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1 **MOVEMENT OF PULSED RESOURCE SUBSIDIES FROM KELP FORESTS TO**
2 **DEEP FJORDS**

3

4 Karen Filbee-Dexter¹, Thomas Wernberg², Kjell Magnus Norderhaug³, Eva Ramirez-Llodra¹,
5 Morten Foldager Pedersen⁴

6

7 1. Norwegian Institute for Water Research (NIVA), Gaustadalléen 21, 0349 Oslo, Norway

8 2. UWA Oceans Institute and School of Biological Sciences, University of Western
9 Australia, Crawley 6009 WA, Australia

10 3. Institute of Marine Research, Nye Flødevigveien 20, NO-4817 His, Norway

11 4. Department of Science and Environment (DSE), Roskilde University, DK-4000 Roskilde,
12 Denmark.

Author Contributions: KFD, TW, and MP conceived and designed the study, and wrote the manuscript. ERL and KM provided editorial advice. All authors conducted the fieldwork. KFD analyzed the data and all authors discussed the results.

13 **Abstract**

14 Resource subsidies in the form of allochthonous primary production drive secondary
15 production in many ecosystems, often sustaining diversity and overall productivity. Despite
16 their importance in structuring marine communities, there is little understanding of how
17 subsidies move through juxtaposed habitats and into recipient communities. We investigated
18 the transport of detritus from kelp forests to a deep Arctic fjord (northern Norway). We
19 quantified the seasonal abundance and size structure of kelp detritus in shallow subtidal (0–
20 12 m), deep subtidal (12–85 m), and deep fjord (400–450 m) habitats using a combination of
21 camera surveys, dive observations, and detritus collections over 1 year. Detritus formed
22 dense accumulations in habitats adjacent to kelp forests, and the timing of depositions
23 coincided with the discrete loss of whole kelp blades during spring. We tracked these blades
24 through the deep subtidal and into the deep fjord, and showed they act as a short-term
25 resource pulse transported over several weeks. In deep subtidal regions, detritus consisted
26 mostly of fragments and its depth distribution was similar across seasons (50% of total
27 observations). Tagged pieces of detritus moved slowly out of kelp forests (displaced 4–50 m
28 (mean 11.8 m ± 8.5 SD) in 11–17 days, based on minimum estimates from recovered pieces),
29 and most (75%) variability in the rate of export was related to wave exposure and substrate.
30 Tight resource coupling between kelp forests and deep fjords indicate that changes in kelp
31 abundance would propagate though to deep fjord ecosystems, with likely consequences for
32 the ecosystem functioning and services they provide.

33

34 Key words (5): seaweeds, connectivity, coastal ecosystems, deep sea, *Laminaria hyperborea*

35 **Introduction**

36 Primary production drives the biodiversity and overall productivity of many ecological
37 communities by controlling the amount of carbon available to propagate through to different
38 trophic levels (Pauly and Christensen 1995; Costanza et al. 2006). On land, most ecosystems
39 receive enough sunlight to sustain carbon fixation and plant growth. In the marine
40 environment, sunlight is rapidly absorbed by the water column and primary production is
41 restricted to the shallow photic zone above 200 m depth (except for localized chemo-
42 autotrophic communities) (Falkowski et al. 1998; Gattuso et al. 1998, 2006; Ramirez-Llodra
43 et al. 2010). The majority of marine ecosystems occur below this zone, and therefore depend
44 on carbon produced elsewhere to support the base of their food webs.

45 In marine ecosystems, much of our understanding of the ecological consequences of
46 the movement of carbon energy across ecosystem boundaries comes from comparisons of
47 ecosystems receiving carbon-based resource subsidies with ecosystems that do not, or by
48 experimentally manipulating subsidies to examine the effects on community structure (Kim
49 1992; Wallace et al. 1997; Polis et al. 1997; Marczak et al. 2007; Bishop et al. 2010). In
50 contrast, the transport of carbon between source and recipient marine communities has
51 received considerably less attention (e.g. Heck et al. 2008; Krumhansl and Scheibling 2012).
52 This is likely due to difficulties in tracking material in ocean environments, challenges
53 associated with connecting an observation of a subsidy in a recipient location to its source,
54 and the complexity of conducting large-scale experiments in these systems. Developing a
55 better understanding of the dynamics of carbon movement is essential to define the spatial
56 and temporal scales over which these linkages operate.

57 Marine resource subsidies often occur as seasonal or pulsed events that provide a
58 temporary surplus of food inputs (Gage 2003; Yang et al. 2008; de Bettignies et al. 2013). In
59 the deep sea, the vertical transport of particulate organic material (e.g. plankton fecal pellets,

60 marine snow, microbial biomass) from the photic zone to the seafloor, following the spring
61 phytoplankton bloom, strongly determines the amount and timing of organic material and
62 nutrients reaching benthic communities (Billett et al. 1983; Platt et al. 1989; Smith et al.
63 1994). Extreme variations in resource supply can have individual-level effects that propagate
64 up trophic levels, with important consequences for recipient ecosystems (reviewed by Ostfeld
65 and Keesing 2000; Yang et al. 2008). Yang et al. (2010) conducted a meta-analysis of 189
66 field studies on resource pulse-consumer interactions, and found that the highest magnitude
67 of consumer response occurred in marine systems. Field observations and manipulations have
68 shown that the overall impact of resource pulses is strongly influenced by their timing
69 (Durant et al. 2007; Armstrong and Bond 2013; Sato et al. 2016), duration, and frequency
70 (e.g. Bode et al. 1997; Bologna et al. 2005; Yeager et al. 2005; Hoover et al. 2006). These
71 trophic linkages are transmitted down to the deep seafloor, where the benthic communities
72 are directly dependent on the seasonal pulses of organic matter produced in the sunlit surface
73 waters (Billett et al. 2001; Smith et al. 2006, 2008).

74 Kelps are large brown seaweeds that have some of the highest rates of productivity on
75 Earth (Mann 1973) and produce large amounts of particulate detritus in the form of detached
76 and eroded organic material (sometimes termed drift kelp). Kelp detritus can range from
77 whole plants, full blades, stipes, and blade fragments of various sizes. On average, 82% of the
78 local primary production from kelp is estimated to enter the detrital food web where it can be
79 exported to adjacent communities (Krumhansl and Scheibling 2012). In Norwegian kelp
80 forests, only 3–8 % of the total kelp production is consumed directly by secondary producers
81 within the kelp forest, while the rest is assumed to be exported (Norderhaug and Christie
82 2011). There are many examples of how the detrital resource subsidy from kelp forests
83 increase secondary production in a diverse range of recipient communities across the depth
84 gradient of marine ecosystems. In South Africa, shore cast subtidal kelp detritus can sustain

85 large populations of limpets (Bustamante et al. 1995). In Western Australia, detrital kelp is a
86 primary food source for sea urchins on shallow subtidal reefs with no kelps (Vanderklift and
87 Wernberg 2008) and is heavily consumed by fish in seagrass beds 100s meters away from
88 reefs (Wernberg et al. 2006). In eastern Canada, detrital kelp in deep subtidal habitats (30–
89 100 m depth) subsidizes sea urchins and influences their reproduction and distribution
90 (Filbee-Dexter and Scheibling 2014, 2017), and in California, USA, detrital kelp supports
91 polychaete communities in 12 m deep sandy areas adjacent to reefs (Kim 1992) and shapes
92 the abundance patterns of benthic fauna in deep canyons (150–500 m) (Vetter 1995; Vetter
93 and Dayton 1998; Harrold et al. 1998). In deep fjord habitats in the Norwegian Arctic,
94 isotopic measures from suspension-feeding bivalves showed that more than 50% of their
95 carbon uptake came from kelps and rockweeds (Renaud et al. 2015), and at 431 m depth in an
96 outer fjord in southern Norway, transplanted drift kelp quickly attracted high densities of
97 crustaceans (Ramirez-Llodra et al. 2016). These studies indicate that deep-water communities
98 adjacent to kelp forests partly depend on transport of food in the form of detrital kelp from
99 the euphotic zone.

