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1 **CARBON EXPORT IS FACILITATED BY SEA URCHINS TRANSFORMING KELP**

2 **DETRITUS**

3

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13 **Abstract**

14 With the increasing imperative for societies to act to curb climate change by increasing
15 carbon stores and sinks, it has become critical to understand how organic carbon is produced,
16 released, transformed, transported, and sequestered within and across ecosystems. In
17 freshwater and open-ocean systems, shredders play a significant and well-known role in
18 transforming and mobilising carbon, but their role in the carbon cycle of coastal ecosystems
19 is largely unknown. Marine plants such as kelps produce vast amounts of detritus, which can
20 be captured and consumed by shredders as it traverses the seafloor. We measured capture and
21 consumption rates of kelp detritus by sea urchins across 4 sampling periods and over a range
22 of kelp detritus production rates and sea urchin densities, in northern Norway. When sea
23 urchin densities exceeded 4 m^{-2} , the sea urchins captured and consumed a high percentage
24 (ca. 80%) of kelp detritus on shallow reefs. We calculated that between 1.3 and 10.8 kg of
25 kelp m^{-2} are shredded annually from these reefs. We used a hydrodynamic dispersal model to
26 show that transformation of kelp blades to sea urchin feces increased its export distance four-
27 fold. Our findings show that sea urchins can accelerate and extend the export of carbon to
28 neighbouring areas. This collector-shredder pathway could represent a significant flow of
29 small particulate carbon from kelp forests to deep-sea areas, where it can subsidize benthic
30 communities or contribute to the global carbon sink.

31

32 Key words (5): shredders, *Laminaria hyperborea*, marine, subsidy, blue carbon

33 **Introduction**

34 Understanding the ways in which organic carbon is transformed, transported and sequestered
35 within and across ecosystems is critical in the Anthropocene, where societies must act to curb
36 climate change by limiting carbon emissions and increasing carbon stores and sinks (Canadell
37 et al. 2007; IPCC 2014). Most research to date has focused on carbon budgets and carbon
38 cycling on land or in the open ocean. However, recently it has been suggested that marine
39 plants in the coastal zone (e.g., seaweeds, seagrasses, and mangroves) may contribute
40 substantially to the amount of carbon sequestered globally (Krause-Jensen and Duarte 2016).
41 The distributions and abundance of these marine plants are changing globally (Orth et al.
42 2006; Wernberg et al. 2019), yet the importance of this ‘blue carbon’ is contentious (Howard
43 et al. 2017; Smale et al. 2018), and the current inability to account for the fate of the large
44 flux of carbon from coastal habitats has been identified as a major unknown in the global
45 carbon budget (Krause-Jensen et al. 2018).

46 Kelp forests are extensive habitats of large seaweeds that are highly productive and
47 represent an important component of the total organic carbon budget along temperate coasts
48 (Mann 1973; Wernberg et al. 2019). On average about 80% of this production enters the
49 detritus pool and can be exported to adjacent habitats where it either supports decomposer
50 communities – returning necessary nutrients to the living part of the ecosystem (Krumhansl
51 and Scheibling 2012) – or it can be buried and stored in marine sediments (Krause-Jensen
52 and Duarte 2016; Abdullah et al. 2017). The dynamics of kelp-carbon movement between
53 kelp forests and sink habitats in the ocean are not well described, but are particularly
54 important for these rocky reefs because detached kelps are not buried locally in sediment, but
55 are often consumed or exported to adjacent regions. This knowledge is therefore essential to
56 determine the potential magnitude and spatial extent of trophic subsidy and sequestration
57 (e.g. Heck et al. 2008; Krumhansl and Scheibling 2012). Large pieces of kelp detritus have

58 been observed in shallow reef and seagrass beds (Vanderklift and Wernberg 2008), on the
59 seafloor in nearshore deep subtidal areas (5 – 90 m depth) (Britton-Simmons et al. 2012;
60 Filbee-Dexter and Scheibling 2016), in deep-fjord habitats (400 m depth) (Filbee-Dexter et
61 al. 2018), and on continental margins and deeper (1000 – 2500 m depth) (Vetter and Dayton
62 1998; Filbee-Dexter and Scheibling 2014a; Krause-Jensen and Duarte 2016). However, we
63 know little about the source locations of these deposits, and have even less of an
64 understanding of transport, which depends on a complex interaction between hydrodynamic
65 conditions and physical characteristics of the detrital kelp (e.g., Wernberg and Filbee-Dexter
66 2018).

67 Of particular interest are the mechanisms controlling carbon transport from productive
68 coastal areas, especially those which are sensitive to environmental change. Shredders are
69 organisms that feed mainly on living or dead plants and that reduce the size of this material.
70 They tend to be much less efficient at assimilation compared to predators and produce
71 numerous small fragments and/or pellets of partly digested (and sometimes still even living)
72 plant material (Wotton and Malmqvist 2001). Sea urchins are important herbivores in many
73 kelp forests globally, and collapse and rapid expansions of sea urchin populations are
74 ongoing in many regions (e.g. Norway, Atlantic Canada, northern California, Tasmania) and
75 many of these changes have been linked to changing environmental conditions (Ling et al.
76 2009; Fagerli et al. 2013; Feehan and Scheibling 2014; Catton 2016). Sea urchins have a
77 solid jaw and calcium carbonate teeth, known as Aristotle's lantern, that enables them to feed
78 on tough kelp tissue, and they likely play an important role in shredding kelp detritus. They
79 generally feed on kelp fragments or whole dislodged blades, stipes, and whole plants that are
80 freely drifting along the seafloor (Harrold and Reed 1985). Under some conditions, sea
81 urchins also destructively graze on attached plants, creating 'barrens' devoid of standing
82 algae (Norderhaug and Christie 2009; Filbee-Dexter and Scheibling 2014b). Most consumed

83 algae pass through the sea urchin's intestine and are egested as feces, which contain relatively
84 large fragments of fresh algal material (Sauchyn and Scheibling 2009), thereby transforming
85 coarse kelp fragments into fine particles. This has at least two important implications for the
86 fate of kelp detritus. First, sea urchin feces sink 20 times slower than large detrital fragments
87 or whole blades, allowing more time for them to be swept away by horizontal water
88 movement, which can extend its dispersal distance (Wernberg and Filbee-Dexter 2018).
89 Capture and shredding of kelp increases its fragmentation rate, which speeds up the release of
90 nutrients because smaller fragments or feces have a larger relative surface area, which is
91 more "attackable" for microorganisms. Second, because kelp that passes through a sea
92 urchin's intestine becomes coated with bacteria from their gut, this egested material is more
93 rapidly degraded or consumed compared to fresh kelp material (Wotton and Malmqvist 2001;
94 Yorke et al. 2019).

95 The extent to which kelp detritus is converted to smaller fecal particles depends on: 1)
96 the ability of sea urchins to capture detritus as it moves out of kelp forests and passes through
97 adjacent habitats; and 2) the consumption rate of this material, which can vary seasonally and
98 spatially (Lauzon-Guay and Scheibling 2010). The capture rate of detritus is expected to be
99 strongly linked with sea urchin density (i.e., Lauzon-Guay and Scheibling 2007; Vanderklift
100 and Wernberg 2008; Filbee-Dexter and Scheibling 2014a). At high densities, sea urchins are
101 often food limited (i.e., they consume most available food), suggesting that some threshold
102 level of density exists where sea urchins capture most available detritus, and any further
103 increases in density should not affect the proportion of detritus shredded.

