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3 **The role of kelp species as biogenic habitat formers in coastal**
4 **marine ecosystems**

5

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16

17 **ABSTRACT**

18 Kelps are ecologically important primary producers and ecosystem engineers, and play a central role
19 in structuring nearshore temperate habitats. They play an important role in nutrient cycling, energy
20 capture and transfer, and provide biogenic coastal defence. Kelps also provide extensive substrata
21 for colonising organisms, ameliorate conditions for understory assemblages, and provide three-
22 dimensional habitat structure for a vast array of marine plants and animals, including a number of

23 commercially important species. Here, we review and synthesise existing knowledge on the
24 functioning of kelp species as biogenic habitat providers. We examine biodiversity patterns
25 associated with kelp holdfasts, stipes and blades, as well as the wider understorey habitat, and
26 search for generality between kelp species and biogeographic regions. Environmental factors
27 influencing biogenic habitat provision and the structure of associated assemblages are considered,
28 as are current threats to kelp-dominated ecosystems. Despite considerable variability between
29 species and regions, kelps are key habitat-forming species that support elevated levels of
30 biodiversity, diverse and abundant assemblages and facilitate trophic linkages. Enhanced
31 appreciation and better management of kelp forests are vital for ensuring sustainability of ecological
32 goods and services derived from temperate marine ecosystems.

33 **Keywords:** benthic communities, epifauna, epiphyte, facilitation, macroalgae, temperate reefs

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36 1. Introduction

37 Kelps dominate rocky reefs in lower intertidal and shallow subtidal zones throughout temperate and
38 subpolar regions of the world (Fig. 1, Steneck et al., 2002). Kelp forests represent some of the most
39 productive and diverse habitats on Earth (Brady-Campbell et al., 1984; Mann, 1973; Reed et al.,
40 2008) and provide humans with ecosystem services worth billions of dollars annually (Beaumont et
41 al., 2008). Kelps are a major source of primary production in coastal zones (Krumhansl and
42 Scheibling, 2012; Mann, 1973). They promote secondary productivity through provision of three-
43 dimensional habitat structure, which supports a vast array of marine life, including species of
44 commercial and conservation importance (Smale et al., 2013; Steneck et al., 2002). The biogenic
45 habitat structure provided by large canopy-forming seaweeds has been shown to offer protection to
46 several commercial fish species (Bologna and Steneck, 1993), and kelp forests in particular serve as
47 important nursery grounds (Holbrook et al., 1990; Tegner and Dayton, 2000). Kelps are ecosystem
48 engineers (Jones et al., 1994) in the truest sense; they alter the environment and resources available
49 to other organisms, playing a crucial role in the functioning of ecosystems. Specifically, kelp
50 canopies alter light (Connell, 2003a), sedimentation (Connell, 2003b), physical abrasion (Irving and
51 Connell, 2006), flow dynamics (Eckman et al., 1989), substratum availability and condition (Christie
52 et al., 2007) and food quantity and quality (Krumhansl and Scheibling, 2012).

53 Strictly speaking, 'kelp' is a taxonomic distinction that refers to members of the Order Laminariales,
54 although several species of large canopy-forming brown algae that perform similar functions are
55 often referred to as kelp in ecological studies (and will be considered here). While the phylogeny of
56 the Laminariales is complex and still uncertain (Bolton, 2010), significant progress has been made
57 towards unravelling evolutionary pathways and relationships. There are currently 9 accepted
58 families of Laminariales, represented by 59 genera and 147 species (Guiry and Guiry 2015). At
59 present, 84% of all described species are found within the 3 most speciose families (Alariaceae,
60 Laminariaceae, Lessoniaceae) and 63% of all kelp species are found within just 5 genera (*Alaria*,

61 *Laminaria*, *Saccharina*, *Ecklonia*, *Lessonia*). Members of these genera are widely distributed across
62 the temperate regions of their respective hemispheres where they serve as foundation species
63 within rocky reef ecosystems (Fig. 1). Other widespread and ecologically important genera include
64 *Macrocystis*, *Nereocystis* and *Undaria* (Fig. 1).

65 Akin to other benthic foundation species, such as hard corals, seagrasses and massive sponges, kelps
66 support elevated biodiversity by increasing habitat volume, heterogeneity and complexity, and
67 through direct provision of food and shelter (Bruno and Bertness, 2001). A great deal of research
68 globally has unequivocally demonstrated that kelps harbour significant biodiversity, even at the scale
69 of an individual. For example, Christie et al. (2003) found, on average, ~130 species and 8,000
70 individuals on individual *Laminaria hyperborea* sporophytes in Norway. As habitat formers, mature
71 thalli directly provide three distinct micro-habitats: the holdfast, the stipe and the lamina/blade
72 (hereafter referred to as blade, see Fig 2). These biogenic habitats differ considerably in structure
73 (Fig. 2) and, as a result, the diversity and composition of their associated assemblages is also highly
74 variable. In addition to variability within individuals, the structure and quantity of biogenic habitat
75 provided by kelps may vary markedly between populations and species, so that the abundance or
76 identity of kelp species within macroalgal canopies influences the structure and diversity of the
77 entire community (Arnold et al., 2016).

78 As well as direct provision of primary habitat, dense stands of epiphytes may develop on some kelp
79 species, such as on *Laminaria* stipes, to provide a secondary habitat which may be utilised by a rich
80 and abundant invertebrate assemblage (Christie et al., 2003). These invertebrate assemblages
81 comprise highly mobile species and prey species for fish and crustacean predators, thereby providing
82 a direct link between lower and higher trophic levels (Norderhaug et al., 2005). The extent of kelp
83 forest habitat is positively related to the abundance of fisheries resources, perhaps due to an
84 increased abundance of prey items and the protection offered to targeted species, especially
85 juveniles, within the kelp canopy (Bertocci et al., 2015). Previous studies on kelp forest biodiversity

86 and utilisation of kelp-derived habitat by marine flora and fauna have tended to focus on a single
87 species and/or region. Here we synthesize existing knowledge of the ecological functioning of kelps
88 (and kelp-like canopy-forming brown algae) as biogenic habitat providers and examine consistency
89 and variability in patterns of associated biodiversity across species and biogeographic regions. We
90 also present novel information on spatial patterns of diversity in kelp forests, estimate the quantity
91 of biogenic habitat provided by kelps in typical coastal ecosystems, identify threats to habitat
92 provision by kelps and highlight knowledge gaps and priority research areas.

93 **2. Direct provision of biogenic habitat**

94 *2.1. Holdfast assemblages*

95 The holdfast structure, which anchors the thallus to the substratum, is the most complex
96 microhabitat offered by kelps (e.g. Arnold et al., 2016). The vast majority of true kelps share a
97 common 'laminarian' holdfast structure, formed by the growth of individual haptera from the diffuse
98 meristematic tissue at the base of the stipe (Novaczek, 1981; Smith et al., 1996). As the plant ages,
99 additional haptera are laid down in layers, growing outwards and downwards, to form a dense mass,
100 in a broadly conical shape (Smith et al., 1996). The upper and outer portions of the holdfast tend to
101 be formed by large, moderately spaced haptera; while towards the base haptera intertwine to form
102 a complex of fine branches and smaller interstitial spaces (Smith et al., 1996). The holdfast changes
103 little over the life span of the kelp. For large perennial species like *Laminaria hyperborea* this is
104 typically ~10 years (Kain, 1979) and may be considerably longer under optimal conditions (up to 20
105 years old; Sjøtun et al., 1995). Although holdfasts of the majority of kelp species are formed in this
106 way, there is considerable interspecific variation in the size, structure, complexity, openness and
107 longevity of the holdfast habitat (Fig. 3).

108 Within the true kelps the volume of the holdfast habitat provided by mature plants may range from
109 $<100 \text{ cm}^3$ for smaller species such as *Ecklonia radiata* (Smith et al., 1996) and *Undaria pinnatifida*

110 (Raffo et al., 2009) to $>3500 \text{ cm}^3$ for *Macrocystis pyrifera* (Rios et al., 2007). The morphology of the
111 structure is also highly variable, being dependent on the density, thickness, complexity and
112 arrangement of the haptera (Fig. 3). For example, *Macrocystis* and *Nereocystis* tend to form
113 intricate holdfast structures, with many fine intertwining haptera, whereas *Laminaria* tend to grow
114 fewer but thicker haptera, with larger interstitial spaces (Fig. 3). *Lessonia* holdfasts are highly
115 atypical, exhibiting poorly defined haptera and a flattened, massive basal holdfast structure. With
116 regards to important 'false-kelps', the holdfast structure of *Saccorhiza polyschides* (Fig. 3) differs
117 much from the laminarian holdfast structure. It characteristically forms a large, hollow, bulbous
118 structure up to 30cm in diameter, of which the upper surface is covered in small protuberances,
119 while the lower surface attaches to the substratum through small, claw-like haptera (Norton, 1969).
120 The bull kelp *Durvillaea antarctica*, being a furoid, forms a solid, robust structure with little
121 morphological differentiation. With regards to intraspecific variation, holdfast structure can vary
122 markedly between populations subjected to different environmental conditions, particularly in
123 response to gradients in wave exposure or current flow (Sjøtun and Fredriksen, 1995). For example,
124 the biomass and internal volume of holdfasts of mature *Laminaria* plants can more than double
125 along a wave exposure gradient (Smale, Teagle, unpublished data). Thus the majority of studies
126 include some measure of habitat volume (i.e. the volume of space available for colonization by fauna
127 between haptera; hereafter called 'habitable space', as opposed to the total space of the holdfast;
128 hereafter 'holdfast volume'); using either a mathematical approach (Jones, 1971), or displacement
129 (Sheppard et al., 1980). Recent work by Walls et al. (2016) suggests that these methods provide
130 similar results, and can, therefore, be compared across studies using these different techniques.

131 The biogenic habitat provided by kelp holdfasts is generally highly complex, extensive (certainly at
132 the scale of kelp forest, see below) and, for many species, temporally stable. The interstitial space
133 between the hard substratum and the haptera represents favourable habitat for colonising fauna, as
134 the holdfast structure offers protection from predators and adverse environmental conditions,
135 accumulates food sources and increases the area of substrata and volume of habitable space

136 available for colonisation (Ojeda and Santelices, 1984). For some species, such as *L. hyperborea*, the
137 holdfast offers a capacious internal habitable space, relative to the overall size of the structure.
138 Within the context of single kelp plants, the holdfast generally supports the greatest diversity of the
139 three primary habitats, with species richness per holdfast typically reaching 30-70 macrofaunal
140 species, but in some cases reaching up to 90 species (Christie et al., 2003; Jones, 1972; Moore,
141 1972a; Thiel and Vásquez, 2000). Invertebrate abundance can exceed 10,000 individuals per
142 holdfast (Christie et al., 2003; Schaal et al., 2012). Reported values for the richness and abundance
143 of holdfast assemblages vary greatly between species and regions (Table 1). Even so, holdfast
144 structures consistently support high levels of biodiversity (Table 1) and the vast majority of studies
145 conclude that invertebrate richness and abundance is elevated within these structures. For
146 example, work on *Ecklonia radiata* in Australia has yielded study-wide total richness values in excess
147 of 350 taxa inhabiting holdfasts (Anderson et al., 2005; Smith et al., 1996). Although variability
148 between kelp species is high, generally those that form large, laminarian type holdfasts (e.g.
149 *Laminaria hyperborea*, *Ecklonia radiata*) support greatest biodiversity (Table 1).

150 Holdfast assemblages are typically dominated by mobile invertebrates taxa including copepods,
151 polychaetes, gastropods and amphipods, and by sessile fauna such as bryozoans, bivalves and
152 sponges (Anderson et al., 2005; Arroyo et al., 2004; Blight and Thompson, 2008; Christie et al., 2003;
153 Christie et al., 2009; Moore, 1972a; Norderhaug et al., 2002; Ojeda and Santelices, 1984; Rios et al.,
154 2007; Schaal et al., 2012). Amphipods and polychaetes are typically numerically dominant, often
155 representing >75% of total faunal abundance (Smith et al., 1996), although the relative abundance
156 of taxonomic groups is strongly influenced by environmental conditions (Moore, 1973a; Sheppard et
157 al., 1980; Smith and Simpson, 1992). A significant proportion of the holdfast fauna is highly mobile
158 and can quickly colonise new available habitat; exchanges between kelp plants and also from kelp to
159 surrounding habitat are thought to occur frequently (Norderhaug et al., 2002; Waage-Nielsen et al.,
160 2003). The composition of the sessile fauna is largely dependent on the availability of dispersal
161 stages in the overlying water column (Marzinelli, 2012), which influences recruitment rates onto

162 holdfasts, as well as local turbidity and sedimentation rates, as many suspension feeding species are
163 susceptible to smothering (Moore, 1973a). Food supply, principally from detrital kelp and other
164 macroalgae and deposited phytoplankton, is rarely thought to be limiting in most kelp forest
165 habitats (Schaal et al., 2012). Kelp holdfasts (particularly laminarian holdfasts) efficiently trap and
166 accumulate sediment (Arroyo et al., 2004; Moore, 1972b), limiting detritus export in highly
167 hydrodynamic areas (Schaal et al., 2012). Species recorded in holdfasts are generally found
168 elsewhere in the surrounding wider habitat, such as amongst epilithic understory algae, rather than
169 being obligate holdfast inhabitants (Christie et al., 2003; Smith et al., 1996). Perhaps the most
170 remarkable exception to this observation is the terrestrial spider (*Desis marina*), which inhabits bull
171 kelp (*Durvillaea antarctica*) holdfasts found on the extreme low shores of New Zealand (McQueen
172 and McLay, 1983). The specific microhabitat provided by the holdfast structure allows the spider to
173 survive submergence during neap tides for at least 19 days (McQueen and McLay, 1983).

174 A range of trophic guilds are represented within holdfasts, including deposit feeders, filter feeders,
175 grazers, scavengers and predators (McKenzie and Moore, 1981), although organisms that feed on
176 detrital organic matter (i.e. deposit feeders and filter feeders) tend to dominate (Schaal et al., 2012).
177 Larger predators, such as the edible crab *Cancer pagurus* (McKenzie and Moore, 1981) and the spiny
178 lobster *Panulirus interruptus* (Mai and Hovel, 2007), commonly shelter in kelp holdfasts. Recent
179 stable isotope analysis has shed light on kelp holdfasts as micro-scale ecosystems, given that the
180 food web within a holdfast may attain 3.5 trophic levels and involve many complex trophic pathways
181 (Schaal et al., 2012). The overall composition of holdfast assemblages in terms of the relative
182 abundance of higher taxa or trophic groups is, to some extent, predictable and consistent across
183 seasons and biogeographic regions where habitats are relatively unimpacted by human activities
184 (Anderson et al., 2005; Christie et al., 2003; Smith et al., 1996). Assemblage composition is,
185 however, sensitive to local environmental factors and predictable shifts in holdfast assemblages
186 (especially at coarser taxonomic levels) occur in response to increased turbidity (Sheppard et al.,
187 1980), pollution from oil spills (Smith and Simpson, 1998), and sewage outfall effluent (Smith and

188 Simpson, 1992). This has led to feasibility studies on the utility of kelp holdfasts as self-contained
189 units for environmental monitoring (Anderson et al., 2005; Sheppard et al., 1980; Smith and
190 Simpson, 1992).

191 The structural complexity and the size (volume) of the holdfast have been shown to impact the
192 diversity and abundance of associated assemblages (Norderhaug et al., 2007). Habitat complexity
193 has been shown to influence assemblage structure in a number of macrophyte groups (Christie et
194 al., 2009); this trend holds true for kelp holdfasts. Indeed, by experimentally altering the complexity
195 of artificial holdfast mimics, Hauser et al. (2006) found significantly higher abundance and diversity
196 on high complexity mimics in comparison to those of a lower complexity. The increase in the
197 complexity potentially providing greater niche space and increased microhabitat availability to
198 inhabiting fauna (Kovalenko et al., 2012).

199 The size of the holdfast habitat (whether quantified by total volume, biomass or internal habitable
200 space) has long been recognised as an important driver of faunal richness and abundance (Moore,
201 1978; Sheppard et al., 1980). However, the reported relationships between habitat volume and
202 faunal richness and abundance are not consistent, and appear to vary between kelp species, regions
203 and locations (e.g. Walls et al., 2016). While all studies report that the total abundance of holdfast
204 fauna increases with habitat size, some studies have found this relationship only holds for smaller,
205 younger holdfasts and abundance is independent of habitat size in older plants (Anderson et al.,
206 2005; Ojeda and Santelices, 1984). Others have reported a consistent positive relationship between
207 faunal abundance and habitat size throughout the entire size range of the kelp holdfast (Christie et
208 al., 2003; Smith et al., 1996; Tuya et al., 2011). Even so, space availability is clearly an important
209 determinant of faunal density. Patterns of faunal richness are also inconsistent, with some studies
210 reporting positive relationships between richness and habitat size (Smith et al., 1996), some
211 reporting asymptotic trends (Anderson et al., 2005; Ojeda and Santelices, 1984) and others reporting
212 no clear trend at all (Christie et al., 2003). Richness patterns are likely to be dependent on the

213 regional/local species pool, the time available for colonisation, and the complexity of the habitat.
214 Several studies have suggested that successional processes within kelp holdfasts do not involve
215 species replacement but rather an additive progression; this is because species recorded in small
216 holdfasts are also recorded in older, larger ones and are not necessarily replaced by competitively
217 superior species (Ojeda and Santelices, 1984; Smith et al., 1996). This may be related to the fact that
218 the habitat is dynamic and grows throughout succession or that the complexity of the holdfast
219 promotes and maintains niche separation. A major impediment in the search for generality in
220 holdfast assemblage structure and functioning is that the methods used to quantify assemblages
221 have been inconsistent, with many studies considering only mobile or sessile fauna (e.g. Christie et
222 al., 2003; Tuya et al., 2011) and other studies focussing on specific taxonomic groups (e.g. peracarid
223 crustaceans; Thiel and Vásquez, 2000), which makes overarching inferences and generalisations
224 difficult.