100 Detrital production rates and arrival in adjacent habitats have been documented
101 previously (Wernberg et al. 2006; Britton-Simmons et al. 2012; de Bettignies et al. 2013;
102 Filbee-Dexter and Scheibling 2016), but the actual movement of this material from the kelp
103 forests into adjacent marine habitats has rarely been quantified. Detrital kelp is produced
104 throughout the year from distal erosion, breakage, and mortality, with shorter periods of high
105 detrital production during peak breakage or dislodgement (reviewed by Krumhansl and
106 Scheibling 2012). Some studies have quantified its export. Filbee-Dexter and Scheibling
107 (Filbee-Dexter and Scheibling 2012) documented a pulse of detrital kelp moving from kelp
108 forests to deep subtidal habitats in the weeks following a strong storm event. Vanderklift &
109 Wernberg (2008) used site-specific morphological markers to identify the source of detrital

110 kelp delivered to urchins at a subtidal temperate reef with no kelp, and found that 10–38% of
111 the kelp originated 6–8 km away. Hobday (2000) used data from ARGOS satellite-tracked
112 drifters in California, USA to mimic the transport of floating rafts of *Macrocystis pyrifera*
113 kelps, and estimated that floating kelps moved an average of 8.5 km d⁻¹, ending up as far as
114 448 km offshore.

115 In this study, we uncover the transport of kelp detritus through an Arctic fjord and
116 investigate what processes drives its movement from the kelp forest to the deepest parts of
117 the fjord. Fjords are good study systems for exploring the dynamics of detrital subsidies
118 because they comprise juxtaposed habitats that differ vastly in primary productivity.
119 Moreover, they typify a situation common throughout the global distribution of kelp
120 communities, where shallow kelp forests fringe deep areas with little to no *in situ* primary
121 production. Fjords usually also host productive fisheries and provide important services to
122 coastal communities (Matthews and Heimdal 1980). Importantly, kelp forests in the Arctic
123 provide a useful opportunity to study the movement of pulsed resource subsidies, because, as
124 a consequences of the strong seasonality, most kelp detachment occurs as a discrete loss of
125 old blades (full blades grown over the previous year that become weakened/tattered during
126 the dark winter), which are shed during rapid growth of new blades between April and May.

127 Here, we aimed to track the pulse of old kelp blades as they moved through habitats
128 and to uncover the extent that shallow and deep marine systems are coupled by the flow of
129 this resource. We tested two competing hypotheses: either 1) the pulsed production of kelp
130 detritus would be retained within the shallow kelp forests until it slowly fragmented and
131 entered deeper habitats in a somewhat steady supply, or 2) it would be flushed into adjacent
132 deep habitats as a short-term pulse of whole blades. To determine the dominant transport
133 processes our study had three main objectives: 1) to quantify seasonal abundance of kelp
134 detritus in shallow and deep-sea habitats, 2) to track the pulse of old blades from shallows to

135 deep-subtidal and deep-fjord habitats, and 3) to determine key biotic and abiotic drivers of
136 the transport of detritus during this pulse.

137

138 **Materials and methods**

139 *Study area*

140 This study was conducted at Malangen fjord, northern Norway (69 °N, 17 °W, Fig. 1), from
141 October 2016 to October 2017. The entrance to Malangen fjord has extensive kelp forests that
142 dominate skerries, shoals and outer shores down to 30 m depth (16.6 ± 3.4 kg m² FW at 4–6 m
143 depth, M.F. Pedersen unpublished data). These rocky shores shelve steeply into a 400–450 m
144 deep basin, bounded from the continental shelf by a shallow sill (<150 m depth). In the more
145 protected inner fjord, sea urchins have overgrazed the shallow subtidal, and kelp forests are
146 restricted to the surf zone or to areas with very high water motion. The dominant kelp in this
147 area is *Laminaria hyperborea*, which has a single digitated blade that is produced annually
148 between April and May, and cast the following spring when the next new blade develops.

149 *Video surveys in shallow and deep habitats*

150 The seasonal abundance of detrital kelp in shallow-subtidal, deep-subtidal, and deep-fjord
151 habitats was quantified using a combination of dive and towed underwater camera transects.
152 Shallow subtidal surveys (ranging from 0–12 m depth) were conducted in kelp forests and
153 habitats adjacent to kelp forests (sand and urchin barrens) by divers at 10 sites in October
154 2016, and March, May, and August 2017. All dive transects began at a submerged float at 4
155 to 6 m depth and extended to the N, E, S and W for 50 m (or until the diver reached the
156 shore). This design encompassed the full depth range of the kelp forest and included adjacent
157 habitats that bordered the kelp forest. Divers swam along each transect at a speed of ~ 1 m s⁻¹
158 using a GoPro camera held under the kelp canopy or approximately 0.5 m above the bottom
159 to video the seafloor.

160 Deep subtidal surveys (<85 m depth) were conducted using an underwater drop
161 camera (Tronitech UVS5080 with VR overlay) towed at an average speed of 0.5 m s⁻¹ from a
162 4 m research vessel and maintained ca. 1 m off the seafloor (field of view ~1 m²). All video
163 transects began at 65 to 85 m depth, extended perpendicularly to shore, and ended at the
164 lower margin of the kelp forest where the seafloor beneath the canopy could not be reliably
165 observed (typically 12–25 m). The depth of the camera and position of the vessel were
166 recorded during each transect using a depth sensor mounted on the camera and a GPS
167 receiver connected to the surface console unit. In total, 10 transects were conducted in March,
168 8 repeated in May and 10 repeated in August 2017. No transects could be recorded in
169 October 2016 as the camera flooded.

170 Deep-fjord surveys were conducted using a Yo-Yo Camera system. The Yo-Yo
171 camera is mounted on a frame which is towed at ~2 m s⁻¹ at 5 m above the seafloor and
172 lowered at regular intervals to 0.5 m above the seafloor. The system has a trigger weight 1 m
173 below the camera, which triggers the camera and strobe when it touches the seafloor (see
174 details in Sweetman and Chapman 2011). A total of 328 images of the seafloor were obtained
175 from 4 Yo-Yo transects conducted in May 2017 on board RV Johan Ruud. The transects ran
176 parallel to shore through the middle of the fjord (400–450 m depth).