104 In this paper we quantify the amount of total detrital production that moves through
105 the sea urchin 'collector-shredder pathway' in kelp forests with varying sea urchin densities
106 and explore how this transformation affects the spatial extent of kelp carbon transfer. This

107 knowledge is required to predict how trophic connectivity and carbon sequestration will vary
108 with changing herbivory, which is currently observed in many kelp forests worldwide.

109

110 **Materials and methods**

111 *Study area.*

112 This study was conducted at Malangen fjord, northern Norway (69 °N, 17 °W), from October
113 2016 to May 2018. The mouth of Malangen fjord has extensive kelp forests that dominate
114 skerries, shoals, and outer shores down to 30 m depth (16.6 ± 3.4 kg m² FW at 4–6 m depth;
115 M. Pedersen, unpublished data). The dominant kelp is *Laminaria hyperborea*, with *Alaria*
116 *esculenta* and *Saccharina latissima* occurring at lower densities in some mixed stands. At the
117 entrance to the fjord, barrens created by overgrazing by the sea urchin *Strongylocentrotus*
118 *droebachiensis* occur at the deep margin (4 – 8 m depth) of many kelp forest patches (Filbee-
119 Dexter et al. 2018). *S. droebachiensis* is a prominent herbivore in kelp forests at northern
120 latitudes in the Atlantic and Pacific Oceans (Dean et al. 2000; Norderhaug and Christie 2009;
121 Filbee-Dexter and Scheibling 2014b; Filbee-Dexter et al. 2019). The sea urchin *Echinus*
122 *esculentus* was also common in this system, occurring under kelp canopies.

123

124 *Detritus capture by sea urchins.*

125 The proportion of detrital kelp captured by sea urchins in shallow subtidal habitats was
126 quantified by scuba divers at 10 sites in October 2016, March, May and August 2017, and at
127 6 sites in May 2018. Transects were conducted in kelp forests and habitats adjacent to kelp
128 forests (sand and overgrazed bedrock). Each transect began at a submerged float at 4 to 6 m
129 depth within a stand of kelp and extended to the N, E, S, and W for 50 m to a maximum
130 depth of 12 m or until the diver reached the shore. Divers swam approximately 1 m s⁻¹ at 0.5
131 m above the bottom and videoed (Go-Pro Hero 3) the seafloor, creating a field of view (FOV)

132 of $0.49 \pm 0.30SD$ m². We estimated the FOV by laying a transect line marked every 0.1 and
133 0.5 m on the seafloor, videoing it in the same manner described above, and then measuring
134 frame area in 40 frames of video using the line as a scaling bar. We analyzed videos in real
135 time and 1) classified bottom type (barrens, kelp forest, sand/other), 2) counted sea urchin
136 number, and 3) recorded observations of kelp detritus, differentiated by type of detritus: stipe,
137 whole blade, or blade fragment; and whether it was associated with sea urchins or free
138 floating. These measures were tabulated every second in an excel Macro, but to ensure non-
139 overlapping measures only data from every 4th second were used. Sea urchin counts was
140 converted to individuals m⁻² using the FOV. Large accumulations of detritus were labeled
141 separately (2% of all observations) and excluded from the analysis due to challenges of
142 identifying sea urchins within them. Small particles and fragments of detritus (< 1 cm length)
143 were difficult to see in videos, and thus were not captured in these measures.

144

145 *Capture and grazing rate.*

146 We measured the capture and grazing rate of kelp detritus by sea urchins in kelp forest and
147 barrens habitats at 4 sites in May and August 2017, and May 2018. At each site, we deployed
148 5-m long chains baited with 4 treatments (2 types of detritus: blades and stipes; 2 modes of
149 attachment: tethered and fixed). We stretched one chain along the seafloor in the barrens and
150 one chain under the kelp canopy at each site. Pre-weighed pieces of kelp blades (7 ± 0.1 g)
151 and stipes (35 ± 0.5 g) (n = 8 of each) were attached either directly to the chain or tethered to
152 the free end of a 20-cm long fishing twine. We used the tethers to determine whether capture
153 rates differed when detritus was freely moving or fixed to the sea floor. Blades were secured
154 with clothes pins and stipes with cable ties. Chains were revisited within 48 – 77 h following
155 deployment, videoed by a diver using a Go-Pro, then collected and brought back to shore. On
156 shore, kelps were carefully removed, weighed, and examined for evidence of grazing (i.e.,

157 bite marks). Grazing rate was measured as change in biomass over deployment time. To
158 measure the percent of detrital kelp pieces captured by sea urchins we counted the number of
159 pieces of detritus in contact with sea urchins from the Go-Pro videos. We also estimated sea
160 urchin densities around the chain by counting the number of adult *S. droebachiensis* (>15
161 mm) and *E. esculentus* within 0.2 m on either side of the chain (using chain links and tethered
162 clothes pins for scale). To investigate whether these grazing rates varied seasonally, we
163 deployed chains at a control site with a stable sea urchin population within a sheltered bay
164 (Sommarøy) 5 times between August 2016 and August 2017. We used this control site
165 because it was easier to access year-round compared to the exposed kelp forest sites, which
166 enabled higher frequency sampling events over time. We also measured hourly temperature
167 over this period using onset HOBO loggers attached to the submerged float at each site.

168

169 *Rates of shredding of kelp detritus.*

170 To estimate how much kelp detritus is captured and shredded annually from reefs with a
171 range of sea urchin densities and detrital kelp production rates, we obtained measures of the
172 formation of blade detritus (dislodged, spring cast, and eroded blades) and stipe detritus
173 (dislodged) at each kelp forest site between August 2016 – August 2017 (Pedersen et al.
174 2019). These were multiplied by capture rates of blade material (whole blades and blade
175 fragments) and stipes by sea urchins measured in this study (Table 1). We estimated the
176 biomass of detrital kelp particles produced per area of reef based on ~50% assimilation of
177 kelp when it is consumed by sea urchins (Larson et al. 1980; Mamelona and Pelletier 2005),

178

179 *Modelling the influence of detrital fragment size on export.*

180 To examine the impact of sea urchin shredding on the export of kelp detritus, we modelled
181 the transport of kelp blades and sea urchin feces (processed kelp) released from shallow reefs.