225 Several studies have examined interspecific variability in holdfast assemblage structure to determine
226 whether different kelps support different levels of biodiversity. McKenzie and Moore (1981)
227 compared holdfast assemblages associated with *Saccorhiza polyschides* with those of *Laminaria*
228 *hyperborea* in the UK and noted marked differences in faunal composition, richness and abundance.
229 *L. hyperborea* supported far greater diversity and abundance, which was attributed to greater
230 complexity and longevity of the holdfast structure; but *S. polyschides* housed larger animals,
231 including several predatory fish and crustaceans that were typically absent from *L. hyperborea*.
232 Some years later, Tuya et al. (2011) repeated the comparison in northern Portugal, where *L.*
233 *hyperborea* is found at its southern range edge and sporophytes are much smaller, and found no
234 differences in faunal composition or abundance between the two host species despite marked
235 differences in holdfast morphology. As such, biogeographic context – in terms of both the structure
236 of the kelps themselves and the regional/local species pool comprising holdfast assemblages – is
237 clearly important. Recent studies have examined whether, outside its native range, the invasive kelp
238 *Undaria pinnatifida* supports impoverished assemblages compared with native habitat-forming

239 macroalgae (Arnold et al., 2016; Raffo et al., 2009). In Argentina, the larger holdfasts offered by *M.*
240 *pyrifera* support higher faunal richness and abundance than *U. pinnatifida* (Raffo et al., 2009). In the
241 UK the longer-lived holdfasts offered by native perennial kelps support greater richness and biomass
242 of sessile fauna (Arnold et al., 2016). Both studies stated, however, that native kelp species may not
243 be negatively impacted by non-native *U. pinnatifida*, which may occupy a different niche both
244 spatially and temporally, and community-wide responses to invasion are likely to be complex and
245 context-specific. With further reference to intraspecific variability, studies on *Macrocystis pyrifera* in
246 Chile have revealed high levels of variation in holdfast assemblage structure and diversity between
247 kelp populations (Ojeda and Santelices, 1984; Rios et al., 2007). Spatial differences in physical
248 disturbance regimes driven by wave exposure and storm intensity were suggested as the most likely
249 driver of associated biodiversity patterns (see below).

250 2.2. Stipe assemblages

251 In contrast to the holdfast, the stipe is relatively simple in structure but also exhibits significant
252 variability between species and populations. The majority of kelps have a defined stipe; a single rigid
253 structure arising from the apex of the holdfast and supporting the blade in the water column. The
254 structure of the stipe itself, in terms of rugosity, rigidity, tensile strength and whether it is branching,
255 terete, solid or hollow, varies considerably between species. The length of the stipe, and therefore
256 the total area of biogenic habitat available for colonisation, also varies considerably between
257 populations and species. For example, the average stipe length of mature *Laminaria hyperborea*
258 plants may more than double along a steep wave exposure gradient (Smale et al., 2016), although
259 smaller differences in water motion between moderately exposed and sheltered habitats may have
260 minimal effect on the rate of stipe elongation (Kregting et al., 2013). Interspecific variation is
261 considerable, with some kelp species exhibiting stipe lengths in excess of 15 (*Ecklonia maxima*) or
262 even 30 m (*Nereocystis luetkeana*). Several species (e.g. *Nereocystis* spp., *Macrocystis pyrifera*) have
263 evolved gas-filled bladders to assist with flotation and some species (e.g. *M. pyrifera*) develop mid-

264 water fronds to facilitate photosynthesis (Graham et al., 2007). Several ecologically-important
265 species, including *Undaria pinnatifida* and *Saccorhiza polyschides* have flattened stipes (Castric-Fey
266 et al., 1999; Norton, 1969; Norton and Burrows, 1969). Although most kelps produce a single stipe,
267 some species (including *Lessonia nigrescens* and *M. pyrifera*) grow multiple stipes from the same
268 holdfast structure. As such, the physical structure and properties of kelp stipes are likely to have a
269 major influence on the structure and diversity of the associated assemblage.

270 Studies on the invertebrate assemblages associated with the surface of kelp stipes are scarce, with
271 most focus on the assemblage associated with secondary epiphytic algae. However, there is
272 emerging evidence to suggest that some species (e.g. *L. hyperborea*) can support rich and abundant
273 assemblages of sessile invertebrates attached directly to the stipe (Leclerc et al., 2015). Within a
274 kelp forest, the total biomass of filter feeders, particularly demosponges, attached to stipes can be
275 substantial, and represents an important link between trophic levels. With regards to flora,
276 epiphytic algae are common on marine macroalgae (Bartsch et al., 2008). Some are obligate
277 epiphytes (e.g. on *Ecklonia maxima* in South Africa; Anderson et al., 2006), while the majority are
278 facultative, simply occupying free space on the surface of larger macroalgae, as well as being found
279 attached to abiotic substrata (Bartsch et al., 2008). Experimental removals of kelp canopies have
280 resulted in early settlement of common epiphytic species in cleared areas, perhaps suggesting that
281 competition for light with canopy algae limits these facultative species to an epiphytic strategy
282 (Hawkins and Harkin, 1985). Studies utilising artificial macrophyte mimics have shown that
283 epiphytes readily grow on abiotic structures, supporting the assertion that the biotic nature of the
284 macrophyte involved is often insignificant (Cattaneo and Klaff, 1979; Harlin, 1973).

285 The diversity and abundance of epiphytic algae colonising kelp is highly variable. Nearly 80 species
286 of epiphytes (red, green and brown algae) have been recorded on *Laminaria* species in the Sea of
287 Japan (Sukhovveeva, 1975), whereas in the North Sea, 7 and 8 species of epiphytes (predominantly
288 red algae) were recorded on *Laminaria digitata* and *L. hyperborea* respectively (Schultze et al.,

289 1990). *L. hyperborea* stipes in Norway support a diverse, red algae dominated, epiphytic community
290 of up to 40 species (Christie et al., 1998; Sørli, 1994). Whittick (1983), however, found that 95% of
291 epiphyte biomass found on samples of *L. hyperborea* in southeast Scotland comprised just 4 species.
292 The diversity and abundance of epiphytes can also be extremely variable between host species, with
293 significant differences observed between closely related and morphologically similar species. For
294 instance, *L. hyperborea* has been shown to support up to 86 times more epiphytes (by weight) than
295 *Laminaria ochroleuca*, in areas where both species co-exist in mixed stands (Smale et al., 2015). In
296 this case, differences were most likely related to variability in surface texture and, perhaps,
297 production of chemical antifoulants (see Jennings and Steinberg, 1997 for *Ecklonia* example; Smale
298 et al., 2015). The composition of epiphytes often changes vertically along the stipe (Whittick, 1983),
299 and also exhibits pronounced differentiation along abiotic gradients (Bartsch et al., 2008). Epiphyte
300 biomass decreases with depth, due to light attenuation in the water column, often by a factor of ten
301 or more (Allen and Griffiths, 1981; Marshall, 1960; Whittick, 1983). Depth (and associated changes
302 in light levels) also plays a part in structuring epiphyte assemblages, with distinct zonation of
303 different epiphytic algal species along depth gradients (e.g. *Palmaria palmata* and *Phycodrys rubens*
304 on *L. hyperborea*; Whittick, 1983). Under certain conditions, specifically where light levels, water
305 motion (particularly tidally-driven currents) and kelp densities are very high, the kelp sporophytes
306 themselves may be epiphytic on older kelp plants (Velimirov et al., 1977), thereby initiating a
307 complex facilitation cascade (Thomsen et al., 2010).

308 The often extensive secondary habitat provided by epiphytic algae on kelp stipes, has been shown to
309 support a diverse and extremely abundant faunal assemblage (Christie, 1995; Christie et al., 2003).
310 While the holdfast generally supports the most diverse assemblage, the stipe/epiphyte complex
311 usually supports the greatest densities of fauna (Table 1). Christie et al. (2003) recorded in excess of
312 55,000 individual mobile macrofauna per kelp on the stipe of *L. hyperborea* in Norway; but noted
313 that the assemblage associated with the stipe was the most variable, with very low abundances
314 observed on some specimens. These assemblages tend to be dominated by amphipods, gastropods,

315 and other molluscs (Norderhaug et al., 2002). Habitat size is very important for stipe and epiphytic
316 algal associated macrofauna, as it is for holdfast fauna. Larger habitats (i.e. larger biomass of
317 epiphytic algae) have been shown to support a more abundant and diverse assemblage (Norderhaug
318 et al., 2007). It is, once again, also important to consider the complexity of the epiphytic algal
319 material concerned when considering the effect of habitat space, not only considering the algal
320 surface itself, but also the interstitial volume (Christie et al., 2009; Hacker and Steneck, 1990). It has
321 been shown that macrofaunal density on epiphytic red algae is higher on structurally complex
322 species (e.g. *Rhodomela* spp. and *Ptilota gunneri*) than those with simple, smooth surfaces (e.g.
323 *Palmaria palmata*; Christie et al., 2009; also see Schmidt and Scheibling, 2006). Similarly, recent
324 work has shown that the diversity and richness of faunal assemblages is greater on large, roughened
325 epiphytes compared with smooth, simple forms (Norderhaug et al., 2014). This assertion is
326 supported by work with artificial mimics of differing complexity (Christie et al., 2007). It is important
327 to note, however, that while habitat size seems to be of importance in driving the abundance of
328 macrofauna, the patterns do not hold true for meiofauna, suggesting that other processes (e.g.
329 predation by macrofauna) may be playing a role in controlling their abundance (Norderhaug et al.,
330 2007), and that meiofauna may be more closely associated with holdfasts than epiphytes (Arroyo et
331 al., 2004).

332 2.3. Blade assemblages

333 The blade, or lamina, provides a large surface area for photosynthesis and also for colonisation by a
334 range of epibionts. Although the blade has the lowest structural complexity of the primary
335 microhabitats, inter and intraspecific variability in morphology is still evident (Arnold et al., 2016;
336 Włodarska-Kowalczyk et al., 2009). Blade structures vary in thickness, rigidity, surface texture, edge
337 formations, presence of a mid-rib, and the number and arrangement of divisions; all of which can
338 differ between species and populations and will have some influence on the settlement, growth and
339 survivorship of epiflora and epifauna.

340 The blade generally supports the lowest diversity of epibionts of the primary habitats (Włodarska-
341 Kowalczyk et al., 2009), although competitively inferior species may persist here due to intense
342 competition for space in other areas (i.e. the stipe; Seed and Harris, 1980). The blade of healthy kelp
343 plants typically support a low coverage of epiphytic algae, which would likely compete for light and
344 nutrients to the detriment of the host alga. However, heavy epiphytic loading on kelps has been
345 observed under stressful conditions, such as periods of intense warming or low light and high
346 nutrients (Andersen et al., 2011; Moy and Christie, 2012; Smale and Wernberg, 2012), and, in
347 perennial species, as the old blade senesces at the end of the growing season (e.g. Andersen et al.,
348 2011). Moreover, kelps with short annual life-cycles (e.g. *Undaria pinnatifida* and *Saccorhiza*
349 *polyschides*) often support dense epiphytic assemblages during the senescent period of the
350 sporophyte stage (e.g. Norton and Burrows, 1969).

351 The low faunal diversity characteristic of kelp blades may be due, in part, to the inherent flexibility
352 and instability of the substratum (Bartsch et al., 2008). However, in certain conditions, epifaunal
353 abundance and spatial cover can be high (Saunders and Metaxas, 2008). The bryozoan
354 *Membranipora membranacea* has been noted to be one of the few, often the only, species of sessile
355 fauna associated with the blade of *Laminaria* species (Seed and Harris, 1980). This is probably due
356 to the growth plan of this species, which develops non-calcified bands of zooids thought to prevent
357 cracking of colonies on a flexible substratum (Ryland and Hayward, 1977). *M. membranacea* is now
358 a common invasive species in the northwest Atlantic, thought to be introduced from Europe via ship
359 ballast water (Lambert et al., 1992). Survival of native northwest Atlantic kelp has been shown to be
360 lower in the presence of invasive *M. membranacea* (Levin et al., 2002), making plants more
361 susceptible to defoliation during intense wave action by making the blade of affected species brittle
362 (Dixon et al., 1981; Lambert et al., 1992; Saunders and Metaxas, 2008; Scheibling et al., 1999). It
363 should be noted, however, that in other settings extensive growth of sessile epiphytic fauna
364 (including *M. membranacea*) have been shown to have no negative impact on the growth of kelps
365 (Hepburn and Hurd, 2005). There is evidence that growth rates increase in heavily colonised fronds

366 during periods of low inorganic nitrogen concentrations in seawater, potentially due to the provision
367 of ammonium excreted by sessile fauna (e.g. hydroids on *Macrocystis pyrifera*; Hepburn and Hurd,
368 2005). Recent work on four kelp species by Arnold et al. (2016) reported a maximum of just five or
369 six sessile invertebrate species attached to kelp blades, which were predominantly bryozoans. Other
370 work conducted at larger scales have, however, reported considerably higher richness values
371 (Włodarska-Kowalczyk et al., 2009). Clearly, richness of blade epifauna varies considerably between
372 host species and location (Table 1).

373 Larger mobile organisms can also be locally abundant on blade surfaces, some of which have a very
374 high affinity to kelp species. For example, the blue-rayed limpet, *Patella pellucida* (previously
375 *Helcion pellucidum*), is a common and locally abundant grazer found on *Laminaria* spp., where it
376 feeds predominantly on the kelp tissue (Christie et al., 2003; Vahl, 1971). Similarly, the gastropod
377 *Lacuna vincta* can colonise laminae in high densities (Johnson and Mann, 1986) and, although the
378 direct impacts of grazing may be relatively minor and spatially restricted across the blade surface,
379 the indirect effects of tissue weakening may promote defoliation of kelp canopies during intense
380 storms (Krumhansl and Scheibling, 2011b). Other conspicuous and ecologically important
381 macroinvertebrates include the sea urchin *Holopneustes* spp. found within *E. radiata* canopies
382 (Steinberg, 1995) and the turban snails *Tegula* spp., which inhabit *M. pyrifera* fronds (Watanabe,
383 1984). More generally, the mid-water fronds and surface canopies of the giant kelp *M. pyrifera* can
384 form mini-ecosystems that support high abundances of invertebrates and fish (see Graham et al.,
385 2007 and references therein).

386 Crucially, many invertebrates associated with kelp thalli maintain their association with the host
387 plant even if it becomes detached from the substratum. Detached kelp may be transported great
388 distances from source populations and, as a result, aid the dispersal of fauna that remains affiliated
389 and viable. Positively buoyant kelps, such as *M. pyrifera* and *Durvillaea antarctica*, form kelp rafts
390 which can drift many hundreds of km, facilitating the dispersal of associated invertebrate

391 assemblages (Fraser et al., 2011; Hobday, 2000; Ingólfsson, 1995). Such rafts are particularly
392 numerous in the Southern Ocean (Smith, 2002) and may have played an important role in species
393 dispersal and colonisation of novel habitats over both ecological and evolutionary timescales (Fraser
394 et al., 2011). Rafting may also be an effective means of long-range dispersal for positively buoyant
395 species of invasive algae (e.g. *Sargassum muticum*; Kraan, 2008; Rueness, 1989).

396 2.4. Habitat preference of kelp fauna

397 Although most species of kelp associated fauna are found in more than one micro-habitat (e.g. stipe
398 and holdfast), there is some evidence of habitat 'preference' among a number of taxa. A study of *L.*
399 *hyperborea* along an extensive stretch of the Norwegian coastline found no species associated solely
400 with the blade, but that around 70 species were exclusively associated with either the holdfast or
401 the epiphytes on the stipe (Christie et al., 2003). This pattern has also been shown in other studies
402 of *L. hyperborea* (Norton et al., 1977; Schultze et al., 1990). It is important to note that these
403 patterns are consistent in highly mobile groups that have the means to move throughout the entire
404 plant (Christie et al., 2003). Dispersal beyond a single plant has, however, been documented with
405 both holdfast and stipe epiphyte associated species (Jorgensen and Christie, 2003). Jorgensen and
406 Christie (2003) found, using artificial substrata, that holdfast related species tended to disperse close
407 to the seabed, but that stipe epiphyte associated fauna travelled throughout the kelp forest as a
408 whole, and even above the canopy layer. Some of these very mobile fauna (e.g. amphipods and
409 isopods) have been shown to actively emigrate from kelp forest systems in relatively high numbers
410 (1 - 2% total biomass daily; Jorgensen and Christie, 2003), and kelp associated fauna represent a
411 large source of food for adjacent systems (Bartsch et al., 2008). Thus kelp forests can be considered
412 ecologically important near shore export centres (Bartsch et al., 2008).

413 While the majority of mobile kelp associated fauna can be found on other macroalgae, a number of
414 species may be considered 'kelp specialists'. For instance, the limpets *Cymbula compressa* and
415 *Patella pellucida* are found almost exclusively on kelps (*C. compressa* on *E. radiata* in South Africa;

416 Anderson et al., 2006; and *P. pellucida* on laminarian kelps in the northeast Atlantic; Marques de
417 Silva et al., 2006). Although *P. pellucida* spat settle on crustose algae and later migrate to
418 macroalgae, including *Mastocarpus stellatus* (McGrath, 2001), those individuals found on *Laminaria*
419 *spp.* have been shown to have higher growth rates than those found elsewhere (McGrath, 1992).

