change (Wernberg et al. 2011,
116 Krumhansl et al. 2016).

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

128 The current downward trajectory of more than one-third of the world’s kelp forests
129 (Krumhansl et al. 2016) will cause major reductions in the quality and quantity of ecosystem
130 services that these foundation species provide (e.g. loss of tourism, closures of recreational or
131 commercial fisheries, and removal of carbon sink, cf. Table 1). There is therefore a pressing need
132 to understand the processes that are driving these regime shifts. Here we provide an overview of
133 the transformation of kelp forests to turf seascapes. We begin by reviewing the global literature
134 on shifts from kelp forests to turf-dominated reefs. We map out the growing global extent of the
135 problem and synthesize available information on global and regional drivers and dynamics of
136 these shifts, developing a generalized conceptual model of the interacting mechanisms. Finally,
137 we examine in more detail, the feedback mechanisms that prevent recovery of kelp forests. We
138 suggest that efforts to reduce local anthropogenic impacts may be an effective strategy for
139 curbing the degradation of kelp forests in many of these systems. However, a deeper, more

140 mechanistic understanding of the drivers, and recovery potential of kelp forests following these
141 shifts is required to ensure cost-effective and successful management into the future.

142

143 **The rise of turf algae**

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

157 The large-scale replacement of kelp forests with turf algae is a new phenomenon (Fig. 2,
158 3). Another important and extensively studied phenomenon of kelp loss is direct consumption
159 by sea urchins, which can destructively graze erect macroalgae and trigger regime shifts to
160 coralline algal-dominated 'barrens' (Steneck et al. 2002, Filbee-Dexter and Scheibling 2014).
161 Regime shifts from kelp forests to urchin barrens have been studied for decades on temperate
162 rocky reefs worldwide (Filbee-Dexter and Scheibling 2014). These shifts are largely triggered
163 by population explosions of sea urchins due to removal of top predators, urchin recruitment
164 pulses, or altered environmental conditions (Steneck et al. 2002, Filbee-Dexter and Scheibling

165 2014). Following collapse to barrens, kelp forests can reestablish years or decades later, when
166 sea urchin densities decline and grazing intensity is once again reduced to levels where kelps can
167 recruit and reestablish (Watson and Estes 2011, Filbee-Dexter and Scheibling 2014). In contrast,
168 large-scale shifts from kelp forests to turfs have not shown recovery, but reefs have remained in
169 a degraded turf state. It is unclear what is responsible for these new dynamics of persistent kelp
170 loss. Potentially, human driven environmental changes such as ocean warming or coastal
171 eutrophication are favoring growth and survival of turfs over kelps, and decoupling the kelp loss
172 and recovery processes from top down control by urchins and/or their predators. Key questions
173 now facing ecologists are: (1) what are the main drivers of shifts to turfs, (2) what feedbacks are
174 maintaining them and how permanent are they, and (3) what strategies are available for moving
175 forward towards solutions to the problem?

176

177 **The global flattening of kelp forests**

178 The shift from kelp forests to turfs has been increasingly documented along many temperate
179 coasts globally. Early observations of these shifts were reported in the late 1990s and 2000s in
180 localized areas of South Australia (Connell et al. 2008), the Baltic Sea and Skagerak (e.g.
181 Middelboe and Sand-Jensen 2000, Eriksson et al. 2002), and Atlantic Canada (Filbee-Dexter et
182 al. 2016). However, in the last decade, more widespread disappearance of kelp forests has been
183 reported along 100s km of coastline in Atlantic Canada (Filbee-Dexter et al. 2016), Europe (Moy
184 and Christie 2012, Voerman et al. 2013), and Australia (Wernberg et al. 2016a) (Table 2, Fig. 2,
185 3).

186 In the Indian Ocean, *Ecklonia radiata* kelp forests (Fig. 2a) collapsed along the coast of
187 Western Australia during an extreme marine heatwave in the austral summer of 2010/11,
188 following four decades of background warming in this ocean warming hotspot (Smale and
189 Wernberg 2013, Wernberg et al. 2013, 2016a). Kelp forests were completely wiped out and
190 replaced by turfs and *Sargassum* spp., along 100 km coast at their range margin (Fig. 2b), where

191 the cover of turfs increased from less than 10% to more than 80% in less than two years. The
192 kelp forests to the north succumbed to acute thermal stress as temperature anomalies exceeded
193 their physiological capacity (Smale and Wernberg 2013, Wernberg et al. 2016b) and thermal
194 safety margins (Bennett et al. 2015a). At the same time, there was a substantial influx of tropical
195 fish herbivores (Fig. 2c) resulting in a 400% increase in grazing rates to levels equivalent to
196 healthy coral reefs. This increased herbivory facilitated the expansion of turfs while preventing
197 the kelp from recovering (Bennett et al. 2015b). The tropical fishes also recruited farther south,
198 beyond the acute catastrophic impacts of the heatwave. Here they actively grazed the kelp
199 canopy, reducing its cover by almost 70% in less than five years at localized reefs (Zarco-Perello
200 et al. 2017), paving the way for an equivalent expansion of turfs (T. Wernberg, personal
201 observation). In contrast, kelp forests in colder waters farther south did not experience similar
202 canopy loss and proliferation of turfs even though temperature anomalies during the heatwave
203 were similar (Wernberg et al. 2013, 2016a).