182 We simulated dynamic ocean circulation for our study area from August 2015 to August
183 2016 using the open-source Regional Ocean Modeling System with a 160 m x 160 m
184 horizontal resolution and a 35-layer vertical resolution (ROMS, myroms.org, see examples
185 Shchepetkin and McWilliams 2005; Haidvogel et al. 2008) (Online Resource 1). To
186 determine the vertical movement of the detritus, we used a particle tracking individual-based
187 model (IBM), which calculated the movement of individual blades and feces, accounting for
188 turbulent mixing at 1 second resolution, and using the ocean model as an input. The sizes and
189 sinking speeds were measured *in situ* for kelp blades and freshly egested sea urchin feces
190 collected in our study area (Wernberg and Filbee-Dexter 2018). We used these measures to
191 select a range of material densities that represented blades and fecal particles in the model.
192 All pieces of kelp detritus were negatively buoyant. The detrital kelp pieces (18 000 blades
193 and 2000 feces) were released at 1 m height above the sea-floor from randomly selected
194 points within the source kelp forest polygons. This 1 m distance corresponded to the height of
195 the kelp canopy in our area. Detrital kelp pieces were released 6 times a day, every 7 days,
196 over a 1-year period. The cumulative distance traveled by each piece was calculated until it
197 reached the seafloor (< 20 cm from the bottom) and stopped moving along the bottom (speed
198 < 1 m s⁻¹ for 2 h). The source kelp forest polygons are based on a predictive model of kelp
199 forests (Bekby et al. 2013), and covered a total area of 20.4 km².

200

201 *Analyses.*

202 We compared sea urchin densities measured from dive surveys in different habitats (kelp
203 forest or barrens), sampling periods, and sites by fitting a mixed effects model with habitats
204 as fixed effects and sites and campaigns as random effects using Restricted Maximum
205 Likelihood (REML) (lme4 package; Pinheiro et al. 2018). To identify factors influencing the
206 capture of detritus by sea urchins from field observations and experimental detritus additions,

207 we assessed how the percentage of detritus captured in surveys and the percentage of detritus
208 attached to chains with bite marks varied with sea urchin density, habitat type, and detritus
209 type (fragment, stipe, blade) using a mixed effects model, with habitat and detritus type as
210 fixed effects and sampling period as a random effect. We observed that capture rates of
211 detritus increased with increasing sea urchin density until a threshold level where almost all
212 detrital pieces within the habitat were captured. To test whether this breakpoint was
213 significant, we fitted a piecewise regression model to our data and compared it to a fitted
214 linear model (segmented package; Muggeo 2017). Grazing rates on detritus attached to
215 chains in barrens and kelp forests habitats were fitted to linear models. Differences in grazing
216 rates on tethered and untethered stipe and blade material deployed at a sheltered bay site for 5
217 time periods were analyzed using a 3-way ANOVA with time as a fixed factor as it was the
218 variable of interest in this control site. All analyses were performed in R version 3.4.2.

219

220 **Results**

221 *Sea urchin density and kelp detritus.*

222 Sea urchins formed a dominant component of the benthic community, and often captured or
223 consumed kelp detritus under the kelp canopy and within the surrounding barrens (Fig. 1).
224 Sea urchin densities ranged from 0.5 to 7 individuals m⁻² at the 10 kelp habitats and 3 to 10
225 individuals m⁻² at the 6 adjacent barren habitats (Fig. 2). Sea urchin densities within sites did
226 not vary seasonally over the 4 sampling periods (random effect SD = 0.24), but were different
227 among sites (random effect SD = 1.76) (based on mixed effect model with residual error SD
228 = 1.64). Densities were higher in barrens than adjacent kelp forests ($F_{1,65} = 22.5$, $p < 0.001$).

229 The mean density of kelp blade fragments was ca. 0.10 fragments m⁻² within kelp
230 forests and ca. 0.20 m⁻² in adjacent barrens when averaged across sites and sampling periods
231 (Online Resource 1; Fig. S1A). The abundances of detached whole blades in kelp forests

232 were similar to barren habitats, averaging ca. 0.09 blades m⁻² (Online Resource 1; Fig. S1B),
233 while the abundance of detached stipes was very low, averaging 0.03 stipes m⁻² across sites
234 (kelp and barrens) and sampling periods (Online Resource 1; Fig. S1C).

235

236 *Detritus capture by sea urchins.*

237 There was a strong positive relationship between the percent of drifting pieces of detritus
238 captured by sea urchins in kelp forest and barrens habitats and the background sea urchin
239 density at those sites (Fig. 3). Capture rates were not significantly different for blades,
240 fragments, and stipes ($F_{2,43} = 0.55$, $p = 0.55$). However, because capture rates of stipes were
241 highly variable, we plotted them separately for ease of interpretation (Fig. 3C). Capture rates
242 were ca. 22% higher in barrens than in kelp forest habitats ($F_{1,45} = 0.6$, $p = 0.011$) and were
243 positively influenced by sea urchin density ($F_{1,45} = 19.7$, $p < 0.001$). The piecewise regression
244 model showed that capture rates of detritus increased with increasing sea urchin density, until
245 a threshold level where almost all pieces of detritus were captured. The model explained
246 more variance in our response compared to a linear model with no breakpoint ($R^2 = 0.65$ vs.
247 $R^2 = 0.52$, $p = 0.001$) and estimated a single breakpoint at 3.8 ± 0.6 SE sea urchins m⁻² above
248 which capture rate did not increase (slope = 2.4% captured urchin⁻¹ m⁻²) (Fig. 3). The smallest
249 detrital fragments that we observed in contact with sea urchins were ~1 cm long; and held to
250 their aboral side by their tube feet. The only other large (i.e., visible in videos) detritivores
251 observed in contact with kelp detritus were sea cucumbers (*Cucumaria frondosa*), and these
252 were not nearly as common as sea urchins and not visibly shredding the kelp detritus.

253 In our field studies, sea urchins consumed kelp detritus at similar rates across seasons,
254 and captured detrital fragments that were both attached and freely moving on the seafloor
255 with similar efficiency (tethered vs. untethered). Grazing rates by sea urchins on kelp blades
256 and stipes deployed on chains at the control site in the sheltered bay in August and October

257 2016, and March, May, and August 2017 ranged from 0.2 to 1.9 g WW d⁻¹, and did not differ
258 significantly between sampling events ($F_{4,210} = 2.22$, $p = 0.068$) (Online Resource 1; Fig. S2).
259 Bottom temperatures during the study period were highest in August (11.5°C) and lowest in
260 April (4.2°C). Grazing rates were similar between tethered and untethered treatments ($F_{1,210} =$
261 0.74, $p = 0.391$), with no interaction between detritus type and tethering ($F_{1,210} = 0.082$, $p =$
262 0.78). Grazing was significantly lower on stipes compared to blades ($F_{1,210} = 156$, $p < 0.001$).

263 For detritus addition experiments at our 5 study sites, the proportion of blades with
264 bite marks at the time of retrieval increased sharply with urchin density until around 2 to 3
265 sea urchins m⁻² (Fig. 4A). In barrens, more than 50% of the deployed blades had grazing
266 marks, even at low sea urchin densities. This positive relationship between sea urchin density
267 and grazing rate was evident for stipes, but no clear threshold was detected (Fig. 4B).
268 However, in barrens with more than 5 urchins per m², >80% of the stipes had bite marks. The
269 proportion of detrital pieces with bite marks was significantly influenced by habitat type
270 (kelp forest < sea urchin barren; $F_{1,300} = 361$, $p < 0.001$), detritus type (blades > stipes; $F_{1,300} =$
271 102 $p > 0.001$), and background sea urchin density ($F_{1,300} = 204$, $p > 0.001$) (Linear Mixed
272 Effects Model accounting for random effect of campaign = 10.3 SD; residual error SD =
273 20.4). There was no significant difference in these results when we used densities of *S.*
274 *droebachiensis* alone or the summed densities of both *E. esculentus* and *S. droebachiensis*, so
275 the latter are presented.