177 *Video analysis*

178 Each video transect was viewed in real time, and bottom type and occurrence of detritus
179 along the transect were recorded using an Excel macro, synchronized with the video time.
180 The program tabulated records every 3 seconds to avoid frame overlap. The bottom in all
181 surveys was classified as either kelp forest, bare rock, sediment and rock, or sediment. All
182 frames along each transect were classified into presence/absence observations of detrital kelp.
183 The number of stipes, and blades observed along each transect were counted (whole plants
184 were rarely observed). All frames with accumulations (defined as dense amounts of detritus

185 (>50% cover) that could not be differentiated into individual pieces) were also counted.
186 Counts of detritus from drop camera transects were binned into 10-m depth categories and
187 standardized by the number of observations of the seafloor (video frames) in each category.
188 Counts of detritus from dive transects were binned into two habitat categories: within the kelp
189 forest or in habitats adjacent to the kelp forest, and standardized by the number of
190 observations of the seafloor in each category. All observations of kelp detritus in photographs
191 of the deep fjord from Yo-Yo surveys were counted, and the fragment size and amount of
192 degradation visually assessed.

193 *Biomass estimates*

194 To estimate the biomass of detritus per area of seafloor in each depth stratum (excluding
195 accumulations), we multiplied the number of detrital fragments, blades, and stipes by their
196 average respective biomass, and then divided this by the area of seafloor observed in the
197 transect (frame area x number of frames in the depth stratum). The biomass estimates for the
198 detritus were obtained from average biomass measures of detrital fragments (n = 30)
199 collected from 8 m depth at 1 site and weighed to the nearest 0.1 g, and blades and stipes
200 collected adjacent to the subsurface floats at all study sites in May, March, and August (M.F.
201 Pedersen, unpublished data). Note that these are coarse estimates.

202 *Collections*

203 To quantify how the size of detrital kelp pieces varied with season and depth, detritus was
204 collected from shallow habitats (4–12 m depth) by divers and from deep habitats (400–450 m
205 depth) using benthic trawls. In the shallow subtidal, kelp detritus was bagged on encounter
206 from accumulations within or along the margin of the kelp forest during dive surveys in
207 March, May, and August 2017. Detrital kelp was collected from the deep basin in Malangen
208 fjord using otter or beam trawls in March, May, and October 2017. All collected pieces were
209 laid out flat beside a scale and photographed from above. Detritus size was determined from

210 the photographs by measuring the total area of each piece using ImageJ (National Institute of
211 Health). To visually compare between these measures and observations of blades of kelp
212 from video transects, large pieces of collected detritus were separated using a cut-off of >300
213 cm², which captured all full blades and the majority of partial blades, and were plotted.

214 The size structure of detrital kelp was analyzed by calculating 4 size-frequency
215 distribution parameters for each collection: mean size and SD, coefficient of variation, and
216 size at the 95th percentile. These 4 parameters were compared across 3 time periods: before
217 the pulse (March), during the pulse (May), and after the pulse (August/October); and between
218 2 depths (shallow and deep) using a multivariate analyses of variance (MANOVA). Post-hoc
219 comparisons were conducted to examine the effect of time period on each parameter using
220 ANOVAs (Quinn and Keough 2002).

221 *Field measures of export*

222 To quantify the movement of detached kelp out of kelp forests and into adjacent habitats, we
223 released tagged kelp detritus at 6 of the 10 dive sites and tracked its displacement after a ~2-
224 week period. Kelps were collected and cut into blades, stipes, and fragments (~10 cm long
225 digits), and tagged in 2 places with uniquely numbered high-visibility flagging tape. At each
226 site, kelps were bundled together with a line, lowered directly from a small boat over the
227 subsurface float (suspended 0.5 m off the seafloor) used for dive surveys, and released when
228 level with the canopy. Following release, the unbundled kelp sank to the seafloor. A total of
229 390 kelp fragments were released during calm conditions at low tide: 10 stipes, 30 fragments,
230 and 15 blades at two sites on 9-May-2017; and 10 stipes, 30 fragments, and 30 blades at four
231 sites on 10-May-2017. Divers revisited the sites between 11 to 17 days after the release to
232 measure the displacement of kelp fragments. Divers located the tagged kelps by searching the
233 immediate area surrounding the float for ~20 minutes and recording any tagged kelp
234 encountered along the four 50-m video transects (see above). For each recovered kelp, the

235 divers recorded the tag number, the type of detritus (blade, stipe, or fragment), the distance
236 and bearing from the release point, the habitat type (kelp forest, kelp forest margin, barren or
237 sand), and whether it was trapped by one or more sea urchins (*Echinus esculentus* or
238 *Strongylocentrotus droebachiensis*). To estimate export velocity, the total displacement from
239 the float was divided by number of days since release.

240 Relative water movement (RWM) was measured at each site using an accelerometer
241 (Onset HOBO G-logger) attached to the subsurface float used for the kelp release (following
242 the design described by Evans and Abdo 2010). The accelerometer recorded its position in
243 the water column along 2 horizontal axes every second minute during each deployment (each
244 30 days). RWM was calculated as the vector sum for all pair-wise recordings and hourly
245 means and standard deviations were computed. The standard deviations were finally averaged
246 over all sampling periods and used as a relative measure of water motion, encompassing both
247 wave exposure and currents (Figurski et al. 2011).

248 The importance of detritus type, wave exposure, bottom type and sea urchins for the
249 total displacement of tagged kelp was examined using a random forest model (RFM). A RFM
250 is an advanced version of a classification and regression tree that explains the variance in the
251 response variable using decision trees constructed from predictor variables (Breiman 2001).
252 In our RFM the best predictor variable for each split in the data was determined from 2
253 randomly sampled predictor variables. Our model stopped after 3 splits and grew 500 trees.
254 This model was appropriate for our data because it performs well with categorical predictor
255 variables that have strong, but not clearly defined, interactions (Breiman 2001). To better
256 examine the impact of water movement on export velocity, we constructed the RFM using
257 site wave exposure instead of site as a predictor variable.

258 All analyses were conducted using R v.3.1.0. The RFM was constructed using the
259 randomForest package (Breiman and Cutler 2015).

260

261 **Results**

262 *Observations of detritus from shallow and deep video surveys*

263 Our observations show that substantial amounts of kelp detritus accumulated in shallow
264 subtidal habitats (0–12 m) in May, coinciding with the loss of old blades between April and
265 May. In the shallow subtidal, kelp detritus occurred in 38% of all observations of the seafloor
266 from dive surveys in the kelp forest and adjacent habitats (Fig. 2a-b, Fig. 3). Most detritus
267 accumulated along the deeper margins of kelp forests, deposited in depressions or basins
268 around shallow shoals, or was retained in small gullies within the kelp forests. These
269 accumulations largely consisted of *Laminaria hyperborea*, but occasionally included blades
270 of *Saccharina latissima* and *Alaria esculenta*. The percent of frames containing fragments of
271 detritus in dive surveys (mean \pm SD) was highly variable across sites, but relatively similar
272 throughout the year (October $22 \pm 17\%$, March $39 \pm 28\%$, May $18 \pm 14\%$, and August $17 \pm$
273 11%). Accumulations of blades were present in $<6\%$ of all observations of the seafloor in
274 October, March, and August, but were in 26% of all observations in May. At some sites in
275 May, old blades carpeted the seafloor in accumulations that were over 1 m deep and 10s of m
276 in areal extent (Fig 2a). In October, March, and August, most of the detritus was fragmented
277 (Fig 2b, Fig 3) and often trapped by sea urchins. The highest abundances of fragments and
278 detached stipes were found in March where they accumulated at the margin of the kelp forest
279 (Fig. 3). Overall, the abundance of detritus was substantially higher in adjacent shallow
280 habitats compared to inside the kelp forest, and higher in May compared to other periods due
281 to high number of accumulated blades (Fig. 3). The lack of increase in fragmented detritus
282 between March and August does not support the hypothesis that old blades are retained
283 within the shallow kelp forests and slowly fragmented. Conversely, the strong seasonal drop
284 in the abundance of large blades and accumulations of detritus in shallow habitats between

285 May and August supports the competing hypothesis that detritus is flushed out of the
286 shallows relatively quickly.