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

216 western coast (Hartvig Christie, Norwegian Institute for Water Research, Oslo, personal
217 communication, June 2nd, 2017).

218 In the western Atlantic Ocean, in Nova Scotia, Canada, *Laminaria digitata* and *S.*
219 *latissima* forests (Fig. 2g) have disappeared along the central Atlantic coast, with average canopy
220 cover losses of 89% compared to baseline measures from 1982 (Filbee-Dexter et al. 2016). These
221 declines were gradual, beginning in the early 1990s, and reductions in kelp were associated with
222 an increase in turf-forming algae and two invasive algal species, *Fucus serratus* and *Codium*
223 *fragile* subspecies *fragile* (Fig. 2h). This region is a global warming hotspot, and the declines in
224 kelp were largely driven by indirect effects of warming temperatures that increased recruitment
225 and growth of the invasive bryozoan *Membranipora membranacea* (Fig. 2i) (Saunders et al.
226 2010, Krumhansl et al. 2014). *M. membranacea* encrusts kelp fronds leading to higher breakage
227 and mortality during periods of wave action (Krumhansl et al. 2011). Stronger storms, increased
228 intensity of mesograzing, and direct physiological effects of warm temperatures also played a
229 role in eroding the resilience of the kelp forest (Filbee-Dexter and Scheibling 2012, Krumhansl
230 et al. 2014, O'Brien et al. 2015). Shifts to turfs were most dramatic in protected bays where water
231 temperatures are warmer, and kelp forests are still found in cooler, more exposed parts of the
232 coast. Similarly, 300-600 km to the southwest in the Gulf of Maine, USA, shifts to filamentous
233 and corticated red algae occurred during the mid-1990s to mid-2000s (Steneck et al. 2013).
234 Currently, turfs are abundant along sheltered and southern reefs (Steneck et al. 2013), and in
235 some areas kelp forests have been entirely replaced by invasive red turf algae (Dijkstra et al.
236 2017).

237 Most other places that have experienced transitions from macroalgal forests to turfs
238 (Table 2) have followed the same general pattern that emerges from the three examples described
239 above (cf. Fig. 4). For one, many of these habitats are under pressure from the direct effects of
240 abiotic drivers due to warming or nutrient pollution. This pressure can be either lethal, causing
241 kelp mortality, or sub-lethal, causing reduced performance and increasing vulnerability to other

242 drivers (Wernberg et al. 2010). Often, abiotic drivers also lead to changes in other biological
243 components of the ecosystem, which in turn can have indirect negative effects on the kelp.
244 Examples of these biotic drivers include increased grazing intensity from herbivores in
245 southwestern Europe and Mediterranean Sea (Vergés et al. 2014, Franco et al. 2015) and
246 competition from invasive red algae in the Gulf of Maine (Dijkstra et al. 2017) (Fig. 4).

247

248 **Multiple drivers trigger collapse to turfs**

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

256 There is strong evidence that warming, in particular, has played an important role in most
257 shifts to turfs documented in the last decade (Table 2). Ultimately, kelps are cool-water
258 organisms and, towards the warmer ends of their distribution, warming will reduce their growth,
259 weaken their tissue and negatively affect how they deal with other perturbations such as grazing,
260 epiphytism, or mechanical damage (Wernberg et al. 2010, Simonson et al. 2015). Consequently,
261 most of the collapsed kelp forests have been located in warming hotspots, or near the edges of
262 their distribution where they likely are less resilient to additional perturbations [e.g. *L. digitata*
263 in France and Denmark (Raybaud et al. 2013), *S. latissima* in Gulf of Maine and Atlantic Canada
264 (Merzouk and Johnson 2011) and *E. radiata* in Australia (Wernberg et al. 2010, Wernberg et al.
265 2016a)]. In contrast, in the center and cooler ends of their species' distributions, kelp forests in
266 some regions have experienced significant discrete warming events without collapsing (e.g.,
267 Wernberg et al. 2013, Krause-Jensen and Duarte 2014, Araújo et al. 2016, Reed et al. 2016).

268 Canopy removal experiments in Western Australia prior to the collapse of northern kelp forests,
269 showed substantially faster canopy recovery at cooler southern locations compared to warmer
270 northern locations, where turf algae increased in cover before the canopies could recover
271 (Wernberg et al. 2010). Further indirect evidence for the importance of elevated temperatures
272 comes from observational ‘space-for-time’ studies of warming along geographic temperature
273 gradients, where low kelp and high turf cover are more prevalent in warmer regions compared
274 to colder regions (Wernberg et al. 2010, Tuya et al. 2012, Filbee-Dexter et al. 2014). However,
275 in almost all shifts to turf algae, significant kelp loss occurred before temperature thresholds for
276 mortality were passed, suggesting that widespread kelp mortality is not due to direct effects of
277 warming, but instead triggered by cumulative effects of multiple stressors, extreme events or
278 altered biotic interactions that are often indirectly caused by increased temperatures.