276 There was no significant difference in grazing rate on deployed detritus between the
277 two habitat types (GLM, $p = 0.117$) and 3 deployment times (GLM, $p = 0.10$). There was a
278 positive, linear relationship between grazing rate on deployed detritus and sea urchin
279 densities across habitats and sampling periods ($p < 0.001$), and this relationship was stronger
280 for blades compared to stipes (Fig. 5).

281

282 *Production of shredded detritus.*

283 The total production rate of kelp detritus ranged between 3.5 and 29.6 g FW m⁻² d⁻¹ across
284 our 10 study sites (Table 1). This estimate is based on the total detrital blade material
285 (average ± SE = 329 ± 56 g FW m⁻² through dislodgement, 1859 ± 133 g FW m⁻² due to
286 spring cast, and 538 ± 33 g FW m⁻² due to distal erosion) and stipe material (358 ± 79 g FW
287 m⁻² through dislodgement) produced annually between August 2016 – August 2017 at these
288 same sites (Pedersen et al. 2019; Fig. 6). Average capture rates (± SE) of kelp detritus by sea
289 urchins corresponded to 50 ± 11 % of the blades and blade fragments and to 52 ± 12 % of the
290 stipes. The average amount of captured and consumed detritus m⁻² was 15.2 ± 3.1 g FW d⁻¹,
291 and ranged between 3.5 and 29.6 g m⁻² d⁻¹ (Table 1). Assuming ~50% assimilation of kelp
292 when it is consumed by sea urchins (Larson et al. 1980; Mamelona and Pelletier 2005), this is
293 equivalent to a 5 to 47% conversion rate of large pieces of detritus to small sea urchin feces.

294

295 *Modelling the influence of detritus size on export.*

296 The model simulation showed that most detrital blades and feces remained relatively close to
297 shore. 50% of blades deposited after moving 8.5 km from their point of release whereas 50%
298 fecal particles deposited after moving 26.1 km from their point of release (Figs. 7,8). Fecal
299 particles with slower sinking rates were transported much further than large blades (90th
300 percentiles = 214 km for feces compared to 56 km for whole blades), moving as far as 321
301 km before reaching the seafloor. In shallow habitats, higher local settlement occurred in
302 gently sloping environments and when detritus was produced in the form of quickly sinking
303 large pieces and not small, slower sinking fragments. Beyond the shallow subtidal, detritus
304 accumulated in deep basins on the coastal shelf, in the deepest areas of the fjord and in
305 regions with local topographic features (Fig. 8).

306

307 **Discussion**

308 Macroalgae forests produce an estimated 170 millions of tons of organic carbon each year
309 (Krause-Jensen and Duarte 2016). Discovering the fate of that major pool of carbon is a key
310 step towards understanding its importance in the global carbon sink and role as a resource
311 subsidy to benthic communities (Renaud et al. 2015; Krause-Jensen et al. 2018). Because no
312 kelp-carbon is buried within kelp forests, the transport and processing of kelp detritus is vital
313 to determine its ultimate fate (Smale et al. 2018).

314 The field surveys and experimental manipulations in this study, combined with
315 tagging studies from the same area, indicate that sea urchins are highly effective at capturing
316 kelp material moving freely in kelp forests and barren areas. We measured high association
317 rates between the amount of captured kelp detritus and sea urchin densities in both field
318 surveys and in manipulative experiments. Beyond densities of 4 urchins m⁻², sea urchins
319 captured most observed pieces of kelp detritus within these habitats. The strong relationship
320 between sea urchin density and the presence of sea urchin bite marks on deployed stipes and
321 blade detritus, suggests high encounter rates of detrital material when it occurs within the
322 vicinity of sea urchins and confirms that these organisms are highly important shredders in
323 the system. This efficient capture rate is further supported by the lack of difference between
324 tethered and untethered kelps in our manipulative experiments, which show that sea urchins
325 can capture moving kelp as easily as anchored kelp.

326 The higher percentage of detrital kelp pieces captured in barrens compared to kelp
327 habitats with similar sea urchin densities suggests that elements of the habitat type (e.g.,
328 canopy cover, food supply, predators, water movement) influence the capture of kelp by sea
329 urchins. This is consistent with findings from other systems that sea urchins in barrens are
330 more food-limited, and therefore more active feeders compared to sea urchins within kelp
331 forests (Harrold and Reed 1985). Finally, the lack of grazing on detrital kelp deployed at sites

332 with low sea urchin densities suggests that the impact of sea urchins is localized, and that
333 they do not respond to food cues or search for kelp over large distances. This was also
334 documented in Atlantic Canada (Filbee-Dexter and Scheibling 2014a). The low grazing on
335 kelp stipes (compared to kelp blades) by sea urchins may be because it was difficult for sea
336 urchins to capture the heavy rolling stipes in a kelp forest. The amount of supportive tissue,
337 including lignins and structural compounds in the outer cortex, may also be higher in stipes
338 compared to blades, making them less palatable (Leclerc et al. 2013). For other *Laminaria*
339 species, stipes are less palatable and attract less grazers than blades do, which may explain
340 this preference (Johnson and Mann 1986).

341 High *in situ* grazing rates of kelp detritus by sea urchins suggest that most detritus
342 captured by urchins is rapidly converted to small fecal particles. Grazing rates of deployed
343 blades on chains were high, matching or exceeding those measured for other sea urchins in
344 the North Atlantic, e.g., 0.7 to 3.5 g ind.⁻¹ d⁻¹ (Lauzon-Guay & Scheibling 2007a) and 1.7 g
345 ind.⁻¹ d⁻¹ (Sauchyn & Scheibling 2009a). However, not all kelp captured by sea urchins is
346 necessarily consumed, but may also be fragmented and exported as small undigested
347 particles. Filbee-Dexter & Scheibling (2012) estimated that 2.6% of the mass lost each day by
348 deployed kelp detritus was due to fragmentation alone. The lack of strong seasonal variability
349 in capture rates and grazing rates suggests that our measures from August and May can be
350 used to estimate transformation rates of kelp blades to feces over the annual cycle of carbon
351 production and export.

352 Sea urchins may play a similar role to invertebrate collectors and shredders in other
353 aquatic ecosystems (e.g., streams) (Wotton and Malmqvist 2001), by stimulating the
354 breakdown and transport of carbon (Sauchyn and Scheibling 2009; Wernberg and Filbee-
355 Dexter 2018). The food quality of feces increases over time, which – combined with its
356 smaller size – will impact how it is used by benthic organisms (Yorke et al. 2019). The

357 content of organic matter and energy in freshly egested *S. droebachiensis* feces (pellets of
358 *Laminaria digitata*) deployed at 6 to 16 m depth in the Northwest Atlantic declined over the
359 first 3 days but then increased over the next 16 days in total and labile organic matter and
360 available energy content (Sauchyn and Scheibling 2009). Similarly, *S. droebachiensis* that
361 consumed fresh *Nereocystis luetkeana* kelp egested feces with higher lipid content compared
362 to fresh *N. luetkeana* (Schram et al. 2018). Shredding plant material into smaller fragments
363 that are easily accessible for microbial colonisation and activity, may further increase
364 degradation of kelp material. Shredded macroalgae and egested phytoplankton by benthic
365 suspension feeders, gastropods and zooplankton in coastal and open ocean ecosystems,
366 rapidly host diverse communities of bacteria and protozoa, which increase its nutritional
367 quality by taking up inorganic nutrients from the surrounding water and accelerating
368 degradation (Peduzzi and Herndl 1986; Hansen et al. 1996; Povero et al. 2003; Thor et al.
369 2003). Based on relationship between the lost proportion of *Strongylocentrotus*
370 *droebachiensis* fecal dry weight (material = *Saccharina latissima*) after t days ($0.68e^{-0.41t} +$
371 0.32) (Sauchyn and Scheibling 2009) and the average time until settlement of feces in our
372 model (11.7 ± 6.7 h), we estimate that ~12.5% of the fecal material is remineralized in
373 transport.

