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CARBON EXPORT IS FACILITATED BY SEA URCHINS TRANSFORMING KELP DETRITUS

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Abstract

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

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

Introduction

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

Kelp forests are extensive habitats of large seaweeds that are highly productive and represent an important component of the total organic carbon budget along temperate coasts (Mann 1973; Wernberg et al. 2019). On average about 80% of this production enters the detritus pool and can be exported to adjacent habitats where it either supports decomposer communities – returning necessary nutrients to the living part of the ecosystem (Krumhansl and Scheibling 2012) – or it can be buried and stored in marine sediments (Krause-Jensen and Duarte 2016; Abdullah et al. 2017). The dynamics of kelp-carbon movement between kelp forests and sink habitats in the ocean are not well described, but are particularly important for these rocky reefs because detached kelps are not buried locally in sediment, but are often consumed or exported to adjacent regions. This knowledge is therefore essential to determine the potential magnitude and spatial extent of trophic subsidy and sequestration (e.g. Heck et al. 2008; Krumhansl and Scheibling 2012). Large pieces of kelp detritus have been observed in shallow reef and seagrass beds (Vanderklift and Wernberg 2008), on the seafloor in nearshore deep subtidal areas (5 – 90 m depth) (Britton-Simmons et al. 2012; Filbee-Dexter and Scheibling 2016), in deep-fjord habitats (400 m depth) (Filbee-Dexter et al. 2018), and on continental margins and deeper (1000 – 2500 m depth) (Vetter and Dayton 1998; Filbee-Dexter and Scheibling 2014a; Krause-Jensen and Duarte 2016). However, we know little about the source locations of these deposits, and have even less of an understanding of transport, which depends on a complex interaction between hydrodynamic conditions and physical characteristics of the detrital kelp (e.g., Wernberg and Filbee-Dexter 2018).

Of particular interest are the mechanisms controlling carbon transport from productive coastal areas, especially those which are sensitive to environmental change. Shredders are organisms that feed mainly on living or dead plants and that reduce the size of this material. They tend to be much less efficient at assimilation compared to predators and produce numerous small fragments and/or pellets of partly digested (and sometimes still even living) plant material (Wotton and Malmqvist 2001). Sea urchins are important herbivores in many kelp forests globally, and collapse and rapid expansions of sea urchin populations are ongoing in many regions (e.g. Norway, Atlantic Canada, northern California, Tasmania) and many of these changes have been linked to changing environmental conditions (Ling et al. 2009; Fagerli et al. 2013; Feehan and Scheibling 2014; Catton 2016). Sea urchins have a solid jaw and calcium carbonate teeth, known as Aristotle's lantern, that enables them to feed on tough kelp tissue, and they likely play an important role in shredding kelp detritus. They generally feed on kelp fragments or whole dislodged blades, stipes, and whole plants that are freely drifting along the seafloor (Harrold and Reed 1985). Under some conditions, sea urchins also destructively graze on attached plants, creating ‘barrens’ devoid of standing algae (Norderhaug and Christie 2009; Filbee-Dexter and Scheibling 2014b). Most consumed algae pass through the sea urchin's intestine and are egested as feces, which contain relatively large fragments of fresh algal material (Sauchyn and Scheibling 2009), thereby transforming coarse kelp fragments into fine particles. This has at least two important implications for the fate of kelp detritus. First, sea urchin feces sink 20 times slower than large detrital fragments or whole blades, allowing more time for them to be swept away by horizontal water movement, which can extend its dispersal distance (Wernberg and Filbee-Dexter 2018). Capture and shredding of kelp increases its fragmentation rate, which speeds up the release of nutrients because smaller fragments or feces have a larger relative surface area, which is more "attackable" for microorganisms. Second, because kelp that passes through a sea urchin's intestine becomes coated with bacteria from their gut, this egested material is more rapidly degraded or consumed compared to fresh kelp material (Wotton and Malmqvist 2001; Yorke et al. 2019).