279 In contrast to gradual warming where canopy cover is reduced over longer timescales
280 (years to decades) (Filbee-Dexter et al. 2016), heat waves that exceed physiological tolerance
281 limits of kelp can cause shift to turfs over relatively short time scales (weeks to months)
282 (Wernberg et al. 2013). The most dramatic example of this was the marine heat wave in Western
283 Australia mentioned above (Wernberg et al. 2013, 2016a). Periods of exceptionally warm
284 temperatures have also been implicated in shifts to turfs in Nova Scotia (Filbee-Dexter et al.
285 2016) and Norway (Moy and Christie 2012), both of which experienced higher than normal
286 summer temperatures two to three years preceding the greatest loss of kelp cover. A similar
287 pattern of kelp loss occurred along the coast of northern California when influx of extremely
288 warm waters in 2014 and 2015 caused a dramatic 93% reduction of *Nereocystis luetkeana* kelp
289 forests (Catton et al. 2016). However, unlike Norway, Australia or Nova Scotia, the kelp forest
290 in northern California, shifted to sea urchin barrens due to concurrent booms in purple sea urchin
291 *Strongylocentrotus purpuratus* populations that overgrazed the reefs (Catton et al. 2016). In
292 contrast, in Southern California substantial warming from 2013 to 2015 did not cause kelps to
293 disappear, although their abundance was among the lowest ever recorded following this heat

294 wave (Reed et al. 2016). Across these cases, it is clear that both periods of extreme warming
295 and/or gradual increases in temperature are having increasingly severe direct or indirect effects
296 on the reproduction, growth and survival of kelps (Airoldi and Beck 2007, Wernberg et al. 2010,
297 Filbee-Dexter et al. 2016).

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

305 Biological stressors also play a role in driving loss of kelp and proliferation of turfs. In
306 the north Atlantic, rising temperatures increase the recruitment and growth of epiphytes, which
307 coat the kelp blades in encrusting colonies (Saunders et al. 2010, Andersen et al. 2011). Extensive
308 overgrowth by these epiphytes reduces the strength of the kelp tissue, increasing breakage and
309 canopy loss during storms (Filbee-Dexter and Scheibling 2012), and contributing to shifts to
310 turfs (Krumhansl et al. 2011, 2014). Grazing by fish and invertebrates can also contribute to kelp
311 loss through direct consumption (Vergés et al. 2014, Zarco-Perello et al. 2017), by increasing
312 fragmentation and breakage (Krumhansl et al. 2011), or by reducing the supply of kelp
313 propagules through targeted consumption of reproductive tissue (e.g. *Lacuna vincta*; O'Brien
314 and Scheibling 2016). In addition to favouring growth of turfs, altered environmental conditions
315 can increase the growth or reproduction of invasive species. During shifts to turfs in Nova Scotia
316 (Canada), Gulf of Maine (USA), and Japan invasive algae also increased in abundance, and
317 appear to have prevented recovery of native kelps through competition for light and space, and
318 by reducing the availability of kelp propagules over successive seasons.

319 An important human-driven change that can promote the growth of turfs over canopy
320 forming species is eutrophication. Eutrophication reduces light penetration in coastal waters and
321 can favour the persistence of turf algae (Gorman et al. 2009), which have high growth rates
322 (Airoldi 1998) and rapid nutrient uptake rates compared to larger, canopy forming algae
323 (Pedersen and Borum 1997). In the northern Mediterranean Sea, Sweden, Denmark and South
324 Australia, the disappearance of canopy kelps and other macroalgae were largely attributed to
325 increases in coastal nutrients and sediment loading (Table 2). Similar dynamics have been
326 documented in Kola Bay (Russia) and New South Wales (Australia), but in these regions the
327 impacts were further compounded by sewage and urban pollution, favouring turf algae (Table
328 2).

329

330 **Feedbacks providing resilience to turfs**

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

344 Once kelps are lost, many of the feedbacks reinforcing their dominance are also lost, and
345 as turf algae start to proliferate new feedbacks are established (Fig. 4). Turf algae can prevent
346 establishment and survival of early life-stages kelps in two ways. First, turf algae are able to
347 quickly overgrow and monopolize primary substrate, limiting the availability of suitable hard
348 substratum required for kelp spore settlement (Airoldi 1998, 2003, Gorgula and Connell 2004,
349 Connell and Russell 2010). Second, sediment accumulation by turfs (e.g., Isaeus et al. 2004,
350 Filbee-Dexter et al. 2016) reduces rates of germination and survival of kelp and canopy forming
351 macroalgae recruits (Reed 1990, Isaeus et al. 2004, Gorman and Connell 2009). Even juveniles
352 that manage to recruit on to mats of turf are more susceptible to dislodgement due to weak
353 attachment (John O'Brien, Dalhousie University, Halifax, personal communication, June 2nd,
354 2017).