374 The transformation from large blades to small detrital particles not only has important
375 consequences for how rapidly kelp is incorporated into benthic food webs (Yorke et al.
376 2019), but it also influences the fate of the exported kelp (Wotton and Malmqvist 2001).
377 Small particles sink slower than large blades, stipes, or whole thalli, allowing more time for
378 them to be swept away by horizontal water movement. Older feces are even more likely to be
379 suspended and transported horizontally because feces rapidly lose labile organic compounds,
380 become less dense and, as a result, sink even slower over time (Sauchyn and Scheibling
381 2009). Our model showed that this transformation can extend mean dispersal distance by 4

382 times, increasing the likelihood that this carbon will move off the coastal shelf and into deep
383 basins. In terms of the role kelps play in moving organic carbon to sink habitats,
384 sequestration can occur when detritus is exported and buried in soft sediment depositional
385 areas or is transported beyond the 1000 m deep sequestration horizon, where it is stored in the
386 long-term (Krause-Jensen and Duarte 2016). Our current model and our past observations of
387 the detritus on the seafloor (Filbee-Dexter et al. 2018), suggest that most large pieces of
388 detritus (e.g., blades and stipes) move slowly and remain close to shore. As a result, they
389 would therefore require substantial cross shelf movement for large pieces of detritus to reach
390 beyond 1000 m depth. In coastal areas such as Malangen fjord, which are bounded by a large
391 coastal shelf with no submarine canyons to link to the deep sea, burial in fjord sediments may
392 be an important process by which large pieces of detritus are taken out of the short-term
393 carbon cycle (Smith et al. 2015). In contrast, smaller detrital fragments and particles have
394 larger potential for long distance export, and thus fragmentation and grazing may be critical
395 processes by which macroalgae reach deep coastal sediments (Queirós et al. 2019) or are
396 exported off the shelf and below the 1000 m depth sequestration horizon (Krause-Jensen and
397 Duarte 2016).

398 Based on detrital production rates measured from our study sites, we estimate that
399 between 1.3 and 10.8 kg of kelp m⁻² are collected and shredded annually from reefs with a
400 range of urchin densities and detrital kelp production rates. This estimate is based on average
401 capture rates of 50% of detrital blades/fragments and 52% of detrital stipes within kelp
402 forests habitats, which may either overestimate the amount converted because it does not
403 include kelp that is immediately exported or kelps that deposit in large accumulations, or
404 underestimate the amount because it does not include kelp collected and shredded in adjacent
405 habitats (e.g., barrens). However, Filbee-Dexter et al. (2018) tracked slow movement of
406 whole kelp blades, blade fragments, and stipes in our study area, and recovered 53% of

407 tagged kelps within 2 weeks after they were released at 6 m depth, 79% of which were
408 associated with sea urchins, supporting the assertion that a substantial portion (>50%) of kelp
409 detritus is retained and captured by urchins in these shallow habitats. Further, our model
410 suggests that a substantial proportion of large pieces of detritus settle on the sea floor rapidly
411 (< 1 km from release point) where there is a high chance they will land in habitats with sea
412 urchins. The extent that detritus does not settle locally, but is transported away from shallow
413 grazers and into pelagic/deep sea areas depends on a combination of the sinking speed of the
414 piece of detritus, the hydrodynamic environment at its release site, and the vertical distance it
415 can fall before reaching the seafloor. These considerable sources of variability are partly
416 captured in our estimates, which are taken from study sites with a range of exposures and
417 diverse topographies, using different types of detritus, and using a model with high spatial-
418 temporal resolution that captures periods of both strong and weak water movement.

419 Sea urchin grazing is one of the most pervasive ecological processes in kelp forests
420 globally, and has changed dramatically in many regions due to anthropogenic climate change
421 (Steneck et al. 2002; Filbee-Dexter and Scheibling 2014b; Wernberg et al. 2019). In mid-
422 Norway, sea urchin recruitment is now failing with increasing temperatures and increased
423 mesopredator populations (Christie et al. 2019)(Fagerli et al. 2013, 2014). In Nova Scotia,
424 Canada sea urchins have been effectively removed from the system as a result of climate-
425 driven disease (Feehan and Scheibling 2014). The southern movement of the eastern
426 Australia current into Tasmania (Ling et al. 2009) and an extreme marine heatwave ('the
427 blob') in Northern California (Rogers-Bennett and Catton 2019)(Catton 2016) have led to sea
428 urchin population explosions, which triggered destructive overgrazing and large-scale kelp
429 forest loss. The concomitant change in capture (collection) and shredding rates of kelp
430 detritus associated with changing sea urchin densities is likely to have substantially altered
431 the amount of detritus moving through different export pathways, with a higher percentage

432 detritus leaving shallow reefs as small particles when sea urchin densities are high. This will
433 impact the magnitude, transport pathways, and endpoints of detrital deposits. Of course, the
434 importance of sea urchins for kelp carbon export depend on a delicate balance between sea
435 urchins being abundant enough to capture significant amounts of kelp detritus and being too
436 abundant to persist by grazing detritus alone (Harrold and Reed 1985). When sea urchins are
437 too abundant they can destructively graze attached kelps, decreasing overall standing stock of
438 carbon, and drastically reducing the amount of kelp available to be exported as detritus
439 (Krumhansl et al. 2014). If they are absent, an important collector-shredder is absent from the
440 ecosystem, and the distance of carbon transfer from intact kelp forests is reduced. Either way,
441 these organisms appear to be of central importance for the breakdown and relocation of
442 organic material along many temperate coasts and should be considered when studying the
443 fate of this detritus.

444 In conclusion, we show that the capture and consumption of kelp detritus by sea
445 urchins plays a major role in determining the transport pathway and rate of export of kelp
446 carbon to adjacent ecosystems. Grazing by sea urchins is one of the most pervasive processes
447 across kelp forests. Sea urchins consumed a large percentage of the total kelp production, and
448 arguably, provided the most important process by which large pieces of detritus are
449 transformed into fragments. Furthermore, it is likely that *S. droebachiensis* (and other sea
450 urchins) play a similar role in other kelp forests within their distributional area (i.e., the cold
451 temperate Atlantic, north Pacific, and Arctic), which would result in a substantial amount of
452 kelp carbon moving through this collector-shredder pathway at a broader scale.