420 2.5. The quantity of biogenic habitat provided by kelps

421 Kelp species are widespread throughout temperate and subpolar regions, where they provide vast,
422 complex habitat for a myriad of other organisms. Although estimating the actual standing stock of
423 kelps is problematic and subject to some uncertainty, it is possible to use a combination of high-
424 resolution fine scale sampling techniques and larger-scale survey approaches to generate useful
425 approximations of kelp distribution and biomass. For example, the estimated standing biomass of
426 *Laminaria spp.* along the northwest coastline of Europe is in excess of 20 million tonnes (wet weight,
427 Burrows et al., 2014; Werner and Kraan, 2004). The biomass and volume of habitat provided by
428 kelps varies considerably between species, sites and regions, and is strongly influenced by
429 environmental factors including wave exposure, light availability and substratum characteristics
430 (Smale et al., 2016). Even so, it is possible to use existing data on kelp populations to illustrate the
431 quantity of biogenic habitat provided on representative kelp-dominated rocky reefs. At a relatively
432 wave sheltered site in Plymouth Sound (Firestone Bay), subtidal rocky reefs support a mixed kelp
433 bed comprising *Laminaria ochroleuca*, *Saccharina latissima*, *Undaria pinnatifida* and *Saccorhiza*
434 *polyschides* (Arnold et al. 2016). While the total biomass, internal holdfast volume and surface area
435 (annual means) provided varies considerably between species, the total kelp canopy generates
436 significant biogenic habitat (Table 2). Within a typical 1 m² area of rocky substrata, kelps supply an
437 average (wet weight) biomass of >2.5 kg, holdfast habitable space of ~380 ml and a surface area
438 available for colonisation of >4 m² (Table 2). To contextualise, the total biomass and surface area of
439 biogenic habitat provided by kelps exceeds most reported values for mature seagrass meadows (~95

440 g dry weight m^2 and $\sim 3.7 m^2$ respectively; Duarte and Sand-Jensen, 1990; Larkum et al., 1984;
441 McKenzie, 1994).

442 At the more wave exposed site, which is dominated by *Laminaria hyperborea* but also supports
443 populations of *L. ochroleuca*, *S. latissima* and *S. polyschides* (Smale et al., 2015), the quantity of
444 biogenic habitat provided by kelps is even greater, particularly with regards to total biomass and
445 internal holdfast habitable space (Table 2). Due to the much larger holdfasts, the internal habitable
446 space generated ($>1.7 L m^{-2}$) is almost 5 times that of the wave-sheltered site, and represents sizable
447 high-quality protective habitat. For both examples, when values are scaled-up to the site level
448 (which is prone to error but still a valuable 'best guess' approach), it is clear that kelps yield
449 substantial biogenic habitat (Table 2) and that deforestation of such reefs (see 5. Threats to biogenic
450 habitat provided by kelps) would result in significant loss of three-dimensional structure and habitat
451 complexity, as has been observed in kelp forests in many regions in response to contemporary
452 stressors (Ling et al., 2009; Moy and Christie, 2012; Wernberg et al., 2013).

453 **3. Physical and biological regulation of habitat provision**

454 *3.1. Physical regulation*

455 Hydrodynamic forces (i.e. wave action and currents) have long been recognised to influence the
456 structure of marine communities (Ballantine, 1961; Brattström, 1968; Knights et al., 2012). With
457 regards to macroalgae-associated assemblages, wave action represents a physical disturbance, and
458 can result in considerable loss of fauna due to dislodgement and mortality (Fenwick, 1976; Fincham,
459 1974). Such disturbance may, however, increase overall diversity of the community by preventing
460 superior competitors from outcompeting other, less competitive, species and by creating a mosaic of
461 habitats at different stages of succession (Connell, 1978). The intermediate disturbance hypothesis
462 (Connell, 1978) would suggest that moderately exposed sites would harbour the highest diversity of
463 flora and fauna (Dial and Roughgarden, 1998), a prediction supported by experimental work in some

464 areas (e.g. England et al., 2008; Norderhaug et al., 2014). Hydrodynamics also influence the
465 availability of food and rates of sedimentation, which can influence biotic assemblages by limiting
466 access to food, or through the smothering of some filter feeding fauna (Moore, 1973a).

467 Wave exposure can also have an effect on the kelps themselves, and therefore a subsequent indirect
468 effect on associated communities. A number of kelp species have been shown to exhibit changes in
469 morphology in response to changes in wave exposure (Fowler-Walker et al., 2006; Molloy and
470 Bolton, 1996; Wernberg and Thomsen, 2005). Adaptations to exposed environments can result in an
471 increase in holdfast size and volume (Sjøtun and Fredriksen, 1995, Smale, Teagle, unpublished data),
472 increased stipe length (Smale et al., 2016) and thickness (Klinger and De Wreede, 1988), and
473 increased blade thickness (Kregting et al., 2016; Molloy and Bolton, 1996). Such strength-increasing
474 adaptations may reduce the probability of dislodgement, or other damage caused by wave action
475 (Wernberg and Thomsen, 2005). An increase in overall thallus size is also a common adaptation to
476 increased wave exposure in kelps (Klinger and De Wreede, 1988; Pedersen et al., 2012; Wernberg
477 and Thomsen, 2005; Wernberg and Vanderklift, 2010); 'going with the flow' with a long, flexible
478 thallus reduces hydrodynamic forces (Denny et al., 1998; Denny and Hale, 2003; Friedland and
479 Denny, 1995; Koehl, 1999). Some species, however, also exhibit an increase in overall thallus size in
480 very sheltered conditions (e.g. *Laminaria hyperborea*; Sjøtun and Fredriksen, 1995; and *L. digitata*;
481 Sundene, 1961). Faunal abundances generally increase with increasing habitat size (Norderhaug et
482 al., 2007); thus a relationship exists between local hydrodynamic conditions, and the diversity of
483 communities found in association with kelps (Anderson et al., 2005; Christie et al., 1998; Christie et
484 al., 2003; Norderhaug and Christie, 2011; Norderhaug et al., 2012; Norderhaug et al., 2007;
485 Norderhaug et al., 2014; Schultze et al., 1990; Walls et al., 2016). Water movement can dislodge
486 epiphytic algae, but also increases algal growth by transporting nutrients over algal surfaces
487 (Norderhaug et al., 2014). The abundance of kelp-associated assemblages depends on both the
488 amount of habitat provided by the algae (Norderhaug et al., 2007) and on algal morphology (Christie
489 et al., 2007). Christie et al. (2003) found that the volume of epiphytic algae on the stipe of *L.*

490 *hyperborea* increased by a factor of 35, and the number of algal species increased by a factor of 1.7,
491 in response to increasing wave exposure. The abundance of associated fauna increased by a factor
492 100 (Christie et al., 2003). It is important to note, however, that most studies conducted along wave
493 exposure gradients have not sampled 'extremely' exposed sites (e.g. remote offshore islands which
494 are rarely visited due to logistical constraints) and under such conditions the morphology of kelp
495 sporophytes and the composition and density of the kelp canopy will be distinct (e.g. Rockall, see
496 Holland and Gardiner, 1975).

497 At high latitudes physical disturbance by ice-scour can limit the distribution of some species of kelp,
498 reducing available biogenic habitat significantly. For example, *Durvillaea antarctica* is absent from
499 severely ice-scoured areas around the Antarctic and sub-Antarctic islands (Fraser et al., 2009; Pugh
500 and Davenport, 1997). *Macrocystis pyrifera*, however, will persist in such areas as its holdfast can
501 anchor below the maximum keel depth of ice-bergs (Pugh and Davenport, 1997).

502 Increased temperature and decreased nutrients (e.g. during El Niño events) can also reduce the
503 quality or quantity of habitat provided by kelps by increasing mortality and reducing recruitment of
504 kelps (Edwards and Hernández-Carmona, 2005), and reducing growth rates (Dean and Jacobsen,
505 1986). Recent work from Norway has highlighted how increased temperature and nutrient levels
506 may interact to influence host kelp species and their associated communities, reducing overall
507 benthic diversity (Norderhaug et al., 2015).

508 Alongside temperature and nutrient availability, light defines where kelps, and in turn their
509 associated assemblages, can develop (Steneck and Johnson, 2013). Kelps are constrained to shallow,
510 well-illuminated coastal areas; in areas lacking herbivores or other disturbance, kelp densities and
511 thallus size decline rapidly with depth (Steneck et al., 2002). High levels of turbidity reduce the
512 amount of light that can penetrate the water column, thus restricting the photic zone and therefore
513 the habitable area for kelps (Steneck et al., 2002; Vadas and Steneck, 1988). As such, levels of light
514 (whether as a function of latitude, depth or water clarity) can control the amount of habitat

515 provided by kelps. Singularly, turbidity can also impact on kelp associated assemblages, reducing
516 diversity by to the increased dominance of few species in turbid waters (e.g. Moore, 1978), or
517 through the increased provision of particulate organic matter as a food source (Moore, 1972b).

518 3. 2. *Biological regulation*

519 The longevity of individual kelp plants can have an effect on the faunal assemblages associated with
520 them. Age has been shown to have significant impacts on the epiphytes growing on the stipe of
521 *Laminaria hyperborea* (Whittick, 1983), and the diversity and abundance of epiphytes has been
522 shown to increase with the age of the host (Christie et al., 1994); a pattern also shown in other
523 species (e.g. *Saccharina latissima*; Russell, 1983). Epiphytes are often confined to the older, more
524 rugose, basal parts of the stipe (Whittick, 1983), and the distal, older parts of the blade (Bartsch et
525 al., 2008; Christie et al., 2003; Norton et al., 1977). The holdfasts of *L. hyperborea*, however, have
526 been shown to reach maximal diversity at around six years old, despite the plant persisting for up to
527 15 years, potentially due to reduced habitable space within the holdfast as encrusting fauna increase
528 in size and coverage (Anderson et al., 2005), or to the more accessible nature of larger holdfasts to
529 predators (Christie et al., 1998). Age structure of entire kelp populations can be affected by local
530 environmental conditions, particularly wave exposure. Studies of *Laminaria setchellii* (Klinger and
531 De Wreede, 1988) and *L. hyperborea* (Kain, 1971, 1976) have documented a higher proportion of
532 younger plants at more exposed sites, suggesting a higher mortality of plants in these areas. Thus
533 the influences of wave exposure, kelp size, and kelp age are intrinsically linked and highly dependent
534 on both the species and the local conditions involved.

535 A major factor limiting the abundance and diversity of the assemblages associated with kelps,
536 particularly the blade microhabitat, is the longevity of the substrata. While the stipe (excluding the
537 epiphytes) and holdfast structures persist for the life span of the kelp (in excess of 15 years for some
538 species), the blade is a more ephemeral structure and in many species is replaced annually, which
539 can limit the persistence and accumulation of species (Christie et al., 2003; Norton et al., 1977). For

540 kelp species with blades that persist for multiple years, the age of the substratum may influence the
541 diversity and structure of the associated epibiotic assemblage (Carlsen et al., 2007). Carlsen et al.
542 (2007) found that the number of epifaunal species found on the blade of *Laminaria digitata* and
543 *Saccharina latissima* in Svalbard was negatively correlated with increasing age, possibly due to a
544 reduction of substrate (blade) surface area, increased physical stress at the distal tips, and increased
545 tissue decay with age.

546 While assemblages associated with the holdfast seem to be relatively stable throughout the year,
547 stipe epiphytes are prone to a high degree of variability between seasons (Christie et al., 2003). The
548 biomass of epiphytic algae tends to decline in the winter, reducing available habitat (Whittick, 1983)
549 and therefore faunal diversity and abundance (Christie et al., 2003). Christie et al. (2003), however,
550 found no reduction in the volume of epiphytic algae growing on *Laminaria hyperborea* in winter,
551 instead suggesting that other factors may also be responsible for the observed reduction in the
552 abundance of faunal assemblages (e.g. reduced habitat complexity, greater predation pressure,
553 increased exposure to winter storm events, and emigration; Christie et al., 2003; Christie and
554 Kraufvelin, 2004). Increases in the abundance of holdfast fauna have also been observed in winter
555 months, suggesting that stipe/epiphytic algae associated species may migrate down to the holdfast
556 during the winter (Christie et al., 2003); holdfasts represent a year round stable habitat and a source
557 of food (i.e. through retention of sediment; Moore, 1972b). Faunal species in epiphyte-associated
558 assemblages generally have higher dispersal rates than those found within the holdfast (Norderhaug
559 et al., 2002), perhaps partly in response to this annual cycle. Epibiotic assemblages associated with
560 kelp blades also exhibit seasonality as they are strongly influenced by processes occurring in the
561 overlying water column, such as seasonal variability in phytoplankton production and related
562 patterns of invertebrate larvae density (Carlsen et al., 2007).

563 While patterns in the abundance, diversity and structure of faunal assemblages inhabiting kelps can
564 vary at small scales, similarities can be seen at much larger spatial scales. Comparisons between

565 studies carried out in the northeast Atlantic show that the species utilising kelps as habitat in this
566 area are relatively consistent (Blight and Thompson, 2008; Christie et al., 2003; Jones, 1971; Moore,
567 1973a, b; Schultze et al., 1990). Similarly, Anderson et al. (2005) examined assemblages in *Ecklonia*
568 *radiata* holdfasts in New Zealand and reported high levels of consistency in structure and diversity at
569 large spatial scales. At coarser taxonomic levels, and global scales, Smith et al. (1996) commented
570 that the dominant faunal groups found within *E. radiata* in Australia were comparable to those
571 inhabiting *Laminaria hyperborea* holdfasts in the UK. Conversely, early work on *Macrocystis pyrifera*
572 in the eastern Pacific reported pronounced large-scale variability in holdfast assemblage structure,
573 which was attributed to biogeographic differences in faunistic composition (Ojeda and Santelices,
574 1984; Santelices, 1980). Similarly, holdfast assemblages in the high Arctic are impoverished and
575 distinct from those at lower latitudes, most likely due to a smaller species pool arising from
576 ecological and evolutionary processes (Włodarska-Kowalczyk et al., 2009).

577 While kelp detritus is an important source of carbon and nitrogen for both subtidal (Fielding and
578 Davis, 1989; Mann, 1988) and intertidal consumers (Bustamante and Branch, 1996; Krumhansl and
579 Scheibling, 2012), the majority of fauna inhabiting kelps do not directly feed on fresh kelp material,
580 due in part to their high C:N ratios (Norderhaug et al., 2003; Schaal et al., 2010) and the presence of
581 anti-herbivory compounds in their tissues (Bustamante and Branch, 1996; Duggins and Eckman,
582 1997; Norderhaug et al., 2003). There is evidence that palatability, and thus the susceptibility to
583 grazing, of kelp differs between species, which may be related to the phlorotannin concentration of
584 the tissue, but also to tissue toughness, the area of the kelp concerned and overall nutritive values
585 (Dubois and Iken, 2012; Macaya et al., 2005; Norderhaug et al., 2006). Nevertheless, a number of
586 species do feed directly on fresh kelp material. The blue-rayed limpet, *Patella pellucida*, for
587 example, is commonly found on laminarian kelps (McGrath, 1997, 2001) and it is known for those
588 that are to feed exclusively on kelp tissue (Vahl, 1971). Two forms of the species exist; the annual
589 *pellucida* form is found solely on the blade, while the *laevis* form migrates downwards where it
590 grazes the stipe, and excavates the base of the stipe within the holdfast where it can persist for 2

591 years (Graham and Fretter, 1947; McGrath and Foley, 2005). As such, this species may cause
592 considerable mortality of host kelps due to the weakening of the holdfast (Kain and Svendsen, 1969).
593 Grazing by larger invertebrate herbivores (e.g. sea urchins) can reduce the amount of biogenic
594 habitat available to the wider community by over-grazing kelp sporophytes and in extreme instances
595 can cause phase shifts from structurally and biologically complex and diverse habitats to
596 depauperate “barrens” (Filbee-Dexter and Scheibling, 2014; Johnson et al., 2011; Ling et al., 2015;
597 Steneck et al., 2002).

598 Competition for suitable hard substratum, light and nutrients can also influence biogenic habitat
599 provision by kelps. Shading by neighbouring canopy-forming macroalgae and epibionts can restrict
600 light availability, while dense epibiont assemblages can limit the exchange of nutrients and/or gases
601 by blocking the surface of thallus cells (Wahl et al., 2015), potentially reducing growth rates, altering
602 morphology and, in extreme cases, leading to mortality.

603 **4. Understorey assemblages and wider biodiversity**

604 At spatial scales greater than a single kelp, multiple individuals form extensive canopies that provide
605 three-dimensional habitat for a vast array of larger marine organisms (Smale et al., 2013), a number
606 of which are of ecological (e.g. sea urchins; Kitching and Thain, 1983) or economical (e.g. the
607 European Lobster; Johnson and Hart, 2001) importance. Kelp forests have long been recognised to
608 be important in regards to a number of fish species, which utilise them as nursery and feeding areas,
609 and as refugia from predators (Bodkin, 1988; Norderhaug et al., 2005; Reisewitz et al., 2006).

610 Elevated abundances of fish species consequently attracts larger piscivores, such as seabirds and sea
611 otters, whose distribution may be closely linked to kelp forests (Estes et al., 2004; Graham, 2004;
612 Steneck et al., 2002). Stable isotope analysis has shown that a number of species of seabird derive a
613 high proportion of their carbon from local kelps (e.g. the great cormorant and the eider duck;
614 Fredriksen, 2003).

615 The kelp canopy ameliorates conditions for the development of diverse epilithic, understorey algal
616 assemblage (Maggs, 1986; Norton et al., 1977), which provides habitat for an array of invertebrate
617 fauna. Understorey assemblages are generally dominated by red algae, with commonly over 40
618 species present (Clark et al., 2004; Flukes et al., 2014; Maggs, 1986). For example, recent
619 biodiversity surveys within kelp forests in the UK and Australia have recorded between 40 and 108
620 species of understorey macroalgae with richness values generally in the order of 50-60 species (Fig.
621 4). Spatial variability in the richness of understorey algal assemblages is likely to be influenced by
622 both local (e.g. wave exposure, turbidity) and regional (e.g. available species pool) processes (Fig. 4).
623 It is clear, however, that understorey assemblages are generally species-rich (Dayton, 1985). They
624 have been shown to be more diverse than comparable assemblages on reefs lacking a canopy
625 (Melville and Connell, 2001; Watt and Scrosati, 2013), most likely because canopies increase habitat
626 heterogeneity and ameliorate environmental conditions.