287 The sharp increase in number and biomass of old, detached blades observed in May in
288 deep subtidal habitats (12–85 m) (Table 1, Fig. 4a), and the decline of blades between May
289 and August, suggest that the pulse of detritus production enters these habitats over a short
290 period (weeks). In deep subtidal habitats, detrital kelp occurred in 50% of all observations of
291 the seafloor from the drop camera transects (Fig 4c). The percent of frames containing an
292 observation of kelp detritus (mean \pm SD across transects) was slightly higher in May (March
293 $40 \pm 22\%$, and May $57 \pm 18\%$, and August $44 \pm 22\%$), and generally increased with depth
294 and, thus, with distance from kelp forest (Fig. 4b). This prevalence of detritus was higher
295 than that observed in the shallow subtidal, however large pieces of detritus (stipes and blades)
296 and accumulations of detritus were less abundant in the deep subtidal and most detritus was
297 fragmented (Fig. 2c). Detritus was most abundant between 25 m and 65 m depth, which
298 captured the sides of the fjord where steep rocky habitats graded into more gently sloping,
299 sediment habitat, which appeared to accumulate detritus (Fig. 2c, 4b,c). In March and
300 August, whole blades were observed in low abundances, primarily between 25–45 m depth,
301 and in similar numbers as stipes. In contrast, in May, old blades were observed in high
302 abundances between 25–75 m depth, and accumulations of blades were commonly observed
303 down to 65 m depth (Fig. 4a). These results support the hypothesis that the pulsed production
304 of detrital kelp blades in the shallows is flushed rapidly into adjacent deep habitats.

305 In the deep fjord (400–450 m), each of the four Yo-Yo Camera transects conducted in
306 May encountered kelp detritus. This detritus was observed at least once in each of the Yo-Yo
307 Camera transects, and in a total of 5 images of the 328 taken (1.5%). However, considering
308 the small field of view of the camera (0.36 m^2) and the vast area of the deep fjord (9,998,363

309 m²), these numbers are fairly large (Table 1). All observations were of full or partial blades,
310 with little evidence of degradation (Fig. 2d).

311 *Collections of kelp detritus*

312 Further evidence that old blades enter deep habitats as a pulsed resource subsidy comes from
313 collections of kelp detritus, which indicate that most export to deep-fjord habitats occurred
314 during the short period between late March and early May, coinciding with the timing of old
315 blade loss. A total of 2580 drift fragments were collected before, during, and after the pulsed
316 loss of old blades: 1948 from accumulations at the kelp forest margin and 634 from the
317 middle of the deep fjord. The average area of all fragments was $66 \text{ cm}^2 \pm 201 \text{ SD}$ (61 ± 208
318 in shallows and 84 ± 178 in the deep). Small fragments of *Laminaria hyperborea* were found
319 in all shallow collections from all 3 periods, and in all deep trawl collections from May.

320 Whole and partial old blades were mainly present in shallow and deep collections in May
321 (Fig. 5). MANOVA comparisons of size frequency parameters from collections showed that
322 detritus size was significantly higher during the period comprising the detritus pulse (May)
323 compared to before (March) and after the pulse (August/October) in both deep and shallow
324 habitats. There was no significant difference in the size composition of detritus between deep
325 and shallow collections in any season (Table 2), indicating a short time-span between detritus
326 leaving the kelp forest and reaching the deep fjord.

327 *Recovery of tagged kelp detritus*

328 We recovered 53% of all tagged kelp pieces released at the sites. At most sites the recovered
329 kelps were found in a narrow line or bundle offshore of the release point (Fig. 6a).

330 Displacement ranged between 4 and 50 m (mean $11.8 \text{ m} \pm 8.5 \text{ SD}$) over the 11–17-day period
331 since release. These represent minimum estimates of displacement as the kelp pieces that
332 were not recovered most likely moved farther from the release point. Of the total recovered

333 kelp, 79% were trapped by sea urchins (Fig. 6b). Kelp found the farthest from the release
334 point were more likely to be trapped by sea urchins.

335 The RFM explained 80.3% of the variance in the export velocity of tagged kelp.
336 Exposure and bottom type were the most important predictors of velocity (both increased the
337 MSE by >22% when they were excluded from the model), with kelps at highly exposed sites
338 and sea urchin barrens displaying the fastest rates of export (Table 3). Site only explained an
339 additional 2.5% of the variance compared to exposure, which indicated that our estimate of
340 site exposure captured most of the influence of site on the response and that other site-
341 specific factors such as topography did not have a strong influence on export velocity of
342 tagged kelp pieces. Sea urchins were the third most important predictor in the RFM (% MSE
343 increase of 2.3). Although stipes tended to move shorter distances than blade or fragments
344 (Fig. 6c), the type of kelp detritus was least important predictor (% MSE increase of 1.3), and
345 there was little difference in mean velocity for different pieces (Table 3; Fig. S1).

346

347 **Discussion**

348 Understanding the ways in which resource subsidies are transported among habitats is critical
349 to understand how this energy is delivered and incorporated into recipient communities.

350 Evidence from surveys and collections throughout our study area indicated that large
351 quantities of kelp detritus entered adjacent deep subtidal habitats beyond the kelp forests,
352 underscoring the importance of kelp as a substantial source of carbon inputs to nearby marine
353 communities.

354 The detrital export during the short period between late March and early May
355 coincided with the timing of old blade loss in *L. hyperborea* (>99% of kelps collected at
356 study sites had old blades in mid-March, compared to <35% of kelps in early May; M. F.
357 Pedersen, unpublished data). The spring timing of this pulse differs from other kelp

358 ecosystems. In Western Australia and Atlantic Canada, De Bettignies et al. (2013) and
359 Krumhansl and Scheibling (2012) measured highest production of kelp detritus in autumn,
360 during periods of strong storm activity and/or when kelp tissue was the weakest. In our study,
361 the peak in the number of stipes and fragments observed in March indicate high rates of
362 dislodgement, breakage and fragmentation also occur during winter, however this mechanism
363 was less important than the loss of old blades in the overall export of detritus. Interestingly,
364 the occurrence of fragments of detritus in the deep subtidal transects did not show as strong
365 of a temporal signal. This may indicate a consistent background supply of detritus in these
366 areas due to erosion or fragmentation of kelp throughout the year. Alternatively, it could be
367 the result of a ‘conveyor belt effect’, where detrital blades or fragments are continually
368 transported through the deep subtidal region and into the deeper fjord at a constant rate,
369 making its occurrence independent of the amount of detritus in shallow accumulations.