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

In this paper we quantify the amount of total detrital production that moves through the sea urchin 'collector-shredder pathway' in kelp forests with varying sea urchin densities and explore how this transformation affects the spatial extent of kelp carbon transfer. This knowledge is required to predict how trophic connectivity and carbon sequestration will vary with changing herbivory, which is currently observed in many kelp forests worldwide.

Materials and methods

Study area.

This study was conducted at Malangen fjord, northern Norway (69 °N, 17 °W), from October 2016 to May 2018. The mouth of Malangen fjord has extensive kelp forests that dominate skerries, shoals, and outer shores down to 30 m depth (16.6 ± 3.4 kg m^2 FW at 4–6 m depth; M. Pedersen, unpublished data). The dominant kelp is *Laminaria hyperborea*, with *Alaria esculenta* and *Saccharina latissima* occurring at lower densities in some mixed stands. At the entrance to the fjord, barrens created by overgrazing by the sea urchin *Strongylocentrotus droebachiensis* occur at the deep margin (4 – 8 m depth) of many kelp forest patches (Filbee-Dexter et al. 2018). *S. droebachiensis* is a prominent herbivore in kelp forests at northern latitudes in the Atlantic and Pacific Oceans (Dean et al. 2000; Norderhaug and Christie 2009; Filbee-Dexter and Scheibling 2014b; Filbee-Dexter et al. 2019). The sea urchin *Echinus esculentus* was also common in this system, occurring under kelp canopies.

Detritus capture by sea urchins.

The proportion of detrital kelp captured by sea urchins in shallow subtidal habitats was quantified by scuba divers at 10 sites in October 2016, March, May and August 2017, and at 6 sites in May 2018. Transects were conducted in kelp forests and habitats adjacent to kelp forests (sand and overgrazed bedrock). Each transect began at a submerged float at 4 to 6 m depth within a stand of kelp and extended to the N, E, S, and W for 50 m to a maximum depth of 12 m or until the diver reached the shore. Divers swam approximately 1 m s^{-1} at 0.5 m above the bottom and videoed (Go-Pro Hero 3) the seafloor, creating a field of view (FOV) of 0.49 ± 0.30SD m^2. We estimated the FOV by laying a transect line marked every 0.1 and 0.5 m on the seafloor, videoing it in the same manner described above, and then measuring frame area in 40 frames of video using the line as a scaling bar. We analyzed videos in real time and 1) classified bottom type (barrens, kelp forest, sand/other), 2) counted sea urchin number, and 3) recorded observations of kelp detritus, differentiated by type of detritus: stipe, whole blade, or blade fragment; and whether it was associated with sea urchins or free floating. These measures were tabulated every second in an excel Macro, but to ensure non-overlapping measures only data from every 4th second were used. Sea urchin counts was converted to individuals m^{-2} using the FOV. Large accumulations of detritus were labeled separately (2% of all observations) and excluded from the analysis due to challenges of identifying sea urchins within them. Small particles and fragments of detritus (< 1 cm length) were difficult to see in videos, and thus were not captured in these measures.

Capture and grazing rate.