355 Allee effects (declines in individual fitness at low population density) on declining kelp
356 populations may also stabilize the turf state. Decreased sporophyte density makes it easier for
357 herbivores to access the kelps and concentrates grazing on fewer remaining plants (e.g., Hoey
358 and Bellwood 2011, Franco et al. 2015, O'Brien and Scheibling 2016), directly and indirectly
359 accelerating kelp loss. Sparse kelp forests experience lower fertilization rates because
360 reproductive sporophytes are rare and farther apart, resulting in a reduction in kelp propagules
361 (Reed 1990, O'Brien and Scheibling 2016). This is compounded by the short dispersal range of
362 kelp spores (typically 1–10 m, Gaylord et al. 2012), which limits the extent of population
363 recovery. Experimental work in *Macrocystis pyrifera* forests suggest that threshold densities of
364 spore settlement (1 spore per mm²) must be achieved for successful fertilization and recruitment
365 of kelps (Reed 1990). Extensive or prolonged kelp loss will reduce propagule supply and could
366 lower spore density below these thresholds, further reinforcing dominance of turfs. Competitive
367 effects of turf-forming algae on canopy species are generally limited to early life stages, but there
368 are some cases where species of turf algae proliferate dramatically under high nutrient conditions
369 and appear to smother adult kelps (Andersen et al. 2011).

370

371 **Is a collapse to turfs a regime shift?**

372 Considerable research has focused on whether degraded reefs could be considered ‘alternative
373 stable states’ of healthy kelp forest ecosystems (Connell and Sousa 1983, Petraitis and Dudgeon
374 2004, Filbee-Dexter and Scheibling 2014). A defining characteristic of regime shifts between
375 alternative stable states is hysteresis, where the initial tipping point to a new state occurs at a
376 critical threshold of environmental or biological stress that is greater than the threshold required
377 to recover the system (Connell and Sousa 1983, Petraitis and Dudgeon 2004). For example, if
378 input of nutrients was the driver of a shift to turfs, hysteresis implies that in order to recover kelp
379 forests, nutrient concentrations would need to be reduced much below the threshold nutrient
380 concentration that triggered the initial shift to turfs. The feedback mechanisms that prevent kelp
381 from reestablishing on turfs suggest that these transitions likely exhibit hysteresis. This has
382 important implications for conservation because management options may be severely limited if
383 strong feedback mechanisms are locking the system into the degraded state (Folke et al. 2004).

384 However, in many shifts to turfs, unprecedented and rapid changes in environmental
385 conditions are driving collapse to new and more degraded reefs (Wernberg et al. 2011 Araújo et
386 al. 2016, Filbee-Dexter et al. 2016, Krumhansl et al. 2016). As a result, turf reefs generally do
387 not persist under similar environmental conditions as the initial kelp forests, and the marine
388 environments are unlikely to return to these prior conditions. This differs from regime shifts to
389 urchin barrens, which are often driven by loss of urchin predators (fish or sea otters) without
390 accompanying environmental change, and can recover the previous kelp state when these
391 predators rebound (Watson and Estes 2011, Filbee-Dexter and Scheibling 2014). This does not
392 mean that barrens are necessarily easier to recover than turfs (e.g. Marzloff et al. 2015), but it
393 does influence how we apply classical ecological theory to understand these shifts. We suggest
394 that, in the context of current environmental change scenarios, it makes little difference to the
395 consequences for ecological and human communities if the impoverished turf state persists

396 indefinitely as a true ‘alternative stable state’ under constant environmental conditions (Petraitis
397 and Dudgeon 2004). What matters is that key drivers of kelp loss are likely to intensify under
398 these scenarios, that these transformations involve feedbacks that are difficult to reverse, and
399 that the consequences will be serious on timescales relevant to humans.

400

401 **Insights for future research**

402 On a global scale, it is clear that local biogeographic and oceanographic conditions play a role
403 in increasing vulnerability or buffering perturbations, allowing some kelp forests to persist, or
404 even expand (Bolton et al. 2012), in the face of changing environmental conditions (Wernberg
405 et al. 2013, Reed et al. 2016). It is striking that kelp to turf transformations have not been
406 documented along the west coast of North or South America or in southern Africa. In these
407 regions, kelp forests exist predominantly within upwelling zones where temperatures remain
408 cool and/or within temperature ranges well inside their physiological capacity (Steneck et al.
409 2002). Insights into the mechanisms that enable kelp to thrive in these areas will be critical when
410 predicting the impacts of future environmental change on kelp forests globally. It is also
411 important to note that threats to kelp forests are not limited to replacement by turfs. Changes in
412 dominant kelp species, commercial kelp harvesting, pollution and increases in kelp pathogens
413 are also impacting the structure and function of these ecosystems (Steneck and Johnson 2013,
414 Krumhansl et al. 2016). Ongoing shifts from kelp forests to urchin barrens are occurring in
415 Tasmania, western Canada, northern California and Alaska (Filbee-Dexter and Scheibling 2014,
416 Catton et al. 2016), suggesting that turfs only establish dominance when kelp is lost under certain
417 conditions (e.g. low urchin abundances). Currently, the mechanisms that drive a kelp forest
418 towards either a turf or barrens state are not clear, but remain important to explore.