627 The influence of canopy-forming macroalgae on understorey assemblages has been examined
628 through both monitoring natural occurrences of canopy removal or thinning (e.g. by grazing; Bulleri
629 and Benedetti-Cecchi, 2006; Ling, 2008; or localised warming events; Smale and Wernberg, 2013;
630 storms; Thomsen et al., 2004; Wernberg et al., 2013), and experimentally by *in situ* removal
631 experiments (Clark et al., 2004; Flukes et al., 2014; Hawkins and Harkin, 1985; Melville and Connell,
632 2001; Reed and Foster, 1984; Toohey et al., 2007). The structure, abundance and diversity of
633 understorey assemblages is regulated by shading (Arkema et al., 2009; Foster, 1982; Kennelly, 1987;
634 Reed and Foster, 1984) and alterations to water flow caused by the canopy (Eckman, 1983), as well
635 as physical disturbance caused by the kelps themselves (i.e. thallus scour, particularly by those
636 species lacking an erect stipe, e.g. *Ecklonia radiata*; Irving and Connell, 2006). The majority of algal
637 species commonly found beneath kelp canopies are tolerant of low light conditions, and often occur
638 below the depth limits of the kelps themselves (Norton et al., 1977). Culture experiments have
639 shown that a number of typical understorey algae grow more rapidly and successfully at lower

640 irradiances (Boney and Corner, 1963; Norton et al., 1977), and suffer mortality at higher irradiances
641 (see Jones and Dent, 1971 and references therein).

642 Changes in hydrodynamics caused by macroalgae and seagrass canopies may alter the supply and
643 dispersal of algal propagules and invertebrate larvae, thereby affecting settlement processes
644 (Eckman, 1983; Eckman et al., 1989). With respect to adult life stages, alterations to water flow can
645 influence feeding activities, and therefore the growth and survival, of filter feeding invertebrates
646 (Knights et al., 2012; Leichter and Witman, 1997) and increased sedimentation has been shown to
647 have a negative impact on the recruitment and survival of sessile invertebrates (Airoldi, 2003; Irving
648 and Connell, 2002). Moreover, physical disturbance caused by the scouring of the seabed by kelp
649 thalli has been shown to have negative effects on the abundance of some morphological (i.e. erect)
650 forms of understory algae (Irving and Connell, 2006).

651 Habitat-forming kelps may also interact with habitat-forming sessile invertebrates, with spatial and
652 temporal variability in their relative abundances influencing the wider community. An interesting
653 example is the sea palm *Postelsia palmaeformis*, an annual kelp which occurs in patches within
654 mussel beds (*Mytilus californianus*) along wave-exposed coastlines of the northeast Pacific
655 (Blanchette, 1996; Dayton, 1973). *P. palmaeformis* has limited dispersal potential and is
656 competitively inferior to *M. californianus*, but can rapidly colonise areas of reef following
657 disturbance to mussel beds (Blanchette, 1996). Moreover, recruitment of *P. palmaeformis*
658 sporophytes onto *M. californianus* individuals increases the probability of their dislodgement during
659 winter storms, which subsequently frees up space on the reef for further *P. palmaeformis*
660 colonisation (Dayton, 1973). As such, the interaction between these species and their environment
661 (i.e. storm disturbance) shapes the wider habitat and influences community structure.

662 All of the governing factors are context dependent and differ between kelp species, reef topography,
663 and local hydrodynamic conditions (e.g. Harrold et al., 1988). For instance, while all kelp canopies
664 regulate the amount of light reaching the seabed, the degree of shading is dependent on the

665 morphological structure of the species. The rigid stipe and relatively small blade of *Laminaria*
666 *hyperborea* can reduce sub-canopy light levels to as little as 10% of surface irradiance in the summer
667 (Norton et al., 1977; Pedersen et al., 2014). The buoyant, extensive fronds of *Macrocystis pyrifera*,
668 however, can reduce light levels to <1% of surface levels (Reed and Foster, 1984). Indeed, within
669 Californian *M. pyrifera* systems the abundance of understory algae beneath the canopy may be
670 light-limited (Foster, 1982; Rosenthal et al., 1974), so that removal of the canopy can lead to
671 increases in both abundance and richness of understory assemblages (Kimura and Foster, 1984;
672 Reed and Foster, 1984). In Chile, however, similar canopy removal experiments deliver a
673 comparatively muted ecological response (Santelices and Ojeda, 1984).

674 Unlike in *M. pyrifera* dominated systems, sessile invertebrates are conspicuously absent from the
675 understory assemblages in temperate Australia (Fowler-Walker and Connell, 2002). It appears that
676 the negative impacts of the constant sweeping of the seabed by the dominant canopy forming kelp,
677 *Ecklonia radiata*, outweighs the positive effects of the canopy, and act to exclude sessile
678 invertebrates (Connell, 2003b). Thus the morphological differences between *M. pyrifera* (large,
679 buoyant species) and *E. radiata* (small, sweeping species) act to provide conditions suitable for vastly
680 different understory assemblages. Within a single species of kelp, wider environmental conditions
681 will also lead to differences in the morphology of individual kelps, and to the population structure of
682 localised forests, and therefore to a difference in conditions experienced by understory species.

683 The age structure of *L. hyperborea* has been shown to be different in more exposed conditions, with
684 generally younger individuals due to the high mortality of larger plants (Kain, 1971, 1976). Young *L.*
685 *hyperborea* plants have a shorter, more flexible stipe, potentially resulting (particularly with the high
686 degree of wave action associated with more exposed locations) more physical disturbance of the
687 seabed, in comparison to older, larger plants (Leclerc et al., 2015). This, again, highlights the
688 importance of context in the study of understory assemblages (see Santelices and Ojeda, 1984).

689 The majority of experimental manipulations of understory assemblages are concerned with a
690 monospecific canopy, and studies on diverse algal canopies are comparatively scarce. Diverse
691 macroalgae canopies may promote greater biodiversity in understory assemblages than
692 monospecific canopies (Smale et al., 2010) due to the enhanced habitat heterogeneity and niche
693 diversification found under mixed canopies (Clark et al., 2004; Smale et al., 2013). The reef itself
694 also plays a role in regulating understories, by altering the structure of the forest canopy (Toohey et
695 al., 2007). Topographically complex reefs have a higher irradiance and greater water motion than
696 simple, flat reefs, and are therefore less likely to impact the degree to which the seabed is shaded by
697 the canopy (Toohey and Kendrick, 2008). Thus, such reef communities are complex, and should be
698 taken into account both in future work on these systems, and in future management decisions
699 (Leclerc et al., 2015).

700 Removal or thinning of kelp forest canopies cannot only serve to alter the structure of understory
701 assemblages, but such disturbances can also provide opportunity for the recruitment and growth of
702 non-native species (Valentine and Johnson, 2003), potentially with detrimental effects on the
703 diversity and habitat structure of these systems (Bax et al., 2001). It has been shown that
704 disturbance to native algal assemblages is required for the colonisation of non-native species such as
705 *Undaria pinnatifida* (Valentine and Johnson, 2003). *U. pinnatifida* has also been shown to host a less
706 diverse, and structurally distinct epibiotic assemblage when compared with native algae (Arnold et
707 al., 2016; Raffo et al., 2009). Thus invasion of native reef assemblages by non-native species may
708 result in impoverished kelp associated assemblages and overall lower local biodiversity (Arnold et
709 al., 2016; Casas et al., 2004).

710 Along urbanised coastlines globally, replacement of natural substrate with artificial structures
711 relating to human activities is common and widespread (e.g. >50% of shores in Sydney Harbour are
712 artificial seawalls; Chapman, 2003). Such structures differ from natural reefs in a number of ways,
713 including their composition, complexity and orientation, and have been shown to support distinct

714 assemblages from those found on natural substrates (Bulleri et al., 2005; Glasby, 1999). Recently
715 there has been a focus on elevating the ecological value of such structures, including the ‘gardening’
716 of habitat-forming species (Firth et al., 2014; Perkol-Finkel et al., 2012). Habitat-forming species
717 growing on artificial substrates, however, support different associated assemblages compared to
718 those growing on natural substrate (Marzinelli et al., 2009; People, 2006). For example, Marzinelli
719 (2012) showed that *Ecklonia radiata* growing on pier-pilings supported different assemblages of
720 bryozoans than those found on natural reefs, and that the abundances of bryozoans, including the
721 invasive *Membranipora membranacea*, were significantly greater on kelps on artificial substrates.
722 This variability in ecological pattern was driven by both direct (through shading) and indirect factors
723 (by altering abundances of sea urchins; Marzinelli et al., 2011). Clearly, the functioning of kelps as
724 habitat forming species varies between natural and artificial habitats and, given the rate of coastal
725 development and habitat modification, this represents an important area of research.

726 **5. Threats to biogenic habitat provided by kelps**

727 Kelp forests are under threat from a range of anthropogenic pressures, such as decreased water
728 quality, climate change and overgrazing driven by trophic cascade effects from overfishing (Brodie et
729 al., 2014; Smale et al., 2013; Steneck et al., 2002; Steneck and Johnson, 2013). Threats to
730 ecosystems services provided by kelp forests have been examined in recent reviews by Smale et al.
731 (2013) and Steneck and Johnson (2013) and will be briefly considered here in relation to biogenic
732 habitat provision. While physical disturbance by wave action is important in maintaining diversity
733 within kelp forests, as well as promoting turnover of nutrients and species (Kendrick et al., 2004;
734 Smale et al., 2010; Smale and Vance, 2015), extreme wave action can cause damage to kelps and
735 associated fauna, leading to high rates of mortality and widespread loss of habitat (Filbee-Dexter
736 and Scheibling, 2012; Krumhansl and Scheibling, 2011a). During intense storms, wave action can
737 cause dislodgement of entire kelp plants, and can lead to large areas of reef being cleared of canopy
738 cover (e.g. Reed et al., 2011; Thomsen et al., 2004). As many climate models predict an increase in

739 the frequency of extreme high-intensity storms in the future, as a consequence of anthropogenic
740 climate change (Easterling et al., 2000; Meehl et al., 2000), increased wave action may reduce kelp
741 forest extent and biodiversity and simplify food webs (Byrnes et al., 2011), and possibly facilitate
742 invasion by non-native species (e.g. Edgar et al., 2004). An increase in the frequency or magnitude
743 of storm events will probably impact the quality and quantity of biogenic habitat available for
744 associated assemblages, as removal of material, from an individual kelp plant to large swathes of
745 kelp forest, represents removal of a vast amount of biogenic habitat from the system. Smaller-scale
746 removal and thinning of kelp forest canopies will also influence associated species, and alter
747 associated structure (Clark et al., 2004; Connell, 2003b; Flukes et al., 2014; Hawkins and Harkin,
748 1985; Santelices and Ojeda, 1984). Furthermore, increased storminess and physical disturbance may
749 interact with other environmental change factors, such as climate-driven range shifts of species
750 (Smale and Vance, 2015) or the spread of non-native species (Krumhansl et al., 2011), to further
751 drive alterations or loss of biogenic habitat.

752 Over-grazing of kelp forests, particularly by sea urchins, can lead to considerable loss of biogenic
753 habitat from temperate ecosystems, in extreme cases causing phase-shifts from structurally complex
754 habitat to depauperate “barrens” (Breen and Mann, 1976b; Filbee-Dexter and Scheibling, 2014;
755 Hagan, 1983; Johnson et al., 2011; Ling et al., 2015; Steneck et al., 2002). The regulation of sea
756 urchin abundances is often linked to the structure and spatial extent of kelp forests (Steneck et al.,
757 2002). Disease (Scheibling et al., 1999), storms (Dayton, 1985) and turbulence (Choat and Schiel,
758 1982) can all influence sea urchin abundances, but predators are the single most important regulator
759 of sea urchin populations (Estes and Duggins, 1995; Johnson et al., 2011; Ling et al., 2015; Sala et al.,
760 1998; Steneck, 1998). Where key sea urchin predators (e.g. lobster; Breen and Mann, 1976a; Ling et
761 al., 2009; and cod; Tegner and Dayton, 2000) are the focus of intensive fishing pressure, a trophic
762 cascade may occur whereby sea urchin populations proliferate and large-scale deforestation of kelp
763 forests ensues.

764 The regularity and intensity of the removal of kelp canopies, through storms or harvesting, is
765 important with regards to the recovery of affected communities. Studies on the impacts of regular
766 harvesting of kelp (e.g. in Norway; Christie et al., 1998) have shown that recovery rates for kelps
767 themselves may not reflect recovery rates for the whole community. While kelp density and
768 morphology may return to a pre-harvested state (> 1 m in height) within 2 – 3 years, associated
769 epiphytic assemblages can take considerably longer to recover (4 - 6 years; Christie et al., 1998).
770 Epiphytic algal communities have been shown to recover particularly slowly and, despite species
771 richness returning to pre-disturbance levels in line with kelp recovery (2 – 3 years), the three-
772 dimensional structure of these assemblages requires a longer period to fully recover, potentially
773 limiting the recovery of associated faunal assemblages (Christie et al., 1998). This level of
774 disturbance has also been shown to impact the abundance of some fish species, as well as impact on
775 the foraging behaviour of some seabirds (Lorentsen et al., 2010). Commercial-scale kelp harvesting
776 (for alginates, food, biofuel and other products) has the potential to severely impact provision of
777 biogenic habitat (e.g. Anderson et al., 2006; Christie et al., 1998), and consequently biodiversity and
778 ecosystem structure, and needs to be carefully managed and regulated into the future. Similarly,
779 aquaculture of kelps and other seaweeds is a rapidly growing global industry (Loureiro et al., 2015)
780 and farming practises have the potential to impact biogenic habitat provision by kelps through the
781 spread of disease (Loureiro et al., 2015) and non-native species (James and Shears, 2016), as well as
782 through interbreeding between wild and farmed populations (Tano et al., 2015). Kelps are cool
783 water species and are stressed by high temperatures (Steneck et al., 2002). As such, seawater
784 warming (in association with global climate change) will impact the distribution, productivity,
785 resilience and structure of kelp forests (Harley et al., 2012; Merzouk and Johnson, 2011; Wernberg
786 et al., 2010). Both increased frequency and severity of extreme warming events (Dayton and
787 Tegner, 1984; Smale and Wernberg, 2013) and longer-term gradual warming (Wernberg et al., 2011)
788 are likely to have significant impacts on habitat structure and, particularly for those species at the

789 equatorial range edge, may cause widespread losses of kelp populations (Fernandez, 2011; Raybaud
790 et al., 2013; Voerman et al., 2013).

791 In addition to increasing temperature, changes in water quality (particularly turbidity) will influence
792 the spatial extent (i.e. both the geographical distribution and maximum depth of populations) and
793 the structure of kelp habitat which, in turn, will influence associated biodiversity patterns.

794 Decreased water quality (i.e. increased nutrients, sediments and turbidity) in coastal environments
795 has led to widespread losses of kelp populations and caused structural shifts in habitats and
796 communities (Connell et al., 2008; Moy and Christie, 2012). As such, human activities influencing
797 processes acting across the land-sea interface, such as coastal development, agricultural practises
798 and catchment management, have the potential to significantly alter kelp forest structure.

799 Physiological stresses are likely to make kelps more susceptible to disease. Disease can cause wide-
800 spread mortality or have sub-lethal impacts, such as reduced growth and fecundity (Wahl et al.,
801 2015), and may induce alterations in community structure and facilitate the spread of non-native
802 species (Gachon et al., 2010). Mass mortality of kelps in New Zealand was attributed to disease,
803 induced by increased physiological stress (Cole and Babcock, 1996). Infected *Saccharina latissima*
804 individuals have been shown to grow more slowly than healthy plants (Schatz, 1984), and infection
805 can cause thallus deformity (Peters and Schaffelke, 1996), and affect depth distributions (Schaffelke
806 et al., 1996). The virulence of many marine microbes is temperature-regulated (Eggert et al., 2010;
807 Harvell et al., 2002). Thus, warmer temperatures may lead to stressed susceptible hosts being
808 exposed to more abundant and virulent pathogens (Wahl et al., 2015), which will ultimately affect
809 biogenic habitat provision. The influence of multiple concurrent stressors will impact habitat
810 provision by kelps in complex and potentially unexpected ways. Thus, more research is required in
811 order to predict how the diversity and abundance of kelp associated flora and fauna will respond to
812 future conditions.

813 In order to alleviate the impacts of current threats and stressors, and to reduce further loss of
814 habitat, there are a few recent examples of management and conservation measures specially
815 targeted at kelp species. In eastern Tasmania, dramatic declines in the extent of *Macrocystis*
816 *pyrifera* have been observed since the 1980s; likely caused by the southward penetration of the
817 warm, nutrient-poor waters of the Eastern Australian Current (Johnson et al., 2011). In August 2012,
818 as a result of these losses, the Australian giant kelp forests were listed as ‘endangered’ under the
819 *Environmental Protection and Biodiversity Conservation Act* (see Bennett et al., 2016 and references
820 therein). Recent evidence also shows that the Adriatic population of the Mediterranean deep-water
821 kelp, *Laminaria rodriguezii*, has suffered a decline of >85% of its historical range, presumably from
822 bottom trawling, and is now present only around the small off-shore island of Palagruža (Žuljević et
823 al., 2016). This has prompted calls for the species to be classified as ‘endangered’ under the IUCN
824 Red List in the Adriatic (Žuljević et al., 2016). In Europe ‘Reefs’ are listed under Annex I of the
825 Habitats Directive as a marine habitat to be protected by the designation of Special Areas of
826 Conservation (SACs). While kelp forests are not specifically targeted in the Habitats Directive,
827 species of the genus *Laminaria* are named components of the ‘Reefs’ habitat (Airoldi and Beck,
828 2007). Additionally, two species of *Laminaria* from the Mediterranean (*L. rodriguezii* and *L.*
829 *ochroleuca*) are listed in Annex 1 of the Bern Convention (Airoldi and Beck, 2007). At the National
830 level, some countries have implemented legislation and policies specifically aimed at kelp
831 populations and communities. For instance, the commercial harvesting of kelp is strictly regulated in
832 France and Norway (Birkett et al., 1998; Christie et al., 1998).