We measured the capture and grazing rate of kelp detritus by sea urchins in kelp forest and barrens habitats at 4 sites in May and August 2017, and May 2018. At each site, we deployed 5-m long chains baited with 4 treatments (2 types of detritus: blades and stipes; 2 modes of attachment: tethered and fixed). We stretched one chain along the seafloor in the barrens and one chain under the kelp canopy at each site. Pre-weighed pieces of kelp blades (7 ± 0.1 g) and stipes (35 ± 0.5 g) (n = 8 of each) were attached either directly to the chain or tethered to the free end of a 20-cm long fishing twine. We used the tethers to determine whether capture rates differed when detritus was freely moving or fixed to the sea floor. Blades were secured with clothes pins and stipes with cable ties. Chains were revisited within 48 – 77 h following deployment, videoed by a diver using a Go-Pro, then collected and brought back to shore. On shore, kelps were carefully removed, weighed, and examined for evidence of grazing (i.e., bite marks). Grazing rate was measured as change in biomass over deployment time. To measure the percent of detrital kelp pieces captured by sea urchins we counted the number of pieces of detritus in contact with sea urchins from the Go-Pro videos. We also estimated sea urchin densities around the chain by counting the number of adult *S. droebachiensis* (>15 mm) and *E. esculentus* within 0.2 m on either side of the chain (using chain links and tethered clothes pins for scale). To investigate whether these grazing rates varied seasonally, we deployed chains at a control site with a stable sea urchin population within a sheltered bay (Sommarøy) 5 times between August 2016 and August 2017. We used this control site because it was easier to access year-round compared to the exposed kelp forest sites, which enabled higher frequency sampling events over time. We also measured hourly temperature over this period using onset HOBO loggers attached to the submerged float at each site.

Rates of shredding of kelp detritus.

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

Modelling the influence of detrital fragment size on export.

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

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

Analyses.

We compared sea urchin densities measured from dive surveys in different habitats (kelp forest or barrens), sampling periods, and sites by fitting a mixed effects model with habitats as fixed effects and sites and campaigns as random effects using Restricted Maximum Likelihood (REML) (lme4 package; Pinheiro et al. 2018). To identify factors influencing the capture of detritus by sea urchins from field observations and experimental detritus additions, we assessed how the percentage of detritus captured in surveys and the percentage of detritus attached to chains with bite marks varied with sea urchin density, habitat type, and detritus type (fragment, stipe, blade) using a mixed effects model, with habitat and detritus type as fixed effects and sampling period as a random effect. We observed that capture rates of detritus increased with increasing sea urchin density until a threshold level where almost all detrital pieces within the habitat were captured. To test whether this breakpoint was significant, we fitted a piecewise regression model to our data and compared it to a fitted linear model (segmented package; Muggeo 2017). Grazing rates on detritus attached to chains in barrens and kelp forests habitats were fitted to linear models. Differences in grazing rates on tethered and untethered stipe and blade material deployed at a sheltered bay site for 5 time periods were analyzed using a 3-way ANOVA with time as a fixed factor as it was the variable of interest in this control site. All analyses were performed in R version 3.4.2.

Results

Sea urchin density and kelp detritus.

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

The mean density of kelp blade fragments was ca. 0.10 fragments m^{-2} within kelp forests and ca. 0.20 m^{-2} in adjacent barrens when averaged across sites and sampling periods (Online Resource 1; Fig. S1A). The abundances of detached whole blades in kelp forests were similar to barren habitats, averaging ca. 0.09 blades m^{-2} (Online Resource 1; Fig. S1B), while the abundance of detached stipes was very low, averaging 0.03 stipes m^{-2} across sites (kelp and barrens) and sampling periods (Online Resource 1; Fig. S1C).

Detritus capture by sea urchins.

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

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

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

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

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

*Production of shredded detritus***.**

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

Modelling the influence of detritus size on export.

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

Discussion

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

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

The higher percentage of detrital kelp pieces captured in barrens compared to kelp habitats with similar sea urchin densities suggests that elements of the habitat type (e.g., canopy cover, food supply, predators, water movement) influence the capture of kelp by sea urchins. This is consistent with findings from other systems that sea urchins in barrens are more food-limited, and therefore more active feeders compared to sea urchins within kelp forests (Harrold and Reed 1985). Finally, the lack of grazing on detrital kelp deployed at sites with low sea urchin densities suggests that the impact of sea urchins is localized, and that they do not respond to food cues or search for kelp over large distances. This was also documented in Atlantic Canada (Filbee-Dexter and Scheibling 2014a). The low grazing on kelp stipes (compared to kelp blades) by sea urchins may be because it was difficult for sea urchins to capture the heavy rolling stipes in a kelp forest. The amount of supportive tissue, including lignins and structural compounds in the outer cortex, may also be higher in stipes compared to blades, making them less palatable (Leclerc et al. 2013). For other *Laminaria* species, stipes are less palatable and attract less grazers than blades do, which may explain this preference (Johnson and Mann 1986).