370 The slow movement of tagged kelp released at our sites indicates that most detritus
371 was exported out of kelp forests relatively slowly. This finding runs counter to our evidence
372 that old blades entered deep fjord habitats within weeks after they were dislodged in the
373 shallows. However, a portion of the tagged kelp was not recovered (despite extensive
374 searching in the vicinity of other tagged kelp), and it is possible that these ‘lost’ fragments
375 could have reached distant habitats. It is also important to note that we measured transport
376 during a period in which no strong storms occurred (using gale warning threshold of wind
377 $>17 \text{ m s}^{-1}$). A remaining gap in our understanding is how transport changes during periods of
378 extreme storm activity, which may flush out accumulations of old blades. Although we did
379 not measure this directly, most detrital kelp observed in deep and shallow subtidal transects
380 in March during stormy conditions ($\sim 13 \text{ m s}^{-1}$ and 2 m wave height) were highly mobile,
381 washing back and forth along the seafloor or suspended in the water column.

382 Transport speed of detritus was largely influenced by wave energy, with higher export
383 rate in exposed sites. As a consequence, exposed kelp forests may export large fragments
384 longer distances. Interactions between substrate type and water movement will also drive
385 patchiness where detrital subsidies accumulate, and create small-scale variation in the
386 structure of recipient communities (e.g. Vetter 1995; Rowe and Richardson 2001; Silver et al.
387 2004). In the deep area, the particular topography at the mouth of the Malangen fjord, where
388 a deep basin (> 400 m) is separated from the continental shelf by a shallow sill (>150 m),
389 should facilitate the retention of large kelp detritus inside the fjord, similarly to what is
390 observed in submarine canyons (Vetter and Dayton 1998).

391 Biotic variables appeared to influence the movement of detritus. In the release
392 experiment, the kelp forest retained much of the tagged detritus, possibly by either reducing
393 currents or by trapping large pieces between attached stipes. This was particularly apparent
394 for tagged stipes, which remained close to release point and were often not trapped by urchins
395 (although their lower rate movement could also be due to their higher material density
396 compared to blades and fragments). Urchins seemed to be more important in retaining
397 detritus as it moved through barrens adjacent to the kelp forests. However, despite their high
398 association with the tagged detritus, urchins did not trap old blades observed in
399 accumulations, and are likely saturated during the peak blade release. Fragmented and
400 consumed kelp (such as urchin feces) have different chemical composition and material
401 properties compared to stipes and fresh or old blades (Smith and Foreman 1984; Sauchyn and
402 Scheibling 2009; Dethier et al. 2014), and the extent that urchins and other grazers shred and
403 consume detritus should strongly influence its export and uptake (Sauchyn and Scheibling
404 2009). This is, however, unknown.

405 The decline in biomass and abundance of detritus from subtidal to the deep-fjord
406 habitats, suggests that only a portion of the detrital material exported from shallow kelp

407 forests reached the deep-fjord. There are a several possible reasons for this. Accumulations of
408 kelp were not observed in the deep Malangen fjord, indicating that the large kelp pieces that
409 reach the seafloor annually are either patchily distributed and accumulations were not
410 captured in our surveys, or that kelps are transported on, sequestered in the sediment,
411 degraded or consumed. It is also possible that a portion of kelp detritus was fragmented into
412 particulate or dissolved organic material, which was not visible on video surveys and would
413 most likely be transported differently compared to large pieces. In fact, the creation and
414 transport of small kelp particles and dissolved organic material is a key unknown in these
415 pathways, and may account for a substantial component of overall detrital production from
416 shallow kelp forests (Krumhansl and Scheibling 2012; Barrón et al. 2014).

417 Once detritus deposits in deep sediment habitats, there are a number of possible fates;
418 it can be consumed by benthic fauna, undergo decomposition, become buried and sequestered
419 in the sediment, or exported to another area (Krumhansl and Scheibling 2012). The reduction
420 in number of old blades found in deep and shallow habitats in August and October compared
421 to May suggests that the supply becomes reduced and/or that the turnover of detritus
422 increases during this period (the material could be either fragmented, consumed, or exported).
423 Deep-sea benthic communities rely on the input of organic matter advected down the slope or
424 through the water column, in the form of small particles (marine snow) or large parcels of
425 organic matter (e.g. fish, cetaceans, wood and macroalgae) (Gage 2003). Although evidence
426 of macroalgal detritus input to deep-sea ecosystem and the response of the benthic fauna is
427 well documented (Wolff 1979; Vetter and Dayton 1998; Harrold et al. 1998; Bernardino et al.
428 2010; Ramirez-Llodra et al. 2016; Krause-Jensen and Duarte 2016), the overall significance
429 of macroalgal input to the energetic budget of deep benthic communities remains uncertain
430 (Gage 2003). The deep basin at the mouth of the Malangen fjord is not that deep and
431 surrounded by highly productive shallow water systems, and thus the benthic communities in

432 the deep fjord are unlikely to be food limited. However, all observations and collections in
433 the Malangen fjord provided evidence of kelp detritus on the deep seafloor, from large blades
434 to small particles collected in sediment grabs (K. Filbee-Dexter, personal observation), and it
435 is arguable that the biomass, and potentially the diversity, of benthic communities supported
436 by the system are influenced by this kelp subsidy.

437 Kelp forests may contribute to global carbon sink by increasing the amount of carbon
438 sequestered in the ocean through the export and burial of detritus (Mcleod et al. 2011;
439 Wilmers et al. 2012). Duarte and Krause-Jensen (2016) used current measures of the
440 production and the proportion of macroalgae exported to deep-sea habitats to estimate the
441 amount of macroalgal-derived carbon sequestered globally. Interestingly, most records of
442 detritus were of large pieces collected from the deep sea. Their estimate was highly uncertain
443 and relied on a number of assumptions, however it exceeded the carbon storage capacity of
444 seagrasses, mangroves, and some terrestrial systems. Still, it is important to note that, in
445 contrast to seagrasses, mangroves and trees, most macroalgae have less structural
446 components in their cell-walls (i.e. lignin, cellulose, etc.) and can be almost completely
447 broken down, which may leave very little refractory carbon to sequester (typically 0–10%,
448 but *L. hyperborea* contains more structural components compared to other kelps) (Enríquez et
449 al. 1993; Nielsen et al. 2004). Field studies such as ours, coupled with degradation
450 experiments, are essential to verify and refine estimates/assumptions on the transport of
451 sinking macroalgal detritus into deeper habitats, which will help us to properly assess the
452 potential of kelp forests to contribute significantly to the global carbon sink.

453 Kelp forests are among the most extensive coastal marine habitats, but their role as a
454 source of carbon for other marine ecosystems is not well explored. Most research on detrital
455 kelp subsidies has focused on measuring the amount of detrital production or quantifying its
456 impact on recipient communities (Krumhansl and Scheibling 2012), and studies on the

457 transport and fate of kelp and other macroalgal detritus are generally limited to the export of
458 detritus from marine to terrestrial systems (Polis et al. 1997; Krumhansl and Scheibling
459 2012). Our results showed that kelp forests and deep fjord habitats appeared to be closely
460 linked by the seasonal production of detritus, challenging the common approach of treating
461 them as closed ecosystems. As a consequence, human activities (e.g. harvesting, pollution,
462 anthropogenic climate change) that reduce or alter timing of resource pulses (e.g. global
463 declines in kelp overviewed by Krumhansl et al. 2016) will have immediate impacts on
464 subsidy reaching deep fjords. In Norway, *L. hyperborea* is increasing along the west coast
465 due to increased crab predation on, and temperature-driven recruitment failure of, sea urchins
466 (Fagerli et al. 2013, 2014), while *S. latissima* is declining in abundance along the southwest
467 and Skagerrak coast, possibly due to heat stress or eutrophication (Moy and Christie 2012).
468 Research on the export of detrital kelp will provide a better understanding of the broader
469 consequences of these changes in kelp detritus abundance. We suggest that maintaining the
470 connectivity between kelp forests and deep fjords may be essential to conserve biodiversity
471 and services (e.g. biomass of commercial species such as the shrimp *Pandalus borealis*)
472 provided by these ecosystems, but additional studies to quantify this link are necessary.