833 **6. Knowledge gaps and recommendations for further research**

834 1. The provision of biogenic habitat by kelp species globally represents a significant and highly-
835 valuable ecological service, which is increasingly under threat from environmental change. While
836 the patterns of change and driving processes have been studied extensively over the last 60 years or
837 so, our current knowledge on the ecology of kelp forests is not evenly spread. The majority of

838 research concerns just a few species (namely *Laminaria hyperborea* in the northeast Atlantic,
839 *Macrocystis pyrifera* in the north Pacific and southern Atlantic, and *Ecklonia radiata* in South Africa
840 and Australasia), and information on others is sparse, or even non-existent. Indeed, several areas of
841 kelp distribution seem to be understudied, with very little information from East Asia currently
842 available or accessible.

843 2. While steps must be taken to form an accurate picture of habitat provision and associated
844 biodiversity patterns from a representative number of kelp species, the experimental design used to
845 do so should also be taken into account. Currently, it is difficult to make overarching inferences or
846 comparisons between kelp species or geographic regions from existing data, due to the different
847 sampling methods, survey designs, habitat metrics (e.g. total habitat volume versus habitable space)
848 and ecological response variables used and presented between studies.

849 3. A standardised sampling approach would allow comparisons to be made between species and
850 across large spatial scales. Given that several key ecological processes operate at large spatial scales
851 (e.g. climate change, global spread of non-native species), consistent and comparable observations
852 of kelp populations and their associated communities across similar spatial scales are needed to
853 advance understanding and improve management of these highly-valuable ecosystems. Adequately
854 resourced international projects or networks would facilitate these goals.

855 4. Recent advances in technology should be employed in order to advance understanding of
856 ecological pattern and processes within kelp forests. For example, previous work unravelling the
857 influence of habitat complexity and size have used simplified mimics of biogenic structures (e.g.
858 holdfasts) that do not accurately represent the complexity seen in nature. Developments in 3D
859 modelling and printing, for example, could be used to manipulate aspects of habitat complexity and
860 size in an ecologically-relevant manner to shed new light on their influence on kelp-associated
861 biodiversity. Similarly, reliable information on the structure and spatial extent of kelp forest habitat
862 is lacking for many regions, partly because shallow rocky reef habitat is logistically-difficult to sample

863 at large spatial scales. Advances in remote sampling technologies, such as Automated Underwater
864 Vehicles (AUVs, see Smale et al., 2012) and Gliders could dramatically increase the spatial and
865 temporal scale of benthic sampling, which would provide more accurate assessment of the structure
866 and distribution of kelp forest habitats. This information would feed into spatial modelling
867 approaches (e.g. Bekkby et al., 2009) and, ultimately, marine management.

868 5. Kelp-dominated habitats provide a wealth of ecosystem goods and services, both directly (such as
869 harvesting of kelp for food, alginates and other products as well as extraction of associated species
870 including crabs and lobsters) and indirectly (such as biogenic coastal defence and nutrient cycling).
871 However, current understanding of the provision of these goods and services, and their value and
872 importance to human society, is limited. A better appreciation of the direct and indirect value of kelp
873 forests, and marine ecosystems generally, to regional industries such as fishing and tourism will
874 benefit conservation and management of these habitats.

875 6. Global environmental change factors, such as the spread of invasive species, overfishing and
876 climate change, are impacting the structure and quantity of biogenic habitat provided by kelp
877 species. Targeted field studies on the wider implications (e.g. changes in primary productivity,
878 biodiversity, coastal geomorphology) of the loss or replacement of habitat-forming species,
879 conducted across multiple spatial scales and trophic levels, is urgently needed to document
880 ecological impacts, and to inform management and support conservation.

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892 **References**

- 893 Airoldi, L., 2003. The effects of sedimentation on rocky coast assemblages. *Oceanogr. Mar. Biol.* 41,
894 161 - 236.
- 895 Airoldi, L., Beck, M.W., 2007. Loss, status and trends for coastal marine habitats of Europe.
896 *Oceanogr. Mar. Biol.* 45, 345 - 405.
- 897 Allen, J.C., Griffiths, C.L., 1981. The flora and fauna of a kelp bed canopy. *S. Afr. J. Zool.* 16, 80 - 84.
- 898 Andersen, G.S., Steen, H., Christie, H., Fredriksen, S., Moy, F.E., 2011. Seasonal patterns of
899 sporophyte growth, fertility, fouling, and mortality of *Saccharina latissima* in Skagerrak, Norway:
900 implications for forest recovery. *J. Mar. Biol.* 2011:690375.
- 901 Anderson, M.J., Diebel, C.E., Blom, W.M., Landers, T.J., 2005. Consistency and variation in kelp
902 holdfast assemblages: Spatial patterns of biodiversity for the major phyla at different taxonomic
903 resolutions. *J. Exp. Mar. Biol. Ecol.* 320, 35-56.
- 904 Anderson, R.J., Rothman, M.D., Share, A., Drummond, H., 2006. Harvesting of the kelp *Ecklonia*
905 *maxima* in South Africa affects its three obligate, red algal epiphytes. *J. Appl. Phycol.* 18, 343 - 349.
- 906 Arkema, K.K., Reed, D.C., Schroeter, S.C., 2009. Direct and indirect effects of giant kelp determine
907 benthic community structure and dynamics. *Ecology* 90, 3126-3137.
- 908 Arnold, M., Teagle, H., Brown, M.P., Smale, D.A., 2016. The structure of biogenic habitat and
909 epibiotic assemblages associated with the global invasive *Undaria pinnatifida* in comparison to
910 native macroalgae. *Biol. Invasions* 18, 661 - 676.
- 911 Arroyo, N.L., Maldonado, M., Perez-Portela, R., Benito, J., 2004. Distribution patterns of meiofauna
912 associated with a sublittoral *Laminaria* bed in the Cantabrian Sea (north-eastern Atlantic). *Mar. Biol.*
913 144, 231 - 242.
- 914 Ballantine, W.J., 1961. A biologically defined exposure scale for the comparative description of rocky
915 shores. *Field Stud.* 1, 1 - 19.
- 916 Bartsch, I., Wiencke, C., Bischof, K., Buchholz, C.M., Buck, B.H., Eggert, A., Feuerpfeil, P., Hanelt, D.,
917 Jacobsen, S., Karez, R., Karsten, U., Molis, M., Roleda, M.Y., Schubert, H., Schumann, R., Valentin, K.,
918 Weinberger, F., Wiese, J., 2008. The genus *Laminaria* sensu lato: recent insights and developments.
919 *Eur. J. Phycol.* 43, 1 - 86.
- 920 Bax, N., Carlton, J.T., Mathews-Amos, A., Haedrich, R.L., Howarth, F.G., Purcell, J.E., Rieser, A., Gray,
921 A., 2001. The control of biological invasions in the world's oceans. *Conserv. Biol.* 15, 1234 - 1246.
- 922 Beaumont, N.J., Austen, M.C., Mangi, S.C., Townsend, M., 2008. Economic valuation for the
923 conservation of marine biodiversity. *Mar. Pollut. Bull.* 56, 386-396.
- 924 Bekkby, T., Rinde, E., Erikstad, L., Bakkestuen, V., 2009. Spatial predictive distribution modelling of
925 the kelp species *Laminaria hyperborea*. *ICES J. Mar. Sci.* 66, 2106 - 2115.
- 926 Bennett, S., Wernberg, T., Connell, S.D., Hobday, A.J., Johnson, C.R., Poloczanska, E.S., 2016. The
927 'Great Southern Reef': social, ecological and economic value of Australia's neglected kelp forests.
928 *Mar. Freshw. Res.* 67, 47 - 56.
- 929 Bertocci, I., Araújo, R., Oliveira, P., Sousa-Pinto, I., 2015. Potential effects of kelp species on local
930 fisheries. *J. Appl. Ecol.* 52, 1216 - 1226.
- 931 Birkett, D.A., Maggs, C.A., Dring, M.J., Boaden, P.J.S., Seed, R., 1998. Infralittoral reef biotopes with
932 kelp species, An overview of dynamic and sensitivity characteristics for conservation management of
933 marine SACs.
- 934 Blanchette, C.A., 1996. Seasonal patterns of disturbance influence recruitment of the sea palm,
935 *Postelsia palmaeformis*. *J. Exp. Mar. Biol. Ecol.* 197, 1 - 14.
- 936 Blight, A.J., Thompson, R.C., 2008. Epibiont species richness varies between holdfasts of a northern
937 and southern distributed kelp species. *J. Mar. Biol. Assoc. U. K.* 88, 469 - 475.
- 938 Bodkin, J.L., 1988. Effects of kelp forest removal on associated fish assemblages in central California.
939 *J. Exp. Mar. Biol. Ecol.* 117, 227 - 238.
- 940 Bologna, P.A.X., Steneck, R.S., 1993. Kelp beds as habitat for American lobster *Homarus americanus*.
941 *Mar. Ecol. Prog. Ser.* 100, 127 - 134.

- 942 Bolton, J.J., 2010. The biogeography of kelps (Laminariales, Phaeophyceae): a global analysis with
943 new insights from recent advances in molecular phylogenetics. *Helgoland Mar. Res.* 64, 263 - 279.
- 944 Boney, A.D., Corner, E.D.S., 1963. The effect of light on the growth of sporelings of the red algae
945 *Antithamnion plumula* and *Brongniartella byssoides*. *J. Mar. Biol. Assoc. U. K.* 43, 319 - 325.
- 946 Brady-Campbell, M.M., Campbell, D.B., Harlin, M.M., 1984. Productivity of kelp (*Laminaria* spp.) near
947 the southern limit in the Northwestern Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 18, 79 - 88.
- 948 Brattström, H., 1968. The importance of water movement for biology and distribution of marine
949 organisms. 2nd European symposium on marine biology. *Sarsia* 34, 9 - 12.
- 950 Breen, P.A., Mann, K.H., 1976a. Changing lobster abundance and the destruction of kelp beds by sea
951 urchins. *Mar. Biol.* 34, 137 - 142.
- 952 Breen, P.A., Mann, K.H., 1976b. Destructive grazing of kelp by sea urchins in Eastern Canada. *J. Fish.*
953 *Res. Board Can.* 33, 1278 - 1283.
- 954 Brodie, J., Williamson, C.J., Smale, D.A., Kamenos, N.A., Mieszkowska, N., Santos, R., Cunliffe, M.,
955 Steinke, M., Yesson, C., Anderson, K.M., Asnaghi, V., Brownlee, C., Burdett, H., Burrows, M.T., Collins,
956 S., Donohue, P.J.C., Harvey, B., Foggo, A., Noisette, F., Nunes, J., Ragazzola, F., Raven, J.A., Schmidt,
957 D.N., Suggett, D., Teichberg, M., Hall-Spencer, J.M., 2014. The future of the northeast Atlantic
958 benthic flora in a high CO₂ world. *Ecol. Evol.* 4, 2787 - 2798.
- 959 Bruno, J.F., Bertness, M.D., 2001. Habitat modification and facilitation in benthic marine
960 communities, in: Hay, M.E., Gaines, S.D. (Eds.), *Marine Community Ecology*. Sinauer, Sunderland,
961 MA., pp. 201 - 218.
- 962 Bulleri, F., Benedetti-Cecchi, L., 2006. Mechanisms of recovery and resilience of different
963 components of mosaics of habitats on shallow rocky reefs. *Oecologia* 149, 482 - 492.
- 964 Bulleri, F., Chapman, M.G., Underwood, A.J., 2005. Intertidal assemblages on seawalls and vertical
965 rocky shores in Sydney Harbour, Australia. *Austral Ecol.* 30, 655 - 667.
- 966 Bunker, F., 2013. Fal and Helford SAC kelp forest condition assessment and maerl studies in August
967 2012. A report to Natural England by MarineSeen, Pembrokeshire, p. 59pp.
- 968 Bunker, F., Mercer, T., Howson, C., 2005. South Wight Maritime European Marine Site sublittoral
969 monitoring 2003-2004. Report by Aquatic Survey & Monitoring Ltd for English Nature (Contract no.
970 FST20-46-16).
- 971 Burrows, M.T., Kamenos, N.A., Hughes, D.J., Stahl, H., Howe, J.A., Tett, P., 2014. Assessment of
972 carbon budgets and potential blue carbon stores in Scotland's coastal and marine environment,
973 Scottish Natural Heritage Commissioned Report No. 761.
- 974 Bustamante, R.H., Branch, G.M., 1996. The dependence of intertidal consumers on kelp-derived
975 organic matter on the west coast of South Africa. *J. Exp. Mar. Biol. Ecol.* 196, 1 - 28.
- 976 Byrnes, J.E., Reed, D.C., Cardinale, B.J., Cavanaugh, K.C., Holbrooks, S.J., Schmitts, R.J., 2011. Climate-
977 driven increases in storm frequency simplify kelp forest food webs. *Global Change Biol.* 17, 2513 -
978 2524.
- 979 Carlsen, B.P., Johnsen, G., Berge, J., Kuklinski, P., 2007. Biodiversity patterns of macro-epifauna on
980 different lamina parts on *Laminaria digitata* and *Saccharina latissima* collected during spring and
981 summer 2004 in Kongsfjorden, Svalbard. *Polar Biol.* 30, 939 - 943.
- 982 Casas, G., Scrosati, R., Piriz, M.L., 2004. The invasive kelp *Undaria pinnatifida* (Phaeophyta,
983 Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina). *Biol. Invasions*
984 6, 411 - 416.
- 985 Castric-Fey, A., Beaupoil, C., Bouchain, J., Pradier, E., L'Hardy-Halos, M.T., 1999. The introduced alga
986 *Undaria pinnatifida* (Laminariales, Alariaceae) in the rocky shore ecosystem of the St Malo area:
987 morphology and growth of the sporophyte. *Bot. Mar.* 42, 71 - 82.
- 988 Cattaneo, A., Klaff, J., 1979. Primary production of algae growing on natural and artificial aquatic
989 plants: a study of interactions between epiphytes and their structure. *Limnol. Oceanogr.* 24, 1031 -
990 1037.
- 991 Chapman, M.G., 2003. Paucity of mobile species on constructed seawalls: effects of urbanization on
992 biodiversity. *Mar. Ecol. Prog. Ser.* 264, 21 - 29.

- 993 Choat, J.H., Schiel, D.R., 1982. Patterns of distribution and abundance of large brown algae and
 994 invertebrate herbivores in subtidal regions of northern New Zealand. *J. Exp. Mar. Biol. Ecol.* 60, 129 -
 995 162.
- 996 Christie, H., 1995. Description of the kelp forest fauna at Froan, Mid Norway; variation in an
 997 exposure gradient. NINA Oppdragsmelding 368, 1 - 22.
- 998 Christie, H., Fredriksen, S., Rinde, E., 1998. Regrowth of kelp and colonization of epiphyte and fauna
 999 community after kelp trawling at the coast of Norway. *Hydrobiologia* 375-76, 49 - 58.
- 1000 Christie, H., Jorgensen, N.M., Norderhaug, K.M., 2007. Bushy or smooth, high or low; importance of
 1001 habitat architecture and vertical position for distribution of fauna on kelp. *J. Sea Res.* 58, 198 - 208.
- 1002 Christie, H., Jorgensen, N.M., Norderhaug, K.M., Waage-Nielsen, E., 2003. Species distribution and
 1003 habitat exploitation of fauna associated with kelp (*Laminaria hyperborea*) along the Norwegian
 1004 coast. *J. Mar. Biol. Assoc. U. K.* 83, 687-699.
- 1005 Christie, H., Kraufvelin, P., 2004. Mechanisms regulating amphipod population density within
 1006 macroalgal communities with low predator impact. *Sci. Mar.* 68, 189 - 198.
- 1007 Christie, H., Norderhaug, K.M., Fredriksen, S., 2009. Macrophytes as habitat for fauna. *Mar. Ecol.*
 1008 *Prog. Ser.* 396, 221-233.
- 1009 Christie, H., Rinde, E., Fredriksen, S., Skadsheim, A., 1994. Ecological consequences of kelp trawling:
 1010 re-establishment of kelp forest, epiphytes and holdfast fauna after kelp trawling at the Rogaland
 1011 coast. NINA Oppdragsmelding 295, 1 - 29.
- 1012 Clark, R.P., Edwards, M.S., Foster, M.S., 2004. Effects of shade from multiple kelp canopies on an
 1013 understory algal assemblage. *Mar. Ecol. Prog. Ser.* 267, 107-119.
- 1014 Cole, R.G., Babcock, R.C., 1996. Mass mortality of a dominant kelp (*Laminariales*) at Goat Island,
 1015 north-eastern New Zealand. *Mar. Freshw. Res.* 47, 907 - 911.
- 1016 Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302 - 1310.
- 1017 Connell, S.D., 2003a. The monopolization of understory habitat by subtidal encrusting coralline
 1018 algae: a test of the combined effects of canopy-mediated light and sedimentation. *Mar. Biol.* 142,
 1019 1065 - 1071.
- 1020 Connell, S.D., 2003b. Negative effects overpower the positive of kelp to exclude invertebrates from
 1021 the understory community. *Oecologia* 137, 97-103.
- 1022 Connell, S.D., Russell, B.D., Turner, D.J., Shepherd, S.A., Kildea, T., Miller, D., Airoidi, L., Cheshire, A.,
 1023 2008. Recovering a lost baseline: missing kelp forests from a metropolitan coast. *Mar. Ecol. Prog.*
 1024 *Ser.* 360, 63 - 72.
- 1025 Dayton, P.K., 1973. Dispersion, dispersal, and persistence of the annual intertidal alga, *Postelsia*
 1026 *palmaeformis* Ruprecht. *Ecology* 54, 433 - 438.
- 1027 Dayton, P.K., 1985. Ecology of kelp communities. *Annu. Rev. Ecol. Syst.* 16, 215 - 245.
- 1028 Dayton, P.K., Tegner, M.J., 1984. Catastrophic storms, El Niño, and patch stability in a southern
 1029 California kelp community. *Science* 224, 283 - 285.
- 1030 Dean, T.A., Jacobsen, F.R., 1986. Nutrient-limited growth of juvenile kelp, *Macrocystis pyrifera*,
 1031 during the 1982 - 1984 "El Niño" in southern California. *Mar. Biol.* 90, 597 - 601.
- 1032 Denny, M., Gaylord, B., Helmuth, B., Daniel, T., 1998. The menace of momentum: dynamic forces on
 1033 flexible organisms. *Limnol. Oceanogr.* 43, 955 - 968.
- 1034 Denny, M.W., Hale, B.B., 2003. Cyberkelp: an integrative approach to the modelling of flexible
 1035 organisms. *Philos. Trans. R. Soc. B.* 358, 1535 - 1542.
- 1036 Dial, R., Roughgarden, J., 1998. Theory of marine communities: the intermediate disturbance
 1037 hypothesis. *Ecology* 79, 1412 - 1424.
- 1038 Dixon, J., Schroeter, S.C., Kastendiek, J., 1981. Effects of the encrusting bryozoan, *Membranipora*
 1039 *membranacea*, on the loss of blade and fronds by the giant kelp, *Macrocystis pyrifera* (*Laminariales*).
 1040 *J. Phycol.* 17, 341 - 345.
- 1041 Duarte, C.M., Sand-Jensen, K., 1990. Seagrass colonization: biomass development and shoot
 1042 demography in *Cymodocea nodosa* patches. *Mar. Ecol. Prog. Ser.* 67, 97 - 103.