453

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616

617 Table 1. Average daily production of kelp detritus (blades and blade fragments and stipes),
 618 average sea urchin densities, and measures of detritus capture by sea urchins at each kelp
 619 forest site. These data are used to estimate the amount of shredded detritus (i.e., the amount
 620 of detached kelp fragmented/grazed by sea urchins) within kelp forests. Detritus production
 621 measured by Pedersen et al. (in review).

Site	Detritus production (g FW d ⁻¹ m ⁻²)		Sea urchin density (m ⁻²) Kelp forest	Capture in kelp forest (%)		Grazed detritus (g FW m ⁻² d ⁻¹) Blades, fragments, and stipes
	Blades and fragments	Stipes		Blade and fragments	Stipes	
1	22.8±13.0	1.0±0.4	3.9±0.6	72	94	17.3±9.7 (73%)
2	26.0±13.6	1.2±0.5	7.3±0.8	94	100	25.6±13.4 (94%)
3	29.9±21.0	1.2±0.3	5.5±1.0	97	56	29.6±20.5 (95%)
4	32.4±22.7	1.4±0.6	4.4±0.3	86	50	28.6±19.8 (85%)
5	31.3±16.5	3.0±1.2	1.7±0.4	41	50	14.3±7.4 (42%)
6	28.1±13.8	6.6±8.3	2.7±0.3	21	67	10.3±8.4 (30%)
7	25.2±13.1	6.9±2.0	0.6±0.2	21	8	5.8±2.9 (18%)
8	25.1±17.7	2.9±0.7	0.6±0.1	13	8	3.5±2.4 (12%)
9	27.1±9.2	4.9±3.4	0.7±0.3	33	83	13.0±5.8 (41%)
10	24.7±12.0	6.8±2.8	1.4±0.4	17	NA	4.2±2.0 (13%)

622

623 **Figure legends**

624 **Fig 1.** Sea urchins within kelp forest (A) and on barrens (B) habitats at 8 m depth. Kelp
625 fragments attached to a grazing chain (C) and detritus captured by sea urchins on barrens (D).
626 Photographs taken by T Wernberg and K Filbee-Dexter

627

628 **Fig 2.** Sea urchin density in kelp forest (A) and barrens (B) sites during 4 sampling periods.
629 Average \pm SE for observations in all 4 transects at each site (4 x 50 m). For study site
630 locations see Fig. 8

631

632 **Fig 3.** Percent detrital blade fragments and whole blades captured by sea urchins in surveys
633 across kelp forest (A) and barrens habitats (B), and percent stipes captured by sea urchins in
634 kelp forest and barrens habitats (C) (site number = 10). Fitted segmented regression line
635 (Capture % \sim urchin density + habitat type) shown. Points are mean \pm SE averaged over
636 sampling periods)

637

638 **Fig 4.** Percent of detrital blades (A) and stipes (B) with sea urchin bite marks after being
639 deployed on chains in barrens and kelp forests at 5 sites with a range of sea urchin densities
640 (Fig. 2), over 3 campaigns

641

642 **Fig 5.** Sea urchin grazing rate on kelp blade (A) and stipe (B) detritus attached to chains
643 deployed in barrens and in kelp forests with different background sea urchin densities over 3
644 sampling periods. Linear model (\pm SE) fitted to relationship between grazing rate and urchin
645 densities across habitats and sampling periods. All points are average \pm SE for a single chain
646 (n = 8 blades and 8 stipes per chain)

647

648 **Fig 6.** Daily production of kelp detritus through dislodgement, erosion, and spring cast at our
649 10 study sites (ordered by increasing sea urchin density). Data are average fresh weight
650 across 4 sampling periods (\pm SE) between August 2016 and August 2017 from Pedersen et al.
651 (2019)

652

653 **Fig 7** Export distance for detrital kelp. Distance that sea urchin fecal particles (B) and whole
654 blades (A) travelled before settling on the seafloor, as estimated from model simulations
655 (n=18 000 blades, 2000 feces pellets). Note different x axis scales

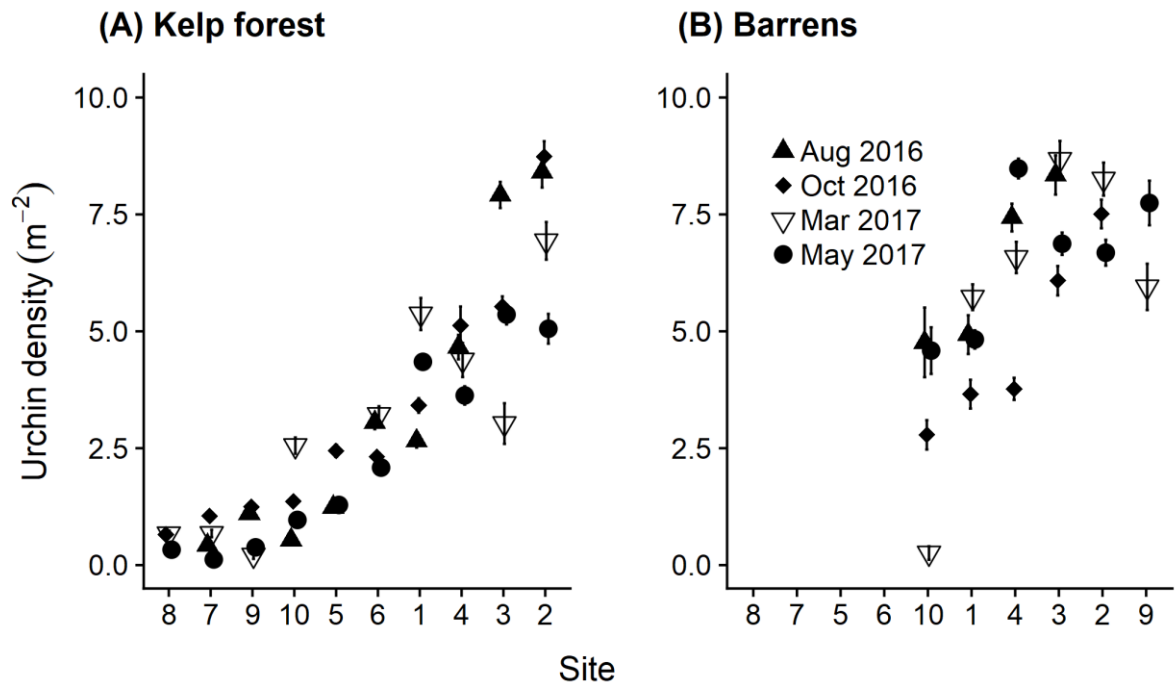
656

657 **Fig 8** Spatial pattern of settlement locations of whole blades and feces (blue points) released
658 from 4 kelp forest areas in the dispersal model (outlined in red). All kelp forest areas (red and
659 orange polygons) were estimated from a predictive kelp model developed by the Norwegian
660 habitat mapping program (Bekkby et al. 2013). The red kelp areas used in the model
661 corresponded to the locations of our field sites (yellow stars; corresponding to site numbers in
662 Fig. 2; site C shows location of sheltered site for the seasonal grazing chains). Deep areas at
663 the fjord entrance and coastal shelf are outlined using the 400 m depth contour