419 On a more localized scale, patches of kelp forests remain within some larger regions that
420 have predominately shifted to turfs. For example, cooler, wave exposed headlands off the coast
421 of Nova Scotia (Filbee-Dexter et al. 2016) and Maine (Steneck et al. 2013), and exposed shoals

422 at the entrance to fjords in western Norway (Moy and Christie 2009) support relatively intact
423 kelp forests compared to nearby regions that have shifted to turfs. An interesting question moving
424 forward is how these spatially fragmented or restricted kelp forests contribute to ecological
425 function compared to more extensive forests. Additionally, these refuge habitats may be critical
426 for supplying spores for kelp recruitment on reefs with high turf cover. Understanding why these
427 areas do not collapse may provide insight on how to build resilience of kelp forests to prevent
428 future shifts.

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

439

440 **Solutions require understanding synergies between local and global drivers**

441 Informed management strategies can either focus on increasing resilience of intact kelp forests
442 by relaxing the drivers of shifts to turfs, or manipulating turf assemblages to promote recovery
443 of kelp following collapse. Our current understanding of the key drivers of these transformations
444 is largely based on correlative linkages between declines in kelp abundance and changes in
445 various abiotic or biotic conditions. A critical next step is to develop a stronger causal and
446 mechanistic understanding of what drives these shifts and their reinforcing feedbacks. This will
447 involve verifying the importance of individual drivers and interactions experimentally or

448 examining impacts along spatial gradients or ranges of environmental conditions. In regions with
449 multiple stressors, reducing local anthropogenic pressure may be an effective strategy for
450 restoring kelp forests (Wernberg et al. 2011, Strain et al. 2014). For example, in Sydney Harbour
451 crayweed forests (*Phyllospora comosa*) were successfully restored by transplanting healthy,
452 fertile adult plants onto turfs after improvements in sewage treatment increased water quality in
453 this area (Campbell et al. 2014). In order to restore kelp forests that have already shifted to turfs
454 it is important to know the strength (or presence) of feedbacks maintaining the degraded turf
455 state. The relative importance and strength of these will likely vary across systems, and will
456 strongly influence the success of restoration initiatives. Specifically, research aimed at
457 understanding the competitive interactions limiting kelp regeneration at early life stages and the
458 establishment potential of kelp on turf reefs across a range of spore densities, patch sizes, or
459 levels of initial juvenile recruitment would enable us to identify threshold levels of kelp
460 abundance necessary for recovery.

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

471

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723 **Table 1. Estimated value of ecosystem goods and services from kelp forests around the**
 724 **world.**

Region	Total value (USD km ⁻¹ yr ⁻¹)	Key services evaluated (percent of total value)	Main species	Reference
Northern Chile, Pacific Ocean ³	811,000	Kelp fishing (76%) Commercial fisheries (15%) Scientific, biological and climate value (9%)	<i>Lessonia</i> spp., <i>Macrocystis pyrifera</i>	Vásquez et al. 2013
Great Southern Reef, Australia, Indian Ocean and Southern Ocean ²	914,000	Tourism (90%) Recreational and commercial fishing (10%)	<i>E. radiata</i> , various endemic fucoids	Bennett et al. 2016
South Africa, South Atlantic Ocean ¹	520,000	Commercial (incl. kelp), recreational and illegal fishing (45%) Ecotourism (30%) Nutrient cycling and carbon sequestration (25%)	<i>Ecklonia maxima</i>	Blamey and Bolton <i>in press</i>