- 1043 Dubois, A., Iken, K., 2012. Seasonal variation in kelp phlorotannins in relation to grazer abundance
1044 and environmental variables in the Alaskan sublittoral zone. *Algae* 27, 9 - 19.
- 1045 Duggins, D.O., Eckman, J.E., 1997. Is kelp detritus a good food for suspension feeders? Effects of kelp
1046 species, age and secondary metabolites. *Mar. Biol.* 128, 489 - 495.
- 1047 Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., Mearns, L.O., 2000. Climate
1048 extremes: observations, modeling, and impacts. *Science* 289, 2068 - 2074.
- 1049 Eckman, J.E., 1983. Hydrodynamic processes affecting benthic recruitment. *Limnol. Oceanogr.* 28,
1050 241 - 257.
- 1051 Eckman, J.E., Duggins, D.O., Sewell, A.T., 1989. Ecology of understory kelp environments. I. Effects of
1052 kelps on flow and particle transport near the bottom. *J. Exp. Mar. Biol. Ecol.* 129, 173 - 187.
- 1053 Edgar, G.J., Barrett, N.S., Morton, A.J., Samson, C.R., 2004. Effects of algal canopy clearance on plant,
1054 fish and macroinvertebrate communities on eastern Tasmanian reefs. *J. Exp. Mar. Biol. Ecol.* 312, 67
1055 - 87.
- 1056 Edwards, M.S., Hernández-Carmona, G., 2005. Delayed recovery of giant kelp near its southern
1057 range limit in the North Pacific following El Niño. *Mar. Biol.* 147, 273 - 279.
- 1058 Eggert, A., Peters, A.F., Küpper, F.C., 2010. The potential impact of climate change on endophyte
1059 infections in kelp sporophytes, Seaweeds and their Role in Globally Changing Environments.
1060 Springer, Netherlands, pp. 139 - 154.
- 1061 England, P.R., Phillips, J., Waring, J.R., Symonds, G., Babcock, R., 2008. Modelling wave-induced
1062 disturbance in highly biodiverse marine macroalgal communities: support for the intermediate
1063 disturbance hypothesis. *Mar. Freshw. Res.* 59, 515 - 520.
- 1064 Estes, J.A., Danner, E.M., Doak, D.F., Konar, B., Springer, A.M., Steinberg, P.D., Tinker, M.T., Williams,
1065 T.M., 2004. Complex trophic interactions in kelp forest ecosystems. *Bull. Mar. Sci.* 74, 621 - 638.
- 1066 Estes, J.A., Duggins, D.O., 1995. Sea otters and kelp forests in Alaska: generality and variation in a
1067 community ecological paradigm. *Ecol. Monogr.* 65, 75 - 100.
- 1068 Fenwick, G.D., 1976. The effect of wave exposure on the amphipod fauna of the alga *Caulerpa*
1069 *brownii*. *J. Exp. Mar. Biol. Ecol.* 25, 1 - 18.
- 1070 Fernandez, C., 2011. The retreat of large brown seaweeds on the north coast of Spain: the case of
1071 *Saccorhiza polyschides*. *Eur. J. Phycol.* 46, 352 - 360.
- 1072 Fielding, P.J., Davis, C.L., 1989. Carbon and nitrogen resources available to kelp bed filter feeders in
1073 an upwelling environment. *Mar. Ecol. Prog. Ser.* 55, 181 - 189.
- 1074 Filbee-Dexter, K., Scheibling, R.E., 2012. Hurricane-mediated defoliation of kelp beds and pulsed
1075 delivery of kelp detritus to offshore sedimentary habitats. *Mar. Ecol. Prog. Ser.* 455, 51 - 64.
- 1076 Filbee-Dexter, K., Scheibling, R.E., 2014. Sea urchin barrens as alternative stable states of collapsed
1077 kelp ecosystems. *Mar. Ecol. Prog. Ser.* 495, 1 - 25.
- 1078 Fincham, A.A., 1974. Periodic swimming behaviour of amphipods in Wellington Harbour. *New Zeal. J.*
1079 *Mar. Freshw. Res.* 8, 505 - 521.
- 1080 Firth, L.B., Thompson, R.C., Bohn, K., Abbiati, M., Airoidi, L., Bouma, T.J., Bozzeda, F., Ceccherelli,
1081 V.U., Colangelo, M.A., Evans, A., Ferrario, F., Hanley, M.E., Hinz, H., Hoggart, S.P.G., Jackson, J.E.,
1082 Moore, P., Morgan, E.H., Perkol-Finkel, S., Skov, M.W., Strain, E.M., van Belzen, J., Hawkins, S.J.,
1083 2014. Between a rock and a hard place: environmental and engineering considerations when
1084 designing coastal defence structures. *Coastal Engineering* 87, 122 - 135.
- 1085 Flukes, E.B., Johnson, C.R., Wright, J.T., 2014. Thinning of kelp canopy modifies understory
1086 assemblages: the importance of canopy density. *Mar. Ecol. Prog. Ser.* 514, 57-70.
- 1087 Foster, M.S., 1982. The regulation of macroalgal associations in kelp forests, Synthetic and
1088 degradative processes in marine macrophytes. Walter de Gruyter, Berlin.
- 1089 Fowler-Walker, M.J., Connell, S.D., 2002. Opposing states of subtidal habitat across temperate
1090 Australia: consistency and predictability in kelp canopy - benthic associations. *Mar. Ecol. Prog. Ser.*
1091 240, 49 - 56.

- 1092 Fowler-Walker, M.J., Wernberg, T., Connell, S.D., 2006. Differences in kelp morphology between
 1093 wave sheltered and exposed localities: morphologically plastic or fixed traits. *Mar. Biol.* 148, 755 -
 1094 767.
- 1095 Fraser, C.I., Nikula, R., Spencer, H.G., Waters, J.M., 2009. Kelp genes reveal effects of subantarctic
 1096 sea ice during the last glacial maximum. *Proc. Natl. Acad. Sci. USA.* 106, 3249 - 3253.
- 1097 Fraser, C.I., Nikula, R., Waters, J.M., 2011. Oceanic rafting by a coastal community. *Proc. R. Soc.*
 1098 *Lond. B.* 278, 649 - 655.
- 1099 Fredriksen, S., 2003. Food web studies in a Norwegian kelp forest based on stable isotope ($\delta^{13}\text{C}$ and
 1100 $\delta^{15}\text{N}$) analysis. *Mar. Ecol. Prog. Ser.* 260, 71 - 81.
- 1101 Friedland, M.T., Denny, M., 1995. Surviving hydrodynamic forces in a wave-swept environment:
 1102 consequences of morphology in the feather boa kelp, *Egregia menziesii* (Turner). *J. Exp. Mar. Biol.*
 1103 *Ecol.* 190, 109 - 133.
- 1104 Gachon, C.M.M., Sime-Ngando, T., Strittmatter, M., Chambouvet, A., Kim, G.H., 2010. Algal diseases:
 1105 spotlight on a black box. *Trends Plant Sci.* 15, 633 - 640.
- 1106 Glasby, T.M., 1999. Differences between subtidal epibiota on pier pilings and rocky reefs at marinas
 1107 in Sydney, Australia. *Estuar. Coast. Shelf Sci.* 48, 281 - 290.
- 1108 Graham, A., Fretter, V., 1947. The life history of *Patina pellucida* (L.). *J. Mar. Biol. Assoc. U. K.* 26, 590
 1109 - 601.
- 1110 Graham, M.H., 2004. Effects of local deforestation on the diversity and structure of southern
 1111 California giant kelp forest food webs. *Ecosystems* 7, 341 - 357.
- 1112 Graham, M.H., Vasquez, J.A., Buschmann, A.H., 2007. Global ecology of the giant kelp *Macrocystis*:
 1113 from ecotypes to ecosystems. *Oceanogr. Mar. Biol.* 45, 39 - 88.
- 1114 Guiry, M.D., Guiry, G.M., 2015. Algaebase, World-wide electronic publication. National University of
 1115 Ireland, Galway.
- 1116 Hacker, S.D., Steneck, R.S., 1990. Habitat architecture and the abundance and body-size-dependent
 1117 habitat selection of a phytal amphipod. *Ecology* 71, 2269 - 2285.
- 1118 Hagan, N.T., 1983. Destructive grazing of kelp beds by sea urchins in Vestfjorden, northern Norway.
 1119 *Sarsia* 68, 177 - 190.
- 1120 Harley, C.D.G., Anderson, K.M., Demes, K.W., Jorve, J.P., Kordas, R.L., Coyle, T.A., 2012. Effects of
 1121 climate change on global seaweed communities. *J. Phycol.* 48, 1064 - 1078.
- 1122 Harlin, M.M., 1973. Transfer of products between epiphytic marine algae and host plants. *J. Phycol.*
 1123 9, 243 - 248.
- 1124 Harrold, C., Watanabe, J., Lisin, S., 1988. Spatial variation in the structure of kelp forest communities
 1125 along a wave exposure gradient. *Mar. Ecol.* 9, 131 - 156.
- 1126 Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S., Samuel, M.D., 2002.
 1127 Climate warming and disease risks for terrestrial and marine biota. *Science* 296, 2158 - 2162.
- 1128 Hauser, A., Attrill, M.J., Cotton, P.A., 2006. Effects of habitat complexity on the diversity and
 1129 abundance of macrofauna colonising artificial kelp holdfasts. *Mar. Ecol. Prog. Ser.*
- 1130 Hawkins, S.J., Harkin, E., 1985. Preliminary canopy removal experiments in algal dominated
 1131 communities low on the shore and in the shallow subtidal on the Isle of Man. *Bot. Mar.* 28, 223 - 230.
- 1132 Hepburn, C.D., Hurd, C.L., 2005. Conditional mutualism between the giant kelp *Macrocystis pyrifera*
 1133 and colonial epifauna. *Mar. Ecol. Prog. Ser.* 302, 37 - 48.
- 1134 Hobday, A.J., 2000. Persistence and transport of fauna on drifting kelp (*Macrocystis pyrifera* (L.) C.
 1135 Agardh) rafts in the Southern California Bight. *J. Exp. Mar. Biol. Ecol.* 253, 75 - 96.
- 1136 Holbrook, S.J., Carr, M.H., Schmitt, R.J., Coyer, J.A., 1990. Effect of giant kelp on local abundance of
 1137 reef fishes: the importance of ontogenetic resource requirements. *Bull. Mar. Sci.* 47, 104 - 114.
- 1138 Holland, G.S., Gardiner, R.A., 1975. The first map of Rockall. *Geogr. J.* 141, 94 - 98.
- 1139 Ingólfsson, A., 1995. Floating clumps of seaweed around Iceland: natural microcosms and a means of
 1140 dispersal for shore fauna. *Mar. Biol.* 122, 13 - 21.

- 1141 Irving, A.D., Connell, S.D., 2002. Sedimentation and light penetration interact to maintain
 1142 heterogeneity of subtidal habitats: algal versus invertebrate dominated assemblages. *Mar. Ecol.*
 1143 *Prog. Ser.* 245, 83 - 91.
- 1144 Irving, A.D., Connell, S.D., 2006. Physical disturbance by kelp abrades erect algae from the
 1145 understory. *Mar. Ecol. Prog. Ser.* 324, 127 - 137.
- 1146 James, K., Shears, N.T., 2016. Proliferation of the invasive kelp *Undaria pinnatifida* at aquaculture
 1147 sites promotes spread to coastal reefs. *Mar. Biol.* 163, 1 - 12.
- 1148 Jennings, J.G., Steinberg, P.D., 1997. Phlorotannins versus other factors affecting epiphyte
 1149 abundance on the kelp *Ecklonia radiata*. *Oecologia* 109, 461 - 473.
- 1150 Johnson, C.R., Banks, S.C., Barrett, N.S., Cazassus, F., Dunstan, P.K., Edgar, G.J., Frusher, S.D.,
 1151 Gardner, C., Haddon, M., Helidoniotis, F., Hill, K.L., Holbrook, N.J., Hosie, G.W., Last, P.R., Ling, S.D.,
 1152 Melbourne-Thomas, J., Miller, K., Pecl, G.T., Richardson, A.J., Ridgway, K.R., Rintoul, S.R., Ritz, D.A.,
 1153 Ross, D.J., Sanderson, J.C., Shepherd, S.A., Slotwinski, A., Swadling, K.M., Taw, N., 2011. Climate
 1154 change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics
 1155 in eastern Tasmania. *J. Exp. Mar. Biol. Ecol.* 400, 17 - 32.
- 1156 Johnson, C.R., Mann, K.H., 1986. The importance of plant defence abilities to the structure of
 1157 subtidal seaweed communities: the kelp *Laminaria longicruris* de la Pylaie survives grazing by the
 1158 snail *Lacuna vincta* (Montagu) at high population densities. *J. Exp. Mar. Biol. Ecol.* 97.
- 1159 Johnson, M., Hart, P., 2001. Preliminary report of the coastal fisheries around the coast of the British
 1160 Isles 1950-1999, Fisheries impacts on North Atlantic ecosystems: catch, effort and national/regional
 1161 datasets. Fisheries Centre Research Report. University of British Columbia, Vancouver, Canada, pp.
 1162 135 - 140.
- 1163 Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373 - 386.
- 1164 Jones, D.J., 1971. Ecological studies on macroinvertebrate populations associated with polluted kelp
 1165 forests in the North Sea. *Helgoland. Wiss. Meer.* 22, 417 - 441.
- 1166 Jones, D.J., 1972. Changes in the ecological balance of invertebrate communities in the kelp holdfast
 1167 habitats of some polluted North Sea waters. *Helgoländer wiss. Meeresunters* 23, 248 - 260.
- 1168 Jones, W.E., Dent, S., 1971. The effect of light on the growth of algal spores, Fourth European Marine
 1169 Biology Symposium. Cambridge University Press, London.
- 1170 Jorgensen, N.M., Christie, H., 2003. Diurnal, horizontal and vertical dispersal of kelp associated
 1171 fauna. *Hydrobiologia* 503, 69 - 76.
- 1172 Kain, J.M., 1971. Synopsis of biological data on *Laminaria hyperborea*. *FAO Fish. Synop.* 87, 1 - 68.
- 1173 Kain, J.M., 1976. The biology of *Laminaria hyperborea*. VIII. Growth on cleared areas. *J. Mar. Biol.*
 1174 *Assoc. U. K.* 56, 267 - 290.
- 1175 Kain, J.M., 1979. A view of the genus *Laminaria*. *Oceanogr. Mar. Biol.* 17, 101 - 161.
- 1176 Kain, J.M., Svendsen, P., 1969. A note on the behaviour of *Patella pellucida* in Britain and Norway.
 1177 *Sarsia* 38, 25 - 30.
- 1178 Kendrick, G.A., Harvey, E.S., Wernberg, T., Harman, N., Goldberg, N., 2004. The role of disturbance in
 1179 maintaining diversity of benthic macroalgal assemblages in southwestern Australia. *Jpn. J. Phycol.*
 1180 52, 5 - 9.
- 1181 Kennelly, S.J., 1987. Physical disturbance in an Australian kelp community. II. Effects on understory
 1182 species due to differences in kelp cover. *Mar. Ecol. Prog. Ser.* 40, 155 - 165.
- 1183 Kimura, R.S., Foster, M.S., 1984. The effects of harvesting *Macrocystis pyrifera* on the algal
 1184 assemblage in a giant kelp forest, Eleventh International Seaweed Symposium. Springer Netherlands,
 1185 pp. 425 - 428.
- 1186 Kitching, J.A., Thain, V.M., 1983. The ecological impact of the sea urchin *Paracentrotus lividus*
 1187 (Lamarck) in Lough Ine, Ireland. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 300, 513 - 552.
- 1188 Klinger, T., De Wreede, R.E., 1988. Stipe rings, age, and size in populations of *Laminaria setchellii*
 1189 Silva (Laminariales, Phaeophyta) in British Columbia, Canada. *Phycologia* 27, 234 - 240.
- 1190 Knights, A.M., Firth, L.B., Walters, K., 2012. Interactions between multiple recruitment drivers: post-
 1191 settlement predation mortality and flow-mediated recruitment. *PLOS ONE* 7, e30596.