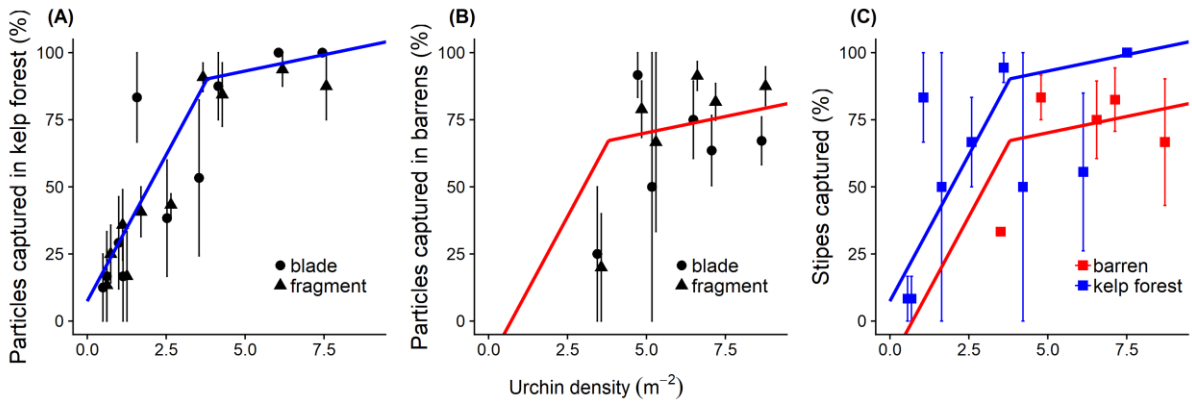
664

665 Fig 1



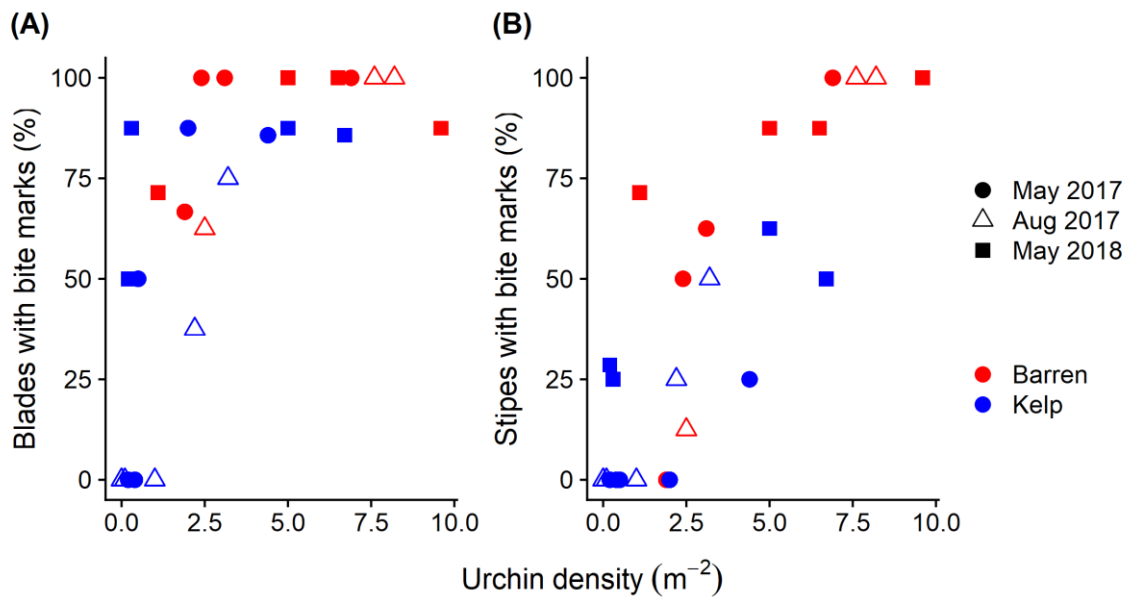
666

667 Fig 2



668

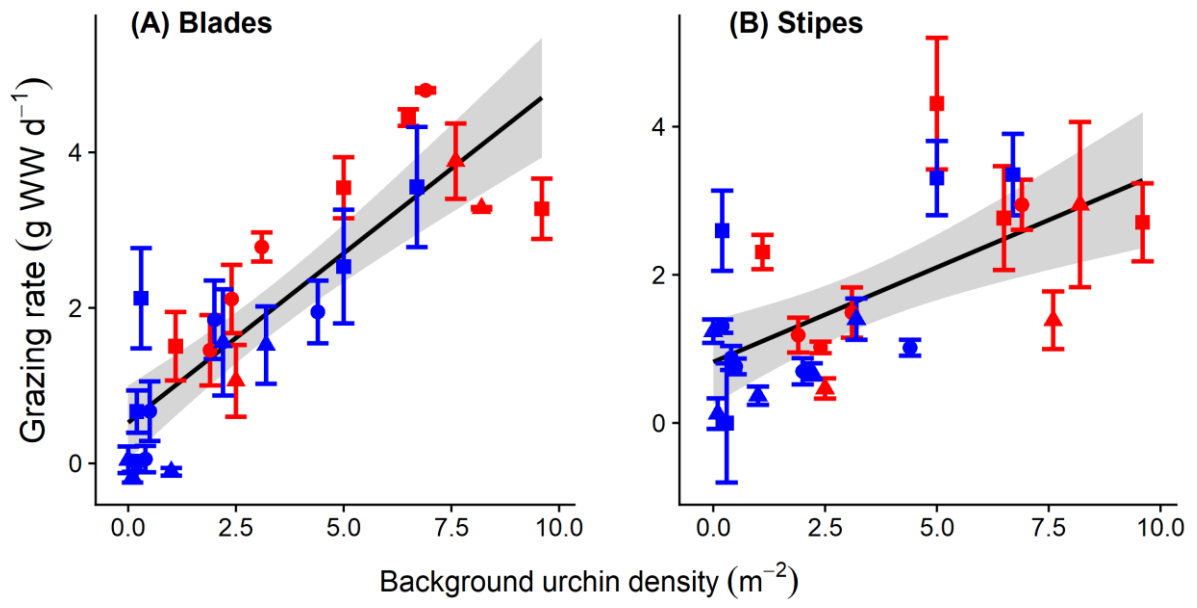
669 Fig 3



670

671 Fig 4

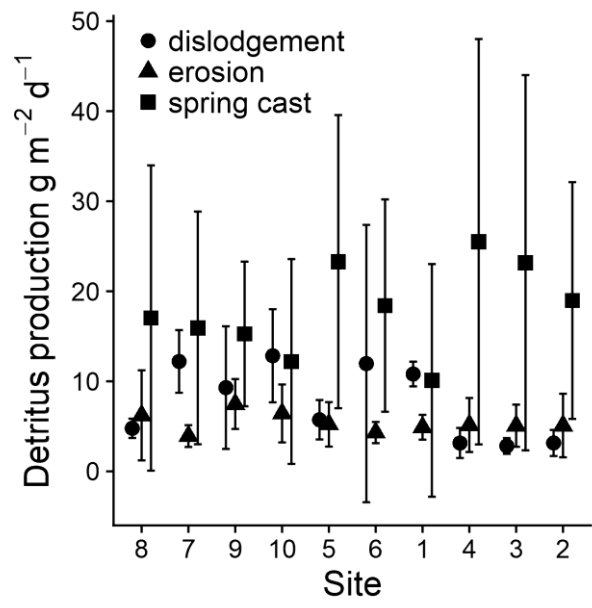
672