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

Sea urchins may play a similar role to invertebrate collectors and shredders in other aquatic ecosystems (e.g., streams) (Wotton and Malmqvist 2001), by stimulating the breakdown and transport of carbon (Sauchyn and Scheibling 2009; Wernberg and Filbee-Dexter 2018). The food quality of feces increases over time, which – combined with its smaller size – will impact how it is used by benthic organisms (Yorke et al. 2019). The content of organic matter and energy in freshly egested *S. droebachiensis* feces (pellets of *Laminaria digitata*) deployed at 6 to 16 m depth in the Northwest Atlantic declined over the first 3 days but then increased over the next 16 days in total and labile organic matter and available energy content (Sauchyn and Scheibling 2009). Similarly, *S. droebachiensis* that consumed fresh *Nereocystis luetkeana* kelp egested feces with higher lipid content compared to fresh *N. luetkeana* (Schram et al. 2018). Shredding plant material into smaller fragments that are easily accessible for microbial colonisation and activity, may futher increase degradation of kelp material. Shredded macroalgae and egested phytoplankton by benthic suspension feeders, gastropods and zooplankton in coastal and open ocean ecosystems, rapidly host diverse communities of bacteria and protozoa, which increase its nutritional quality by taking up inorganic nutrients from the surrounding water and accelerating degradation (Peduzzi and Herndl 1986; Hansen et al. 1996; Povero et al. 2003; Thor et al. 2003). Based on relationship between the lost proportion of *Strongylocentrotus droebachiensis* fecal dry weight (material = *Saccharina latissima*) after *t* days ($0.68e^{-0.41t} + 0.32$) (Sauchyn and Scheibling 2009) and the average time until settlement of feces in our model (11.7 ± 6.7 h), we estimate that ~12.5% of the fecal material is remineralized in transport.

The transformation from large blades to small detrital particles not only has important consequences for how rapidly kelp is incorporated into benthic food webs (Yorke et al. 2019), but it also influences the fate of the exported kelp (Wotton and Malmqvist 2001). Small particles sink slower than large blades, stipes, or whole thalli, allowing more time for them to be swept away by horizontal water movement. Older feces are even more likely to be suspended and transported horizontally because feces rapidly lose labile organic compounds, become less dense and, as a result, sink even slower over time (Sauchyn and Scheibling 2009). Our model showed that this transformation can extend mean dispersal distance by 4 times, increasing the likelihood that this carbon will move off the coastal shelf and into deep basins. In terms of the role kelps play in moving organic carbon to sink habitats, sequestration can occur when detritus is exported and buried in soft sediment depositional areas or is transported beyond the 1000 m deep sequestration horizon, where it is stored in the long-term (Krause-Jensen and Duarte 2016). Our current model and our past observations of the detritus on the seafloor (Filbee-Dexter et al. 2018), suggest that most large pieces of detritus (e.g., blades and stipes) move slowly and remain close to shore. As a result, they would therefore require substantial cross shelf movement for large pieces of detritus to reach beyond 1000 m depth. In coastal areas such as Malangen fjord, which are bounded by a large coastal shelf with no submarine canyons to link to the deep sea, burial in fjord sediments may be an important process by which large pieces of detritus are taken out of the short-term carbon cycle (Smith et al. 2015). In contrast, smaller detrital fragments and particles have larger potential for long distance export, and thus fragmentation and grazing may be critical processes by which macroalgae reach deep coastal sediments (Queirós et al. 2019) or are exported off the shelf and below the 1000 m depth sequestration horizon (Krause-Jensen and Duarte 2016).