473

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480

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676 Table 1. Estimates of detrital kelp biomass per area of seafloor from drop camera surveys (5–
677 85 m depth) in March, May, and August, and Yo-Yo surveys (404–446 m depth) in May.
678 Calculations are based on counts m⁻² of fragments, blades and stipes in each depth stratum,
679 averaged across transects, multiplied by average fragment weight (5.9 g), blade weight (373
680 g), or stipe weight (468 g) from fragments (n=30) and kelps (n =177) collected from the study
681 area. Errors are ± SD.

Depth Month	Fragments (g m ⁻²)	Blades and stipes (g m ⁻²)
12–15 m		
March	2.0±6.3	1.7±3.4
May	0.0±0.0	0.0±0.0
August	0.0±0.0	0.0±0.0
15–25 m		
March	0.5±2.5	0.0±0.0
May	0.2±1.7	3.8±10.7
August	7.7±4.5	4.7±14.5
25–35 m		
March	4.2±8.1	5.5±7.9
May	9.7±14.0	25.8±46.6
August	7.3±5.6	1.0±1.7
35–45 m		
March	18.2±17.1	23.8±23.4
May	8.7±11.9	25.0±25.06
August	6.5±5.8	6.0±13.0
45–55 m		
March	11.9±12.5	7.8±11.4
May	6.8±10.8	36.4±40.0
August	8.4±7.3	2.7±6.4
55–65 m		
March	23.1±13.6	9.5±14.2
May	10.0±13.6	22.7±27.4
August	6.5±12.9	3.1±4.2
65–75 m		
March	17.9±13.7	24.7±25.7
May	16.7±15.4	18.7±15.9
August	15.2±9.9	0.0±0.0
75–85 m		
March	41.8±9.3	15.5±26.9
May	3.6±7.7	18.7±15.9
August	10.7±13.1	7.4±10.5
400–450 m		
May	0.0	12.5

682 Table 2. MANOVA comparing detritus size frequencies parameters (mean, standard
 683 deviation, coefficient of variation, and size at 95th quartile) among period (before, during, and
 684 after pulse) and between shallow and deep collections. ⁿ/_d = numerator and denominator.

Variable	Df	Pillai's Trace	Approx. F	DF (ⁿ / _d)	p
Period	2	0.65	3.3	⁸ / ₅₄	0.004
Depth	1	0.21	1.8	⁴ / ₂₆	0.159
Period*Depth	2	0.19	0.7	⁸ / ₅₄	0.662
Error	29				
Post-hoc ANOVA comparisons for each parameter:					
Mean: During ≠ (Before = After)					
Standard deviation (sd): During, ≠ (Before = After)					
Coefficient of variation: During = Before = After					
95 th quartile: During ≠ (Before = After)					

685

686 Table 3. Variable importance (% increase in MSE and SD) in a random forest model (RFM)
687 of the export velocity of tagged kelp detritus. GINI index is a measure of accuracy for RFM,
688 and denotes the node impurity of the final output groups in a classification and regression
689 tree.

Variable	Importance	Importance SD	GINI index
Bottom	25.9	0.4	28.9
Exposure	22.4	0.4	18.7
Urchin	2.3	0.1	1.8
Detritus type	1.3	0.1	2.3

690

691 **Figure legends**

692 Fig 1. Map of the Malangen fjord study area (left panel) in northern Norway (red arrow, blue
693 country in right panel) with locations of shallow dive sites and transects, drop camera
694 transects, deep trawls, and Yo-Yo camera transects. Depth contours are 50 m

695 Fig 2. Accumulations of kelp blades (a) and fragments (b) observed at margin of kelp forests
696 in May and August (respectively). Detritus fragments at 40 m depth along sides of fjord in
697 March (c). Blade of kelp with little degradation observed at 420 m depth in the deep fjord in
698 May (d)

699 Fig 3. Abundance of detritus in kelp forest (orange) and adjacent shallow habitats (dark blue)
700 from dive transects in October, March, May, and August. Light shading indicates the
701 percentage of frames with observations containing fragments, blades, or stipes. Dark shading
702 indicates the portion of observations that were of accumulations. Error bars are SD. N of
703 frames: October, 6031; March, 8325; May, 3094; and August, 7230

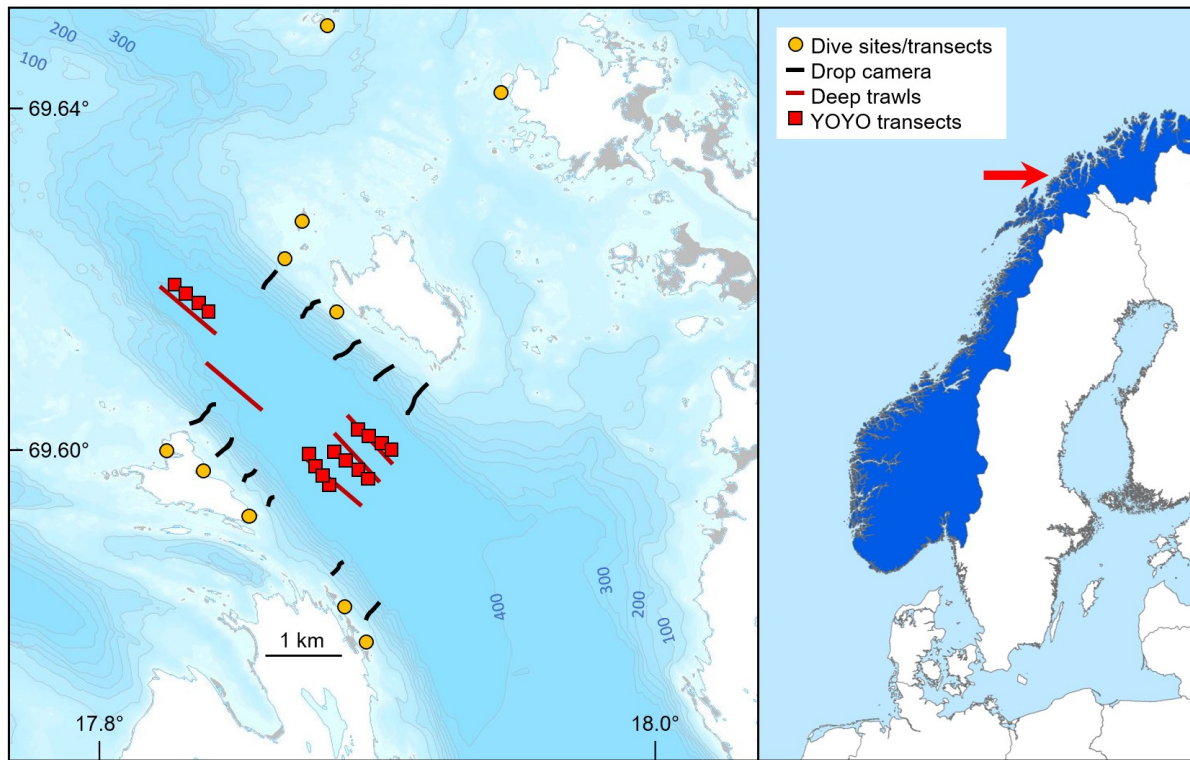
704 Fig 4. Number of observations of blades, stipes, and accumulations of detritus from drop
705 camera transects between 5 and 85 m depth (a). Counts are standardized by number of frames
706 in each depth bin (b). Percent frames with observations of detritus (c) and substrate type (kelp
707 forest, rock, mixed rock and sand, or sand) (c)

708 Fig 5. Size of detrital kelp fragments from shallow collections (a, b) and deep trawls (c, d)
709 before (March, N = 443, 205), during (May, N = 441, 374), and after (August, N = 1064;
710 October, N = 55) the loss of old blades. Left panels show all collections and all sizes, right
711 panels show fragments > 300 cm² pooled by collection times. Boxplots show median (thick
712 line), first and third quartiles.