725 ¹540 million USD, 666 km coastline

726 ²10 billion AUD yr⁻¹, 8,100 km coastline, 0.74 USD

727 ³5.2 billion ZAR yr⁻¹, 700 km coastline, 0.07 USD

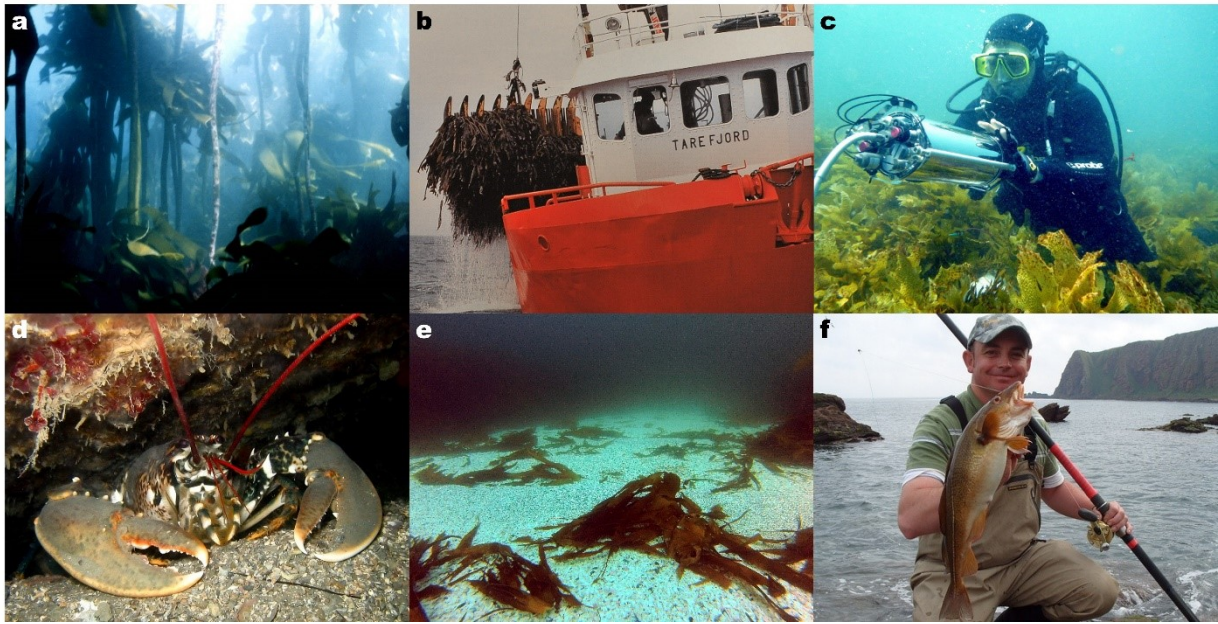
728 **Table 2.** Drivers, dominant species, duration of shift, and description of shifts to turfs
 729 documented throughout range of kelp forests and other canopy forming macroalgae.

Possible drivers	Region	Description	Macroalgal species	Time period	Source
Asia					
Gradual warming	Western Pacific, Japan	Kelp loss and shift in algal community (increased tropical <i>Sargassum</i> spp.) ¹ Herbivorous fish suppress recovery.	<i>Ecklonia</i> spp. and canopy forming temperate <i>Sargassum</i> spp.	1970s–2010; decline: 1990s	Tanaka et al. 2012
Australia					
Eutrophication	Southern Ocean, Australia	Shift to turfs along 70 km. Trapped sediment prevented recruitment.	<i>Ecklonia radiata</i>	1968–1973 ² , 1990s–2007; decline: late-1990s	Connell 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.	<i>E. radiata</i>	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.	<i>Phyllospora comosa</i>	1940s ² –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.	<i>Sargassum</i> 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	<i>Fucus</i> spp	1950s, 1987–1988; decline: pre-1987	Vogt and Schramm 1991
Eutrophication, pollution	Mediterranean Sea, Italy	Shift to turfs.	<i>Cystoseira</i> spp.	Decline: post-1999	Benedetti-Cecchi et al. 2001