- 1192 Koehl, M.A.R., 1999. Ecological biomechanics of benthic organisms: life history, mechanical design
1193 and temporal patterns of mechanical stress. *J. Exp. Biol.* 202, 3469 - 3476.
- 1194 Kovalenko, K.E., Thomaz, S.M., Warfe, D.M., 2012. Habitat complexity: approaches and future
1195 directions. *Hydrobiologia* 685, 1 - 17.
- 1196 Kraan, S., 2008. *Sargassum muticum* (Yendo) Fensholt in Ireland: an invasive species on the move. *J.*
1197 *Appl. Phycol.* 20, 825 - 832.
- 1198 Kregting, L., Blight, A., Elsässer, B., Savidge, G., 2013. The influence of water motion on the growth
1199 rate of the kelp *Laminaria hyperborea*. *J. Exp. Mar. Biol. Ecol.* 448, 337 - 345.
- 1200 Kregting, L., Blight, A.J., Elsässer, B., Savidge, G., 2016. The influence of water motion on the growth
1201 rate of the kelp *Laminaria digitata*. *J. Exp. Mar. Biol. Ecol.* 478, 86 - 95.
- 1202 Krumhansl, K.A., Lee, J.M., Scheibling, R.E., 2011. Grazing damage and encrustation by an invasive
1203 bryozoan reduce the ability of kelps to withstand breakage by waves. *J. Exp. Mar. Biol. Ecol.* 407, 12 -
1204 18.
- 1205 Krumhansl, K.A., Scheibling, R.E., 2011a. Detrital production in Nova Scotian kelp beds: patterns and
1206 processes. *Mar. Ecol. Prog. Ser.* 421, 67 - 82.
- 1207 Krumhansl, K.A., Scheibling, R.E., 2011b. Spatial and temporal variation in grazing damage by the
1208 gastropod *Lacuna vincta* in Nova Scotian kelp beds. *Aquatic Biol.* 13, 163 - 173.
- 1209 Krumhansl, K.A., Scheibling, R.E., 2012. Production and fate of kelp detritus. *Mar. Ecol. Prog. Ser.*
1210 467, 281 - 302.
- 1211 Lambert, W.J., Levin, P.S., Berman, J., 1992. Changes in the structure of a New England (USA) kelp
1212 bed: The effects of an introduced species? *Mar. Ecol. Prog. Ser.* 88, 303 - 307.
- 1213 Larkum, A.W.D., Collett, L.C., Williams, R.J., 1984. The standing stock, growth and shoot production
1214 of *Zostera capricorni* Aschers. in Botany Bay, New South Wales, Australia. *Aquat. Bot.* 19.
- 1215 Leclerc, J.C., Riera, P., Laurans, M., Leroux, C., Leveque, L., Davoult, D., 2015. Community, trophic
1216 structure and functioning in two contrasting *Laminaria hyperborea* forests. *Estuar. Coast. Shelf Sci.*
1217 152, 11 - 22.
- 1218 Leichter, J.J., Witman, J.D., 1997. Water flow over subtidal rock walls: relation to distributions and
1219 growth rates of sessile suspension feeders in the Gulf of Maine - water flow and growth rates. *J. Exp.*
1220 *Mar. Biol. Ecol.* 209, 293 - 307.
- 1221 Levin, P.S., Coyer, J.A., Petrik, R., Good, T.P., 2002. Community-wide effects of nonindigenous
1222 species on temperate rocky reefs. *Ecology* 83, 3182 - 3193.
- 1223 Ling, S.D., 2008. Range expansion of a habitat-modifying species leads to a loss of taxonomic
1224 diversity: a new and impoverished reef state. *Oecologia* 156, 883 - 894.
- 1225 Ling, S.D., Johnson, C.R., Frusher, S.D., Ridgway, K.R., 2009. Overfishing reduces resilience of kelp
1226 beds to climate-driven catastrophic phase shift. *Proc. Natl. Acad. Sci. USA.* 106, 22341 - 22345.
- 1227 Ling, S.D., Scheibling, R.E., Rassweiler, A., Johnson, C.R., Shears, N., Connell, S.D., Salomon, A.K.,
1228 Norderhaug, K.M., Pérez-Matus, A., Hernández, J.C., Clemente, S., Blamey, L.K., Hereu, B.,
1229 Bellestros, E., Sala, E., Garrabou, J., Cebrian, E., Zabala, M., Fujita, R., Johnson, L.E., 2015. Global
1230 regime shift dynamics of catastrophic sea urchin overgrazing. *Philos. Trans. R. Soc. B.* 370, 20130269.
- 1231 Lippert, H., Iken, K., Rachor, E., Wiencke, C., 2001. Macrofauna associated with macroalgae in the
1232 Kongsfjord (Spitsbergen). *Polar Biol.* 24, 512 - 522.
- 1233 Lorentsen, S., Sjøtun, K., Grémillet, D., 2010. Multi-trophic consequences of kelp harvest. *Biol.*
1234 *Conserv.* 143, 2054 - 2062.
- 1235 Loureiro, R., Gachon, C.M.M., Rebours, C., 2015. Seaweed cultivation: potential and challenges of
1236 crop domestication at an unprecedented pace. *New Phytologist* 206, 489 - 492.
- 1237 Macaya, E.C., Rothäusler, E., Thiel, M., Molis, M., Wahl, M., 2005. Induction of defenses and within-
1238 alga variation of palatability in two brown algae from the northern-central coast of Chile: effects of
1239 mesograzers and UV radiation. *J. Exp. Mar. Biol. Ecol.* 325, 214 - 227.
- 1240 Maggs, C.A., 1986. Scottish marine microalgae: a distributional checklist, biogeographical analysis
1241 and literature abstract. Nature Conservancy Council.

- 1242 Mai, T.T., Hovel, K.A., 2007. Influence of local-scale and landscape-scale habitat characteristics on
1243 California spiny lobster (*Panurllirus interruptus*) abundance and survival. *Mar. Freshw. Res.* 58, 419 -
1244 428.
- 1245 Mann, K.H., 1973. Seaweeds: their productivity and strategy for growth. *Science* 182, 975 - 981.
- 1246 Mann, K.H., 1988. Production and use of detritus in various freshwater, estuarine, and coastal
1247 marine environments. *Limnol. Oceanogr.* 33, 910 - 930.
- 1248 Marques de Silva, C., Landau, B.M., Domènech, R., Martinell, J., 2006. Pliocene Atlanto-
1249 Mediterranean biogeography of *Patella pellucida* (Gastropoda, Patellidae): palaeoceanographic
1250 implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 233, 225 - 234.
- 1251 Marshall, W., 1960. An underwater study of the epiphytes of *Laminaria hyperborea* (Gunn.) Fosl.
1252 *Brit. Phycol. Bull.* 2, 18 - 19.
- 1253 Marzinelli, E., Zagal, C.J., Chapman, M.G., Underwood, A.J., 2009. Do modified habitats have direct
1254 or indirect effects on epifauna? *Ecology* 90, 2948 - 2955.
- 1255 Marzinelli, E.M., 2012. Artificial structures influence fouling on habitat-forming kelps. *Biofouling* 28,
1256 339 - 349.
- 1257 Marzinelli, E.M., Underwood, A.J., Coleman, R.A., 2011. Modified habitats influence kelp epibiota via
1258 direct and indirect effects. *PLOS ONE* 6, e21936.
- 1259 McGrath, D., 1992. Recruitment and growth of the blue-rayed limpet, *Helcion pellucidum* (L.), in
1260 south east Ireland. *J. Mollus. Stud.* 58, 425 - 431.
- 1261 McGrath, D., 1997. Colonisation of artificially cleared *Laminaria digitata* (Huds.) Lamour. by the blue-
1262 rayed limpet *Helcion pellucidum* (L.) (Mollusca, Gastropoda). *Biol. Environ.* 97B, 245 - 248.
- 1263 McGrath, D., 2001. Inter-algal movement of marked blue-rayed limpets, *Patella pellucida* L.,
1264 between kelps on the lower shore. *J. Mollus. Stud.* 67, 398 - 400.
- 1265 McGrath, D., Foley, H., 2005. Settlement and recruitment of the blue-rayed limpet *Patella pellucida*
1266 L. in Galway Bay, west coast of Ireland, in: Wilson, J.G. (Ed.), *The intertidal ecosystem: the value of*
1267 *Ireland's shores.* Royal Irish Academy, Dublin, pp. 100 - 114.
- 1268 McKenzie, J.D., Moore, P.G., 1981. The microdistribution of animals associated with the bulbous
1269 holdfasts of *Saccorhiza polyschides* (Phaeophyta). *Ophelia* 20, 201 - 213.
- 1270 McKenzie, L.J., 1994. Seasonal changes in biomass and shoot characteristics of a *Zostera capricorni*
1271 Aschers. dominant meadow in Carins Harbour, northern Queensland. *Aust. J. Mar. Freshw. Res.* 45,
1272 1337 - 1352.
- 1273 McQueen, D.J., McLay, C.L., 1983. How does the intertidal spider *Desis marina* (Hector) remain
1274 under water for such a long time? *New Zeal. J. Zool.* 10, 383 - 392.
- 1275 Meehl, G.A., Zwiers, F., Evens, J., Knutson, T., Mearns, L.O., Whetton, P., 2000. Trends in extreme
1276 weather and climate events: issues related to modelling extremes in projects of future climate
1277 change. *Bull. Am. Meteorol. Soc.* 81, 427 - 436.
- 1278 Melville, A.J., Connell, S.D., 2001. Experimental effects of kelp canopies on subtidal coralline algae.
1279 *Austral Ecol.* 26, 102 - 108.
- 1280 Mercer, T., Howson, C., Bunker, F., 2004. Lundy European Marine Site sublittoral monitoring report
1281 2003/2004. Prepared by Aquatic Survey & Monitoring for English Nature (Contract no. FST20-46-16).
- 1282 Merzouk, A., Johnson, L.E., 2011. Kelp distribution in the northwest Atlantic Ocean under a changing
1283 climate. *J. Exp. Mar. Biol. Ecol.* 400, 90 - 98.
- 1284 Molloy, F.J., Bolton, J.J., 1996. The effects of wave exposure and depth on the morphology of inshore
1285 populations of the Namibian kelp, *Laminaria schinzii* Foslie. *Bot. Mar.* 39, 525-531.
- 1286 Moore, P.G., 1972a. The kelp fauna of northeast Britain. I. Introduction and the physical
1287 environment. *J. Exp. Mar. Biol. Ecol.* 13, 97 - 125.
- 1288 Moore, P.G., 1972b. Particulate matter in the sublittoral zone of an exposed coast and its ecological
1289 significance with special reference to the fauna inhabiting kelp holdfasts. *J. Exp. Mar. Biol. Ecol.* 10,
1290 59 - 80.
- 1291 Moore, P.G., 1973a. The kelp fauna of northeast Britain. II. Multivariate classification: turbidity as an
1292 ecological factor. *J. Exp. Mar. Biol. Ecol.* 13, 127 - 163.

- 1293 Moore, P.G., 1973b. The larger Crustacea associated with holdfasts of kelp (*Laminaria hyperborea*) in
1294 north-east Britain. Cah. Biol. Mar. 16, 493 - 518.
- 1295 Moore, P.G., 1978. Turbidity and kelp holdfast amphipoda. I. Wales and S. W. England. J. Exp. Mar.
1296 Biol. Ecol. 32, 53 - 96.
- 1297 Moy, F.E., Christie, H., 2012. Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral
1298 algae along the south and west coast of Norway. Mar. Biol. Res. 8, 309-321.
- 1299 Norderhaug, K.M., Christie, H., 2011. Secondary production in a *Laminaria hyperborea* kelp forest
1300 and variation according to wave exposure. Estuar. Coast. Shelf Sci. 95, 135-144.
- 1301 Norderhaug, K.M., Christie, H., Andersen, G.S., Bekkby, T., 2012. Does the diversity of kelp forest
1302 macrofauna increase with wave exposure? J. Sea Res. 69, 36-42.
- 1303 Norderhaug, K.M., Christie, H., Fossa, J.H., Fredriksen, S., 2005. Fish - macrofauna interactions in a
1304 kelp (*Laminaria hyperborea*) forest. J. Mar. Biol. Assoc. U. K. 85, 1279 - 1286.
- 1305 Norderhaug, K.M., Christie, H., Fredriksen, S., 2007. Is habitat size an important factor for faunal
1306 abundances on kelp (*Laminaria hyperborea*)? J. Sea Res. 58, 120 - 124.
- 1307 Norderhaug, K.M., Christie, H., Rinde, E., 2002. Colonisation of kelp imitations by epiphyte and
1308 holdfast fauna: A study of mobility patterns. Mar. Biol. 141, 965 - 973.
- 1309 Norderhaug, K.M., Christie, H., Rinde, E., Gundersen, H., Bekkby, T., 2014. Importance of wave and
1310 current exposure to fauna communities in *Laminaria hyperborea* kelp forests. Mar. Ecol. Prog. Ser.
1311 502, 295 - 301.
- 1312 Norderhaug, K.M., Fredriksen, S., Nygaard, K., 2003. Trophic importance of *Laminaria hyperborea* to
1313 kelp forest consumers and the importance of bacterial degradation to food quality. Mar. Ecol. Prog.
1314 Ser. 255, 135 - 144.
- 1315 Norderhaug, K.M., Gundersen, H., Pedersen, A., Moy, F., Green, N., Walday, M.G., Gitmark, J.K.,
1316 Ledang, A.B., Bjerkeng, B., Hjermann, D.Ø., Trannum, H.C., 2015. Effects of climate and
1317 eutrophication on the diversity of hard bottom communities on the Skagerrak coast 1990 - 2010.
1318 Mar. Ecol. Prog. Ser. 530, 29 - 46.
- 1319 Norderhaug, K.M., Nygaard, K., Fredriksen, S., 2006. Importance of phlorotannin content and C:N
1320 ratio of *Laminaria hyperborea* in determining its palatability as food for consumers. Mar. Biol. Res. 2,
1321 367 - 371.
- 1322 Norton, T.A., 1969. Growth form and environment in *Saccorhiza polyschides*. J. Mar. Biol. Assoc. U. K.
1323 49, 1025 - 1045.
- 1324 Norton, T.A., Burrows, E.M., 1969. Studies on marine algae of the British Isles. 7. *Saccorhiza*
1325 *polyschides* (Lightf.) Batt. Brit. Phycol. J. 4, 19 - 53.
- 1326 Norton, T.A., Hiscock, K., Kitching, J.A., 1977. The ecology of Lough Ine: XX. The *Laminaria* forest at
1327 Carrigathorna. J. Ecol. 65, 919 - 941.
- 1328 Novaczek, I., 1981. Stipe Growth Rings in *Ecklonia-Radiata* (C-Ag) J-Ag (*Laminariales*). Brit. Phycol. J.
1329 16, 363-371.
- 1330 Ojeda, F.P., Santelices, B., 1984. Invertebrate communities in holdfasts of the kelp *Macrocystis*
1331 *pyrifera* from southern Chile. Mar. Ecol. Prog. Ser. 16, 65 - 73.
- 1332 Ortega, K.J., Saez, C.A., Macaya, E.C., 2014. Changes in invertebrate assemblages inhabiting *Lessonia*
1333 *spicata* (Phaeophyceae) holdfasts after the 2010 earthquake-mediated coastal uplift in Chile. Rev.
1334 Biol. Mar. Oceanogr. 49, 129 - 134.
- 1335 Pedersen, M.F., Nejrup, L.B., Fredriksen, S., Christie, H., Norderhaug, K.M., 2012. Effects of wave
1336 exposure on population structure, demography, biomass and productivity of the kelp *Laminaria*
1337 *hyperborea*. Mar. Ecol. Prog. Ser. 451, 45 - 60.
- 1338 Pedersen, M.F., Nejrup, L.B., Pedersen, T.M., Fredriksen, S., 2014. Sub-canopy light conditions only
1339 allow low annual net productivity of epiphytic algae on kelp *Laminaria hyperborea*. Mar. Ecol. Prog.
1340 Ser. 516, 163 - 176.
- 1341 People, J., 2006. Mussel beds on different types of structures support different macroinvertebrate
1342 assemblages. Austral Ecol. 31, 271 - 281.