Based on detrital production rates measured from our study sites, we estimate that between 1.3 and 10.8 kg of kelp m^{-2} are collected and shredded annually from reefs with a range of urchin densities and detrital kelp production rates. This estimate is based on average capture rates of 50% of detrital blades/fragments and 52% of detrital stipes within kelp forests habitats, which may either overestimate the amount converted because it does not include kelp that is immediately exported or kelps that deposit in large accumulations, or underestimate the amount because it does not include kelp collected and shredded in adjacent habitats (e.g., barrens). However, Filbee-Dexter et al. (2018) tracked slow movement of whole kelp blades, blade fragments, and stipes in our study area, and recovered 53% of tagged kelps within 2 weeks after they were released at 6 m depth, 79% of which were associated with sea urchins, supporting the assertion that a substantial portion (>50%) of kelp detritus is retained and captured by urchins in these shallow habitats. Further, our model suggests that a substantial proportion of large pieces of detritus settle on the sea floor rapidly (< 1 km from release point) where there is a high chance they will land in habitats with sea urchins. The extent that detritus does not settle locally, but is transported away from shallow grazers and into pelagic/deep sea areas depends on a combination of the sinking speed of the piece of detritus, the hydrodynamic environment at its release site, and the vertical distance it can fall before reaching the seafloor. These considerable sources of variability are partly captured in our estimates, which are taken from study sites with a range of exposures and diverse topographies, using different types of detritus, and using a model with high spatial-temporal resolution that captures periods of both strong and weak water movement.

Sea urchin grazing is one of the most pervasive ecological processes in kelp forests globally, and has changed dramatically in many regions due to anthropogenic climate change (Steneck et al. 2002; Filbee-Dexter and Scheibling 2014b; Wernberg et al. 2019). In mid-Norway, sea urchin recruitment is now failing with increasing temperatures and increased mesopredator populations (Christie et al. 2019)(Fagerli et al. 2013, 2014). In Nova Scotia, Canada sea urchins have been effectively removed from the system as a result of climate-driven disease (Feehan and Scheibling 2014). The southern movement of the eastern Australia current into Tasmania (Ling et al. 2009) and an extreme marine heatwave (‘the blob’) in Northern California (Rogers-Bennett and Catton 2019)(Catton 2016) have led to sea urchin population explosions, which triggered destructive overgrazing and large-scale kelp forest loss. The concomitant change in capture (collection) and shredding rates of kelp detritus associated with changing sea urchin densities is likely to have substantially altered the amount of detritus moving through different export pathways, with a higher percentage detritus leaving shallow reefs as small particles when sea urchin densities are high. This will impact the magnitude, transport pathways, and endpoints of detrital deposits. Of course, the importance of sea urchins for kelp carbon export depend on a delicate balance between sea urchins being abundant enough to capture significant amounts of kelp detritus and being too abundant to persist by grazing detritus alone (Harrold and Reed 1985). When sea urchins are too abundant they can destructively graze attached kelps, decreasing overall standing stock of carbon, and drastically reducing the amount of kelp available to be exported as detritus (Krumhansl et al. 2014). If they are absent, an important collector-shredder is absent from the ecosystem, and the distance of carbon transfer from intact kelp forests is reduced. Either way, these organisms appear to be of central importance for the breakdown and relocation of organic material along many temperate coasts and should be considered when studying the fate of this detritus.