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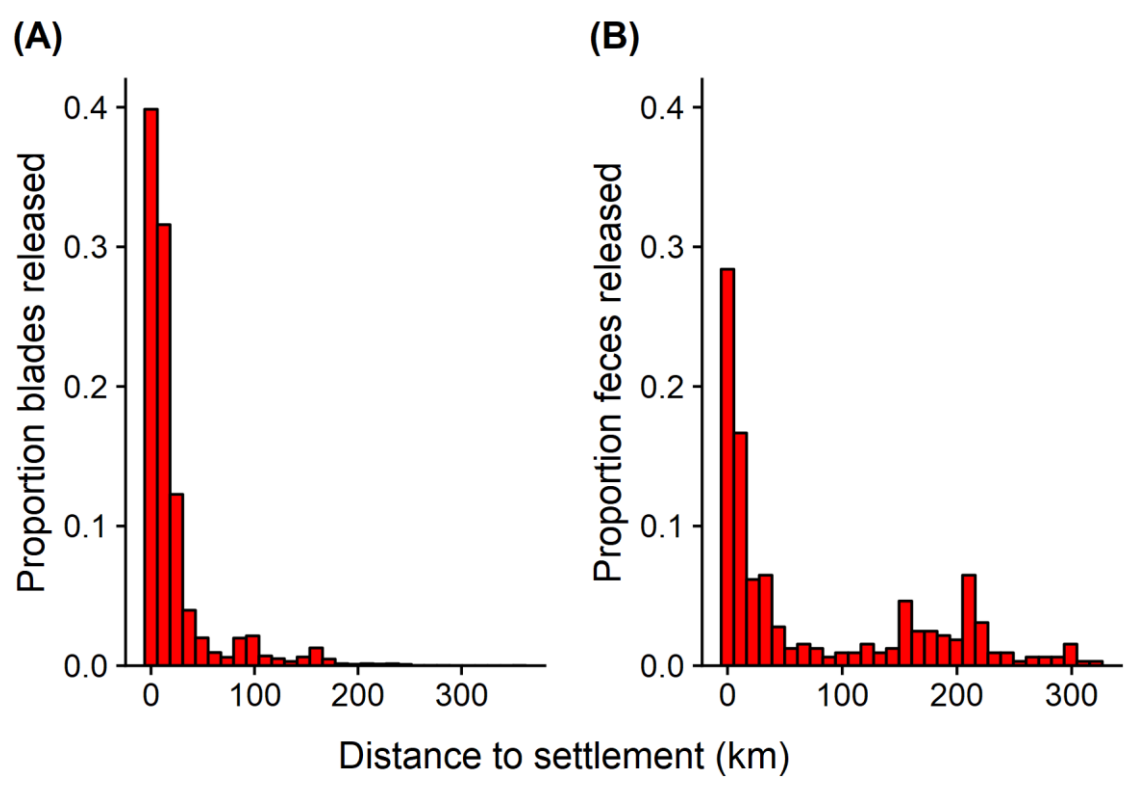
674 Fig 5

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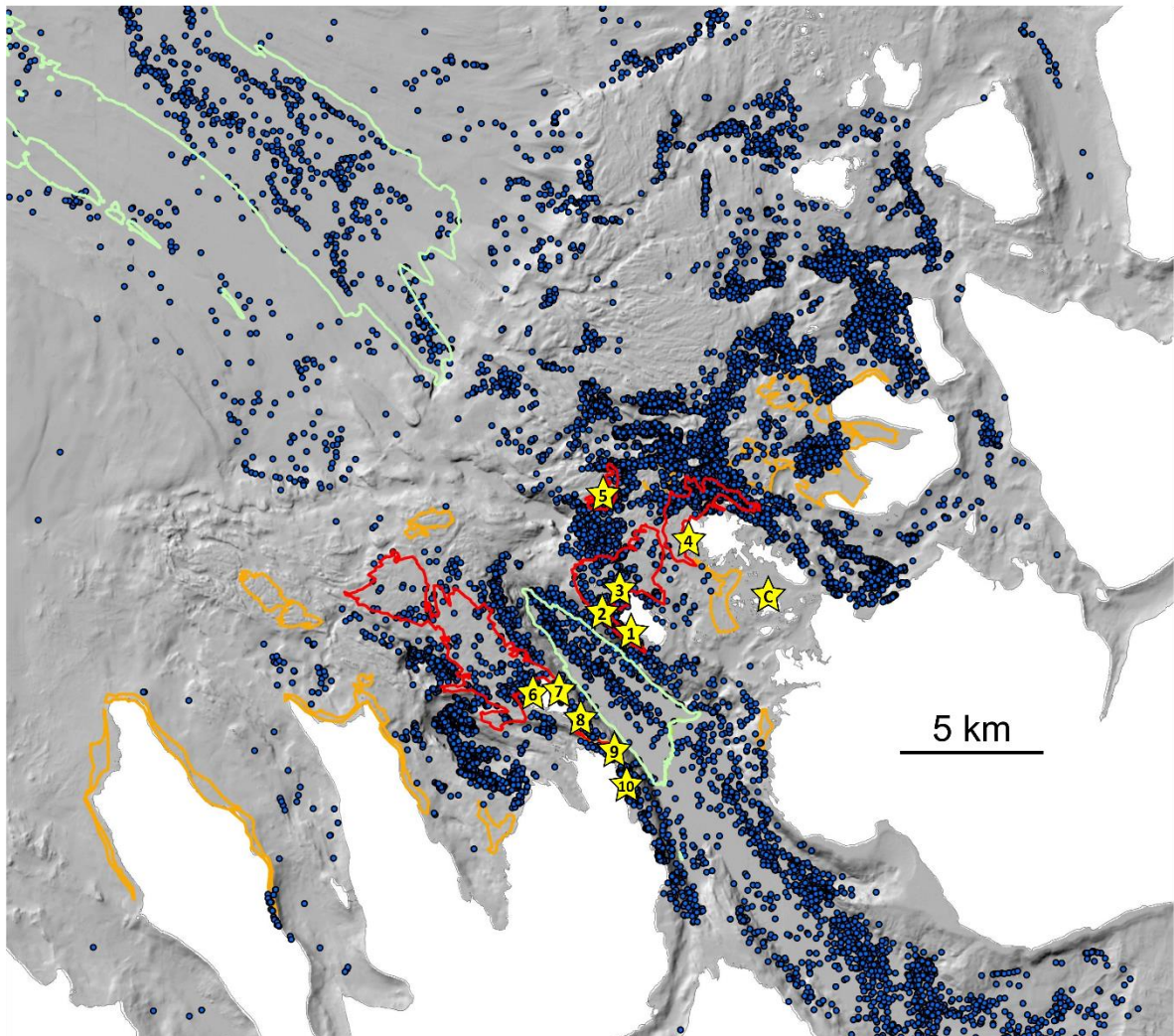
677 Fig 6



679

680 Fig 7

400 m depth (—), Kelp forest (— model source, — other), Detritus ●



681

682 Fig 8