713 Fig 6. Velocity (m d⁻¹) of tagged kelps in relation to (a) detritus type, (b) association with sea
714 urchins (2 species: Ee = *Echinus esculenta*, Sd = *Strongylocentrotus droebachiensis*), and (c)

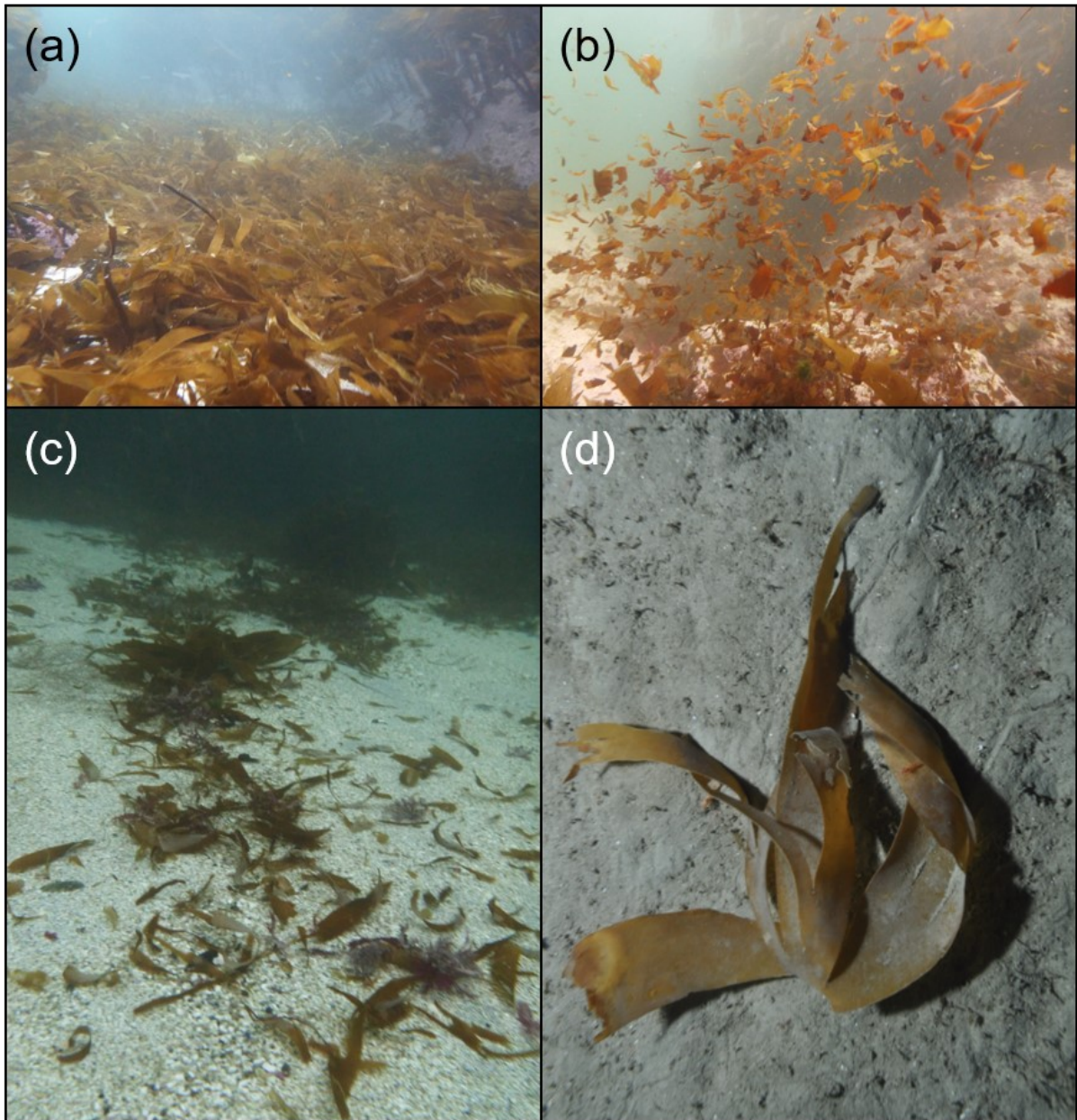
715 habitat it was found in. Velocities are minimum estimates based on tagged kelps recovered
716 during a calm period. Number of pieces recovered shown above boxplots