- 1343 Perkol-Finkel, S., Ferrario, F., Nicotera, V., Airoidi, L., 2012. Conservation challenges in urban
1344 seascapes: promoting the growth of threatened species on coastal infrastructures. *J. Appl. Ecol.* 49,
1345 1457 - 1466.
- 1346 Peters, A.F., Schaffelke, B., 1996. *Streblonema* (Ectocarpales, Phaeophyceae) infection in the kelp
1347 *Laminaria saccharina* (Laminariales, Phaeophyceae) in the western Baltic. *Hydrobiologia* 326, 111 -
1348 116.
- 1349 Pugh, P.J.A., Davenport, J., 1997. Colonisation vs. disturbance: the effects of sustained ice-scouring
1350 on intertidal communities. *J. Exp. Mar. Biol. Ecol.* 210, 1 - 21.
- 1351 Raffo, M.P., Eyra, M.C., Iribarne, O.O., 2009. The invasion of *Undaria pinnatifida* to a *Macrocystis*
1352 *pyrifera* kelp in Patagonia (Argentina, south-west Atlantic). *J. Mar. Biol. Assoc. U. K.* 89, 1571 - 1580.
- 1353 Raybaud, V., Beaugrand, G., Goberville, E., Delebecq, G., Destombe, C., Valero, M., 2013. Decline in
1354 kelp in west Europe and climate. *PLOS ONE* 8, e66044.
- 1355 Reed, D.C., Foster, M.S., 1984. The effects of canopy shading on algal recruitment and growth in a
1356 giant kelp forest. *Ecology* 65, 937 - 948.
- 1357 Reed, D.C., Rassweiler, A., Arkema, K.K., 2008. Biomass rather than growth rate determines variation
1358 in net primary production by giant kelp. *Ecology* 89, 2493 - 2505.
- 1359 Reed, D.C., Rassweiler, A., Carr, M.H., Cavanaugh, K.C., Malone, D.P., Siegel, D.A., 2011. Wave
1360 disturbance overwhelms top-down and bottom-up control of primary production in California kelp
1361 forests. *Ecology* 92, 2108 - 2116.
- 1362 Reisewitz, S.E., Estes, J.A., Simenstad, C.A., 2006. Indirect food web interactions: sea otters and kelp
1363 forest fishes in the Aleutian archipelago. *Community Ecol.* 146, 623 - 631.
- 1364 Rios, C., Arntz, W.E., Gerdes, D., Mutschke, E., Montiel, A., 2007. Spatial and temporal variability of
1365 the benthic assemblages associated to the holdfasts of the kelp *Macrocystis pyrifera* in the Straits of
1366 Magellan, Chile. *Polar Biol.* 31, 89 - 100.
- 1367 Rosenthal, R.J., Clarke, W.D., Dayton, P.K., 1974. Ecology and natural history of a stand of giant kelp,
1368 *Macrocystis pyrifera*, off Del Mar, California. *Fish. Bull.* 72, 670 - 684.
- 1369 Rueness, J., 1989. *Sargassum muticum* and other introduced Japanese macroalgae: biological
1370 pollution of European coasts. *Mar. Pollut. Bull.* 20, 173 - 176.
- 1371 Russell, G., 1983. Parallel growth patterns in algal epiphytes and *Laminaria* blades. *Mar. Ecol. Prog.*
1372 *Ser.* 13, 303 - 304.
- 1373 Ryland, J.S., Hayward, P.J., 1977. British anascan bryozoans. Academic Press, London, UK.
- 1374 Sala, E., Boudouresque, C.F., Harmelin-Vivien, M., 1998. Fishing, trophic cascades, and the structure
1375 of algal assemblages: evaluation of an old but untested paradigm. *Oikos* 82, 425 - 439.
- 1376 Santelices, B., 1980. Phytogeographic characterization of the temperate coast of Pacific South
1377 America. *Phycologia* 19, 1 - 12.
- 1378 Santelices, B., Ojeda, F.P., 1984. Effects of canopy removal on the understory algal community
1379 structure of coastal forests of *Macrocystis pyrifera* from southern South America. *Mar. Ecol. Prog.*
1380 *Ser.* 14, 165 - 173.
- 1381 Saunders, M., Metaxas, A., 2008. High recruitment of the introduced bryozoan *Membranipora*
1382 *membranacea* is associated with kelp bed defoliation in Nova Scotia, Canada. *Mar. Ecol. Prog. Ser.*
1383 369, 139 - 151.
- 1384 Schaal, G., Riera, P., Leroux, C., 2010. Trophic ecology in a Northern Brittany (Batz Island, France)
1385 kelp (*Laminaria digitata*) forest, as investigated through stable isotope and chemical assays. *J. Sea*
1386 *Res.* 63, 24 - 35.
- 1387 Schaal, G., Riera, P., Leroux, C., 2012. Food web structure within kelp holdfasts (*Laminaria*): a stable
1388 isotope study. *Mar. Ecol. Evol. Persp.* 33, 370-376.
- 1389 Schaffelke, B., Peters, A.F., Reusch, T.B.H., 1996. Factors influencing depth distribution of soft
1390 bottom inhabiting *Laminaria saccharina* (L.) Lamour. in Kiel Bay, western Baltic. *Hydrobiologia* 326,
1391 117 - 123.
- 1392 Schatz, S., 1984. The *Laminaria-Phycomelaina* host-parasite association - seasonal patterns of
1393 infection, growth and carbon and nitrogen storage in the host. *Helgolander Meeresun.* 37, 623 - 631.

- 1394 Scheibling, R.E., Hennigar, A.W., Balch, T., 1999. Destructive grazing, epiphytism, and disease: the
 1395 dynamics of sea urchins - kelp interactions in Nova Scotia. *Can. J. Fish. Aquat. Sci.* 56, 2300 - 2313.
- 1396 Schmidt, A.L., Scheibling, R.E., 2006. A comparison of epifauna and epiphytes on native kelps
 1397 (*Laminaria* species) and an invasive alga (*Codium fragile* ssp *tomentosoides*) in Nova Scotia, Canada.
 1398 *Bot. Mar.* 49, 315-330.
- 1399 Schultze, K., Janke, K., Krüß, A., Weidemann, W., 1990. The macrofauna and macroflora associated
 1400 with *Laminaria digitata* and *L. hyperborea* at the island of Helgoland (German Bight, North Sea).
 1401 *Helgolander Meeresun.* 44, 39 - 51.
- 1402 Schuster, M., Konar, B., 2014. Foliose algal assemblages and deforested barren areas: phlorotannin
 1403 content, sea urchin grazing and holdfast community structure in the Aleutian dragon kelp, *Eualaria*
 1404 *fistulosa*. *Mar. Biol.* 161, 2319 - 2332.
- 1405 Seed, R., Harris, S., 1980. The epifauna of the fronds of *Laminaria digitata* Lamour. in Strangford
 1406 Lough, Northern Ireland. *Proc. R. Ir. Acad.* 80B, 91 - 106.
- 1407 Sheppard, C.R.C., Bellamy, D.J., Sheppard, L.S., 1980. Study of the fauna inhabiting the holdfasts of
 1408 *Laminaria hyperborea* (Gunn.) Fosl. along some environmental and geographical gradients. *Mar.*
 1409 *Environ. Res.* 4, 25 - 51.
- 1410 Sjøtun, K., Fredriksen, S., 1995. Growth allocation in *Laminaria hyperborea* (Laminariales,
 1411 Phaeophyceae) in relation to age and wave exposure. *Mar. Ecol. Prog. Ser.* 126, 213 - 222.
- 1412 Sjøtun, K., Fredriksen, S., Rueness, J., Lein, T.E., 1995. Ecological studies of the kelp *Laminaria*
 1413 *hyperborea* (Gunnerus) Foslie in Norway, Ecology of fjords and coastal waters. Elsevier, Amsterdam,
 1414 pp. 525 - 536.
- 1415 Smale, D.A., Burrows, M.T., Evans, A.J., King, N., Yunnice, A.L.E., Moore, P.J., 2016. Linking
 1416 environmental variables with regional-scale variability in ecological structure and standing stock of
 1417 carbon with kelp forests in the United Kingdom. *Mar. Ecol. Prog. Ser.* 542, 79 - 95.
- 1418 Smale, D.A., Burrows, M.T., Moore, P., O'Connor, N., Hawkins, S.J., 2013. Threats and knowledge
 1419 gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecol Evol* 3,
 1420 4016-4038.
- 1421 Smale, D.A., Kendrick, G.A., Harvey, E.S., Langlois, T.J., Hovey, R.K., Van Niel, K.P., Waddington, K.I.,
 1422 Bellchambers, L.M., Pember, M.B., Babcock, R., C., Vanderklift, M.A., Thomson, D.P., Jakuba, M.V.,
 1423 Pizarro, O., Williams, S.B., 2012. Regional-scale benthic monitoring for ecosystem-based fisheries
 1424 management (EBFM) using an autonomous underwater vehicle (AUV). *ICES J. Mar. Sci.* 69, 1108 -
 1425 1118.
- 1426 Smale, D.A., Kendrick, G.A., Wernberg, T., 2010. Assemblage turnover and taxonomic sufficiency of
 1427 subtidal macroalgae at multiple spatial scales. *J. Exp. Mar. Biol. Ecol.* 384, 76 - 86.
- 1428 Smale, D.A., Vance, T., 2015. Climate-driven shifts in species' distributions may exacerbate the
 1429 impacts of storm disturbances on North-east Atlantic kelp forests. *Mar. Freshw. Res.* 66, 1 - 10.
- 1430 Smale, D.A., Wernberg, T., 2012. Ecological observations associated with an anomalous warming
 1431 event at the Houtman Abrolhos Islands, Western Australia. *Coral Reefs* 31, 441.
- 1432 Smale, D.A., Wernberg, T., 2013. Extreme climatic event drives range contraction of a habitat-
 1433 forming species. *Proc. R. Soc. B.* 280, 20122829.
- 1434 Smale, D.A., Wernberg, T., Yunnice, A.L.E., Vance, T., 2015. The rise of *Laminaria ochroleuca* in the
 1435 Western English Channel (UK) and comparisons with its competitor and assemblage dominant
 1436 *Laminaria hyperborea*. *Mar. Ecol.* 36, 1033 - 1044.
- 1437 Smith, S.D.A., 2002. Kelp rafts in the southern ocean. *Global Ecol. Biogeogr.* 11, 67 - 69.
- 1438 Smith, S.D.A., Simpson, R.D., 1992. Monitoring the shallow sublittoral using the fauna of kelp
 1439 (*Ecklonia radiata*) holdfasts. *Mar. Pollut. Bull.* 24, 46 - 52.
- 1440 Smith, S.D.A., Simpson, R.D., 1998. Recovery of benthic communities at Macquarie Island (sub-
 1441 Antarctic) following a small oil spill. *Mar. Biol.* 131, 567 - 581.
- 1442 Smith, S.D.A., Simpson, R.D., Cairns, S.C., 1996. The macrofaunal community of *Ecklonia radiata*
 1443 holdfasts: description of the faunal assemblage and variation associated with differences in holdfast
 1444 volume. *Aust. J. Ecol.* 21, 81 - 95.

- 1445 Sørliie, A.C., 1994. Epifyttiske alger på hapterer og stipes av *Laminaria hyperborea* (Gunn.) Foslie fra
1446 Vega i Nordland fylke. (Epiphytic algae on holdfasts and stipes of *Laminaria hyperborea* (Gunn.)
1447 Foslie from Vega, Nordland County.). University of Oslo.
- 1448 Steinberg, P.D., 1995. Interaction between the canopy dwelling echinoid *Holopneustes purpureus*
1449 and its host kelp *Ecklonia radiata*. Mar. Ecol. Prog. Ser. 127, 169 - 181.
- 1450 Steneck, R.S., 1998. Human influence on coastal ecosystems: does overfishing create trophic
1451 cascades? Trends Ecol. Evol. 13, 429 - 430.
- 1452 Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A., Tegner, M.J.,
1453 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ. Conserv. 29, 436 -
1454 459.
- 1455 Steneck, R.S., Johnson, C.R., 2013. Kelp forests: dynamic patterns, processes and feedbacks, in:
1456 Burtness, M.D., Bruno, J., Silliman, B.R., Stachowicz, J.J. (Eds.), Marine community ecology. Sinauer
1457 Associates, Inc., Massachusetts, USA, pp. 315 - 336.
- 1458 Sukhoveeva, M.V., 1975. Epiphytes on *Laminaria* of the Far East seas. Izvestiya Pacif. Res. Inst. Fish.
1459 Oceanogr. 98, 184 - 192.
- 1460 Sundene, O., 1961. Growth in the sea of *Laminaria digitata* sporophytes from culture. Norw. J. Bot.
1461 11, 83 - 107.
- 1462 Tano, S.A., Halling, C., Lind, E., Buriyo, A., Wikstrom, S.A., 2015. Extensive spread of farmed
1463 seaweeds causes a shift from native to non-native haplotypes in natural seaweed beds. Mar. Biol.
1464 162, 1983 - 1992.
- 1465 Tegner, M.J., Dayton, P.K., 2000. Ecosystem effects of fishing in kelp forest communities. ICES J. Mar.
1466 Sci. 57, 579 - 589.
- 1467 Thiel, M., Vásquez, J.A., 2000. Are kelp holdfasts islands on the ocean floor? - indication for
1468 temporarily closed aggregations of peracarid crustaceans. Hydrobiologia 440, 45 - 54.
- 1469 Thomsen, M.S., Wernberg, T., Altieri, A.H., Tuya, F., Gulbransen, D., McGlathery, K.J., Holmer, M.,
1470 Silliman, B.R., 2010. Habitat cascades: the conceptual context and global relevance of facilitation
1471 cascades via habitat formation and modification. Integr. Comp. Biol. 50, 158 - 175.
- 1472 Thomsen, M.S., Wernberg, T., Kendrick, G.A., 2004. The effect of thallus size, life stage, aggregation,
1473 wave exposure and substratum conditions on the forces required to break or dislodge the small kelp
1474 *Ecklonia radiata*. Bot. Mar. 47, 454 - 460.
- 1475 Toohey, B.D., Kendrick, G.A., 2008. Canopy-understory relationships are mediated by reef
1476 topography in *Ecklonia radiata* kelp beds. Eur. J. Phycol. 43, 133 - 142.
- 1477 Toohey, B.D., Kendrick, G.A., Harvey, E.S., 2007. Disturbance and reef topography maintain high local
1478 diversity in *Ecklonia radiata* kelp forests. Oikos 116, 1618 - 1630.
- 1479 Tuya, F., Larsen, K., Platt, V., 2011. Patterns of abundance and assemblage structure of epifauna
1480 inhabiting two morphologically different kelp holdfasts. Hydrobiologia 658, 373 - 382.
- 1481 Vadas, R.L., Steneck, R.S., 1988. Zonation of deep water benthic algae in the Gulf of Maine. J. Phycol.
1482 24, 338 - 346.
- 1483 Vahl, O., 1971. Growth and density of *Patina pellucida* (L.) (Gastropoda: Prosobranchia) on *Laminaria*
1484 *hyperborea* (Gunnerus) from Western Norway. Ophelia 9, 31 - 50.
- 1485 Valentine, J.P., Johnson, C.R., 2003. Establishment of the introduced kelp *Undaria pinnatifida* in
1486 Tasmania depends on disturbance to native algal assemblages. J. Exp. Mar. Biol. Ecol. 295, 63 - 90.
- 1487 Velimirov, B., Field, J.G., Griffiths, C.L., Zoutendyk, P., 1977. The ecology of kelp bed communities in
1488 the Benguela upwelling system. Helgolander wiss. Meeresunters 30, 495 - 518.
- 1489 Voerman, S.E., Llera, E., Rico, J.M., 2013. Climate driven change in subtidal kelp forest communities
1490 in NW Spain. Mar. Environ. Res. 90, 119 - 127.
- 1491 Waage-Nielsen, E., Christie, H., Rinde, E., 2003. Short-term dispersal of kelp fauna to cleared (kelp-
1492 harvested) areas. Hydrobiologia 503, 77 - 91.
- 1493 Wahl, M., Miolis, M., Hobday, A.J., Dudgeon, S., Neumann, R., Steinberg, P., Campbell, A.H.,
1494 Marzinelli, E., Connell, S., 2015. The responses of brown macroalgae to environmental change from
1495 local to global scales: direct versus ecologically mediated effects. Perspect. Phycol. 2, 11 - 29.

- 1496 Walls, A.M., Kennedy, R., Fitzgerald, R.D., Blight, A.J., Johnson, M.P., Edwards, M.D., 2016. Potential
1497 novel habitat created by holdfasts from cultivated *Laminaria digitata*: assessing the
1498 macroinvertebrate assemblages. *Aquaculture Environment Interactions* 8, 157 - 169.
- 1499 Watanabe, J.M., 1984. The influence of recruitment, competition, and benthic predation on spatial
1500 distributions of three species of kelp forest Gastropods (Trochidae: Tegula). *Ecology* 65, 920 - 936.
- 1501 Watt, C.A., Scrosati, R.A., 2013. Bioengineer effects on understory species richness, diversity, and
1502 composition change along an environmental stress gradient: experimental and mensurative
1503 evidence. *Estuar. Coast. Shelf Sci.* 123, 10 - 18.
- 1504 Wernberg, T., Russell, B.D., Moore, P.J., Ling, S.D., Smale, D.A., Campbell, A., Coleman, M.A.,
1505 Steinberg, P.D., Kendrick, G.A., Connell, S.D., 2011. Impacts of climate change in a global hotspot for
1506 temperate marine biodiversity and ocean warming. *J. Exp. Mar. Biol. Ecol.* 400, 7 - 16.
- 1507 Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T., Bennett, S.,
1508 Rousseaux, C.S., 2013. An extreme climatic event alters marine ecosystem structure in a global
1509 biodiversity hotspot. *Nature Clim. Change* 3, 78 - 82.
- 1510 Wernberg, T., Thomsen, M.S., 2005. The effect of wave exposure on the morphology of *Ecklonia*
1511 *radiata*. *Aquat. Bot.* 83, 61 - 70.
- 1512 Wernberg, T., Thomsen, M.S., Tuya, F., Kendrick, G.A., Staehr, P.A., Toohey, B.D., 2010. Decreasing
1513 resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer
1514 future. *Ecol. Lett.* 13, 685 - 694.
- 1515 Wernberg, T., Vanderklift, M.A., 2010. Contribution of temporal and spatial components to
1516 morphological variation in the kelp *Ecklonia* (Laminariales). *J. Phycol.* 46, 153 - 161.
- 1517 Werner, A., Kraan, S., 2004. Review of the potential mechanism of kelp harvesting in Ireland, Marine
1518 Institute and Taighde Mara Teo report. *Marine Environment and Health Series*, p. 52.
- 1519 Whittick, A., 1983. Spatial and temporal distributions of dominant epiphytes on the stipes of
1520 *Laminaria hyperborea* (Gunn.) Fosl. (Phaeophyta: Laminariales) in S.E. Scotland. *J. Exp. Mar. Biol.*
1521 *Ecol.* 73, 1 - 10.
- 1522 Włodarska-Kowalczyk, M., Kukliński, P., Ronowicz, M., Legeżyńska, J., Gromisz, S., 2009. Assessing
1523 species richness of macrofauna associated with macroalgae in Arctic kelp forests (Hornsund,
1524 Svalbard). *Polar Biol.* 32, 897 - 905.
- 1525 Žuljević, A., Peters, A.F., Nikolić, V., Antolić, B., Despalatović, M., Cvitković, I., Isajlović, I., Mihanović,
1526 H., Matijević, S., Shewring, D.M., Canese, S., Katsaros, C., Küpper, F.C., 2016. The Mediterranean
1527 deep-water kelp *Laminaria rodriguezii* is an endangered species in the Adriatic Sea. *Mar. Biol.* 163, 1
1528 - 12.
- 1529
- 1530
- 1531