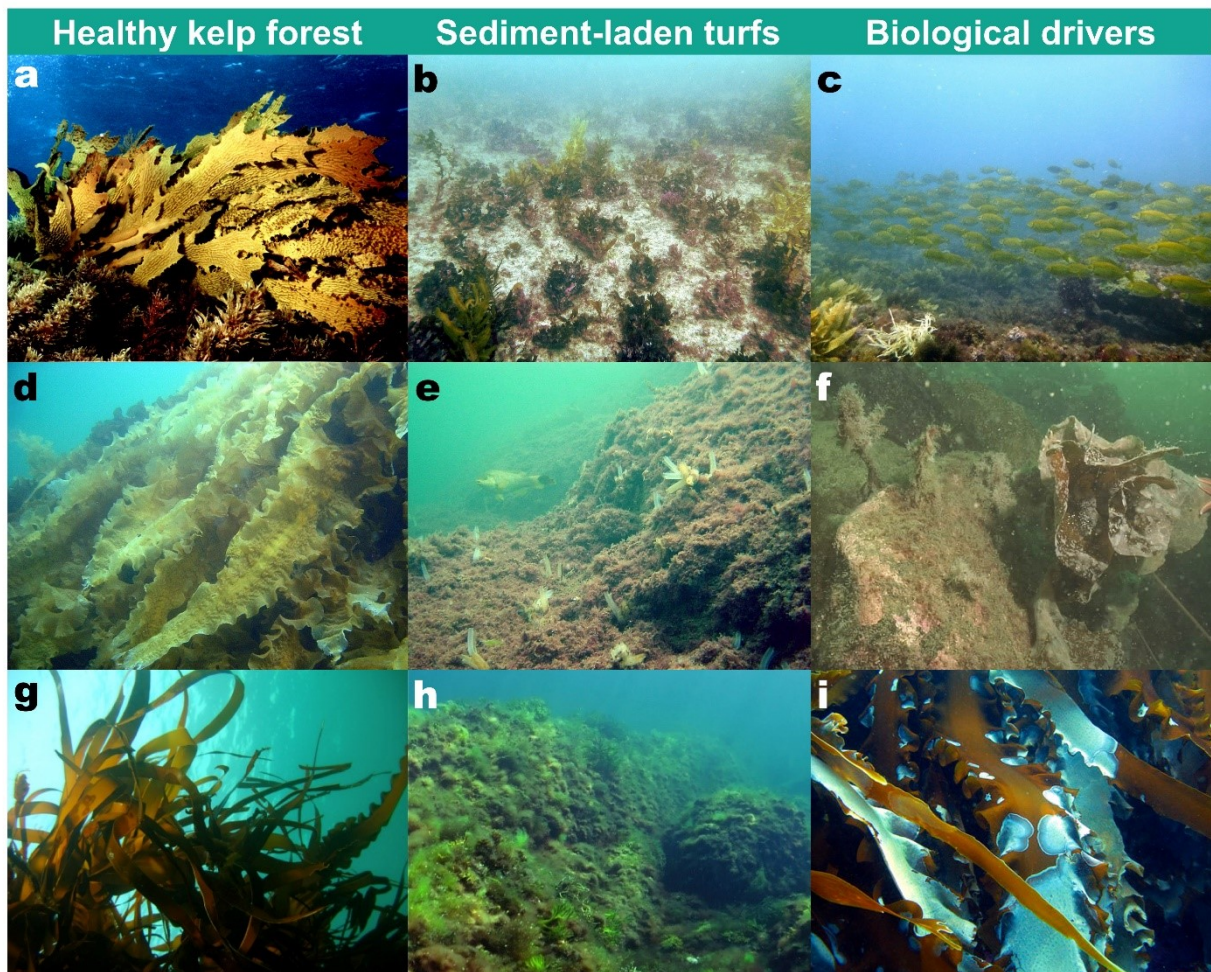
		Loss associated with proximity to urban areas			
Warming, epiphytism, eutrophication	NEA, Western and Southern Norway	Shift to turfs and ephemeral algae. Drivers may vary between western and southern coasts.	<i>S. latissima</i>	1990–2010; decline: 2002	Andersen et al. 2011, Moy and Christie 2012,
Gradual warming, heat waves	NEA, Spain	Decline and replacement by turfs.	<i>L. hyperborea</i> , <i>Laminaria aculeata</i>	1990s–2010; decline: 2007	Voerman et al. 2013
Eutrophication	Denmark	Shift to turfs and green algae.	<i>Fucus</i> 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.	<i>S. latissima</i> (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 <i>Phyllophora truncata</i> .	<i>S. latissima</i> , <i>A. esculenta</i>	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.	<i>L. digitata</i> , <i>S. latissima</i>	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 <i>Dasyisiphonia japonica</i> .	<i>S. latissima</i>	1977–2015; decline: 1990s and 2000s	Steneck et al. 2013, Dijkstra et al. 2017.
South America					
Possibly eutrophication, warming	São Sebastião region, Brazil	Replacement by turfs	<i>Sargassum</i> spp.	1980s–2016	Daniel Gorman, May 3 rd , 2017, University of São Paulo, personal communication, São Paulo

730 ¹Changes in understory following kelp loss not reported. ²Anecdotal or observational evidence of occurrence of
731 macroalgal reefs.