717



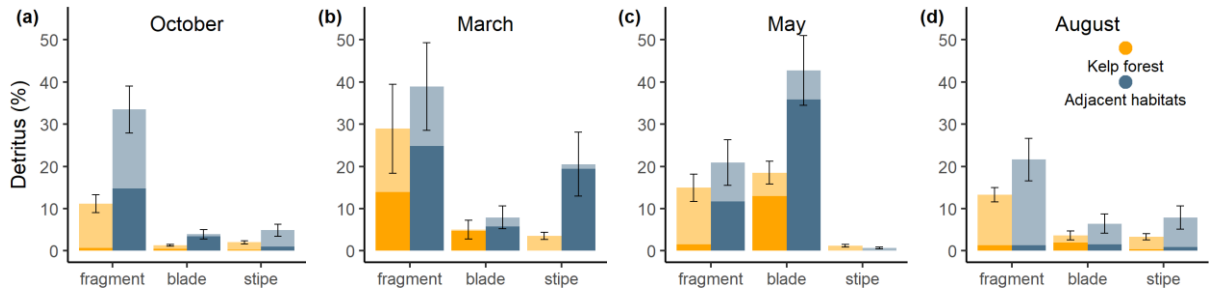
718

719 Fig 1.



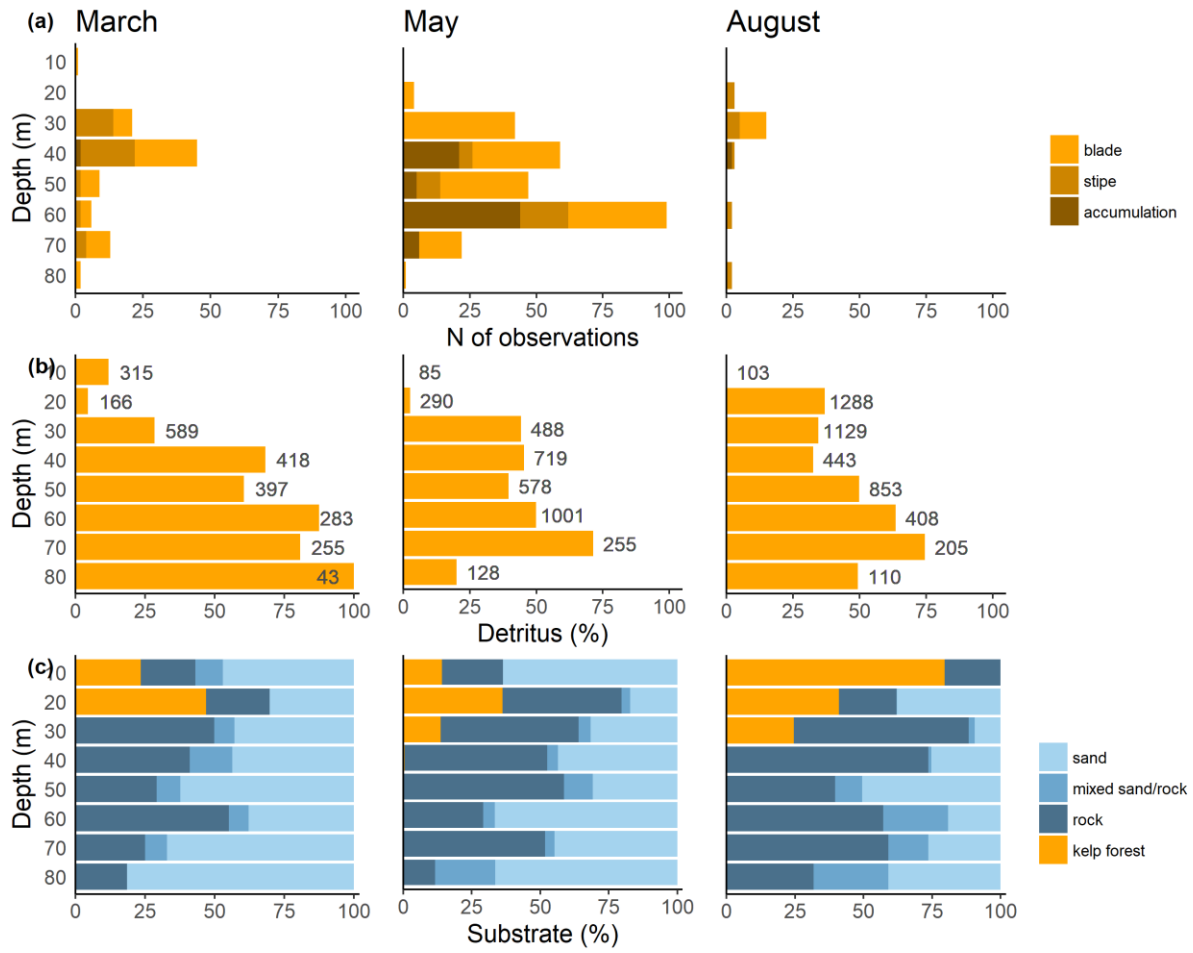
720

721 Fig 2.



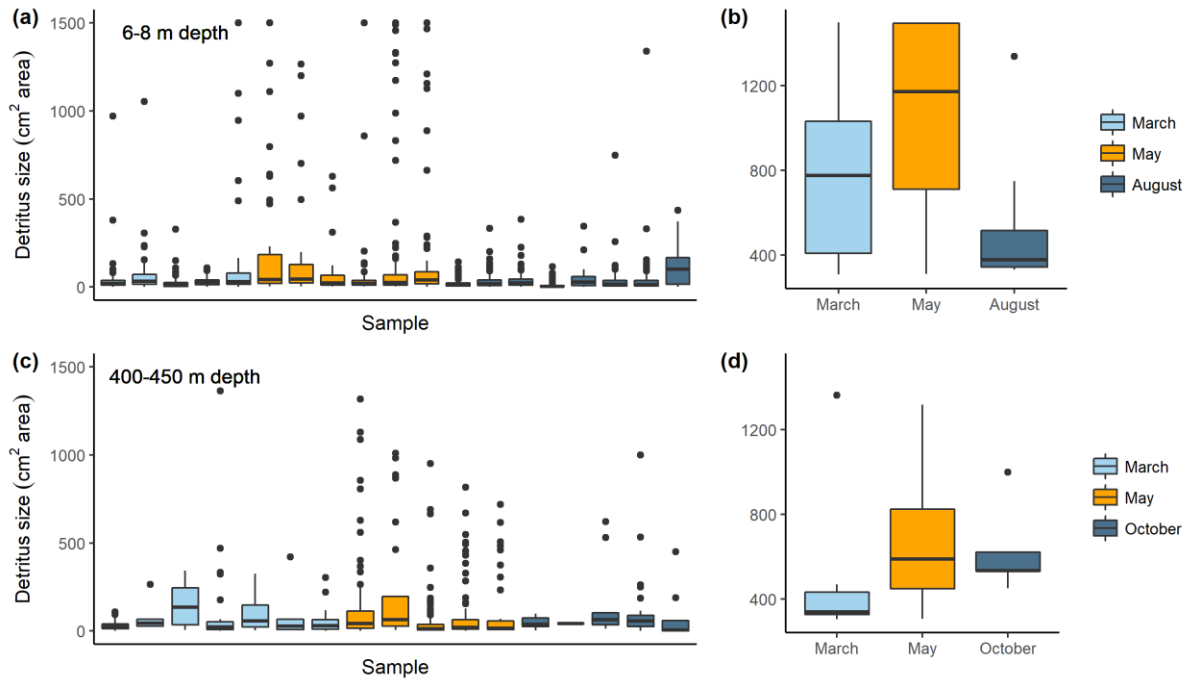
722

723 Fig 3.



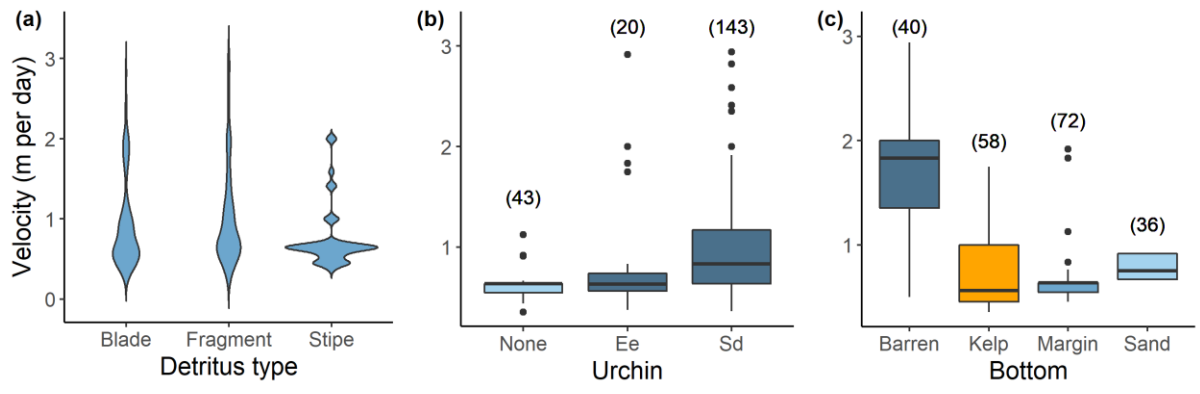
724

725 Fig 4.



726

727 Fig 5.



728

729 Fig 6.