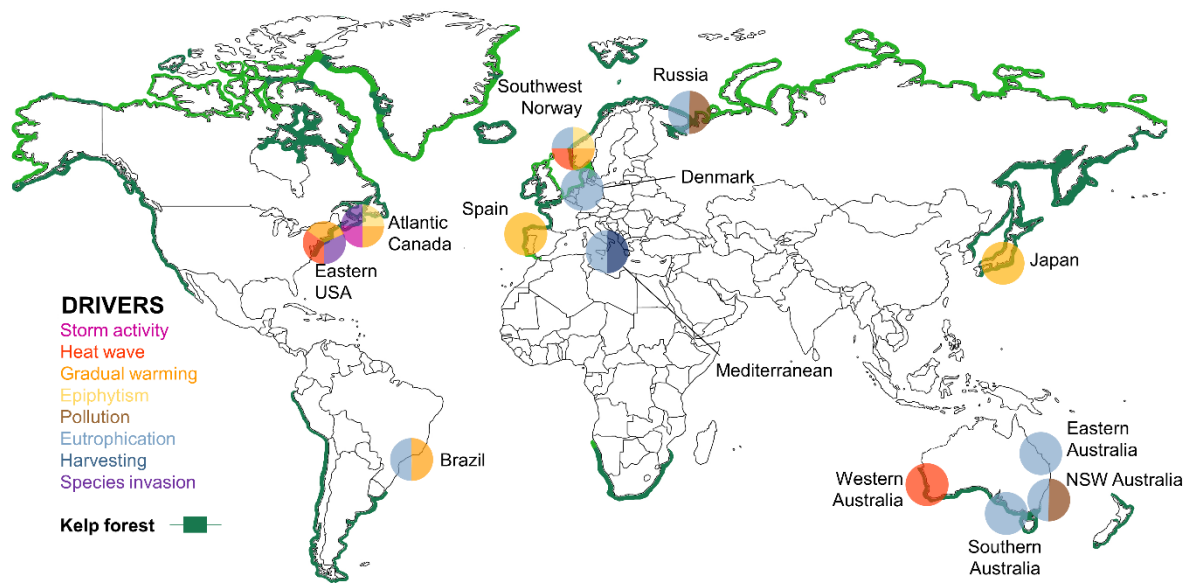
732 **Figures**



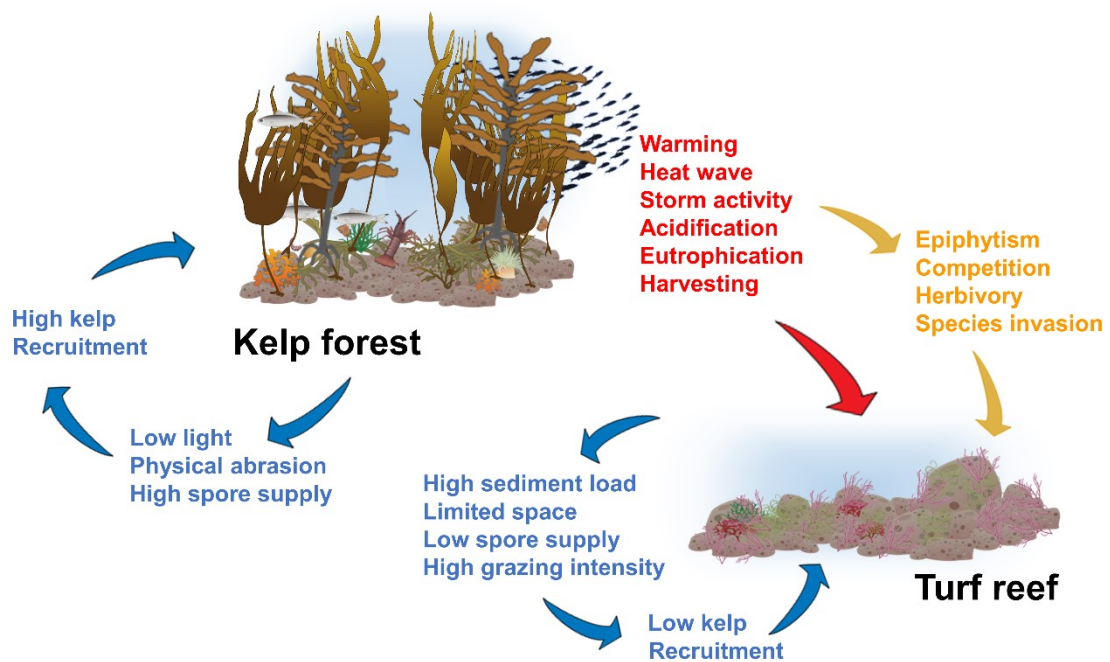
733
734 **Figure 1.** Kelp forests provide many ecological functions and ecosystem services. (a) Kelp
735 forest (*Ecklonia maxima*) in South Africa. (b) Kelp trawler in Norway. (c) Scientific diver
736 undertaking kelp research, Australia. (d) Commercially and recreationally important lobster
737 (*Homarus americanus*) in a kelp forest in Canada. (e) Drift kelp (*Laminaria hyperborea*)
738 accumulation on sand bottom in Arctic Norway. (f) Angler with kelp cod (*Gadus morhua*),
739 United Kingdom. Photographs: Thomas Wernberg (a, c, e), Kåre Foss (b), Karen Filbee-
740 Dexter (d), Whitby Sea Anglers (f).



741
 742 **Figure 2.** Kelp forests have undergone regime shifts from lush, structurally complex forests to
 743 highly simplified, sediment-laden turf reefs. Examples include the disappearance of forests of
 744 *Ecklonia radiata* from Western Australia (top panel), *Saccharina latissima* from southwestern
 745 Norway (middle panel), and *Laminaria digitata* and *S. latissima* from Atlantic Canada (bottom
 746 panel). The photographs show healthy kelp forests (a, d, g), sediment-laden turf reefs (b, e, h)
 747 and biological drivers - (c) tropical herbivores (*Siganus fuscescens*) cropping kelp recruits, (f)
 748 epiphytes smothering kelps and (i) the invasive bryozoan (*Membranipora membranacea*)
 749 encrusting and weakening kelp fronds. Photographs: Thomas Wernberg (a, b, c), Hartvig
 750 Christie (d, e, f), Karen Filbee-Dexter (g), and Robert Scheibling (i, h).



751
 752 **Figure 3.** Global map showing locations of shifts from habitat-forming macroalgae to turfs
 753 (circles) overlaid on the approximate distribution of global kelp forests (green; light green
 754 unknown but inferred from habitat requirements; Filbee-Dexter and Scheibling 2014). Slice
 755 colours of circles indicate different drivers implicated in the shift. See Table 2 for further
 756 details.



757

758 **Figure 4.** Schematic overview of the direct (red) and indirect (orange) drivers and feedbacks
759 (blue) implicated in regime shifts from kelp forests to turf algae globally (Table 2). The arrows
760 indicate the positive effect of these drivers on kelp loss and replacement by turfs, and the
761 positive feedbacks on either the kelp or turf state.