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

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Literature cited

Abdullah M, Fredriksen S, Christie H (2017) The impact of the kelp (*Laminaria hyperborea*) forest on the organic matter content in sediment of the west coast of Norway. Mar Biol Res 13:151–160

Bekkby T, Moy FE, Olsen H, et al (2013) The Norwegian Programme for Mapping of Marine Habitats - providing knowledge and maps for ICZMP. In: Global Challenges in Integrated Coastal Zone Management. John Wiley & Sons, Ltd, Oxford, UK, pp 19–30

Britton-Simmons KH, Rhoades AL, Pacunski RE, et al (2012) Habitat and bathymetry influence the landscape-scale distribution and abundance of drift macrophytes and associated invertebrates. Limnol Oceanogr 57:176–184. doi: 10.4319/lo.2012.57.1.0176

Canadell JG, Le Quéré C, Raupach MR, et al (2007) Contributions to accelerating atmospheric CO2 growth from economic activity, carbon intensity, and efficiency of natural sinks. Proc Natl Acad Sci U S A 104:18866–70. doi: 10.1073/pnas.0702737104

Catton C (2016) "Perfect Storm" Decimates Northern California Kelp Forests | CDFW Marine Management News. In: Calif. Dep. Fish Wildl. Mar. Manag. News. https://cdfwmarine.wordpress.com/2016/03/30/perfect-storm-decimates-kelp/. Accessed 25 Feb 2018

Christie H, Gundersen H, Rinde E, et al (2019) Can multitrophic interactions and ocean warming influence large-scale kelp recovery? Ecol Evol 9:2847–2862. doi: 10.1002/ece3.4963

Dean TA, Bodkin JL, Jewett SC, et al (2000) Changes in sea urchins and kelp following a reduction in sea otter density as a result of the Exxon Valdez oil spill. Mar Ecol Prog Ser 199:281–291

Fagerli C, Norderhaug K, Christie H (2013) Lack of sea urchin settlement may explain kelp forest recovery in overgrazed areas in Norway. Mar Ecol Prog Ser 488:119–132. doi:

10.3354/meps10413

Fagerli C, Norderhaug KM, Christie H, et al (2014) Predators of the destructive sea urchin grazer (Strongylocentrotus droebachiensis) on the Norwegian coast. Mar Ecol Prog Ser 502:207/218

Feehan C, Scheibling R (2014) Disease as a control of sea urchin populations in Nova Scotian kelp beds. Mar Ecol Prog Ser 500:149–158. doi: 10.3354/meps10700

Filbee-Dexter K, Scheibling RE (2014a) Detrital kelp subsidy supports high reproductive condition of deep-living sea urchins in a sedimentary basin. Aquat Biol 23:71–86. doi: 10.3354/ab00607

Filbee-Dexter K, Scheibling RE (2016) Spatial patterns and predictors of drift algal subsidy in deep subtidal environments. Estuaries and Coasts 39:1724–1734. doi: 10.1007/s12237-016-0101-5

Filbee-Dexter K, Scheibling RE (2014b) Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. Mar Ecol Prog Ser 495:1–25. doi: 10.3354/meps10573

Filbee-Dexter K, Wernberg T, Fredriksen S, et al (2019) Arctic kelp forests: Diversity, resilience and future. Glob Planet Change 172:1–14. doi: /doi.org/10.1016/j.gloplacha.2018.09.005

Filbee-Dexter K, Wernberg T, Norderhaug KM, et al (2018) Movement of pulsed resource subsidies from kelp forests to deep fjords. Oecologia 187:291–304. doi: 10.1007/s00442-018-4121-7

Haidvogel DB, Arango H, Budgell WP, et al (2008) Ocean forecasting in terrain-following coordinates: Formulation and skill assessment of the Regional Ocean Modeling System. J Comput Phys 227:3595–3624. doi: 10.1016/j.jcp.2007.06.016

Hansen B, Fotel FL, Jensen NJ, Madsen SD (1996) Bacteria associated with a marine planktonic copepod in culture. II. Degradation of fecal pellets produced on a diatom, a nanoflagellate or a dinoflagellate diet. J Plankton Res 18:275–288. doi: 10.1093/plankt/18.2.275

Harrold C, Reed DC (1985) Food availability, sea urchin grazing, and kelp forest community structure. Ecology 66:1160–1169. doi: 10.2307/1939168

Heck KL, Carruthers TJB, Duarte CM, et al (2008) Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. Ecosystems 11:1198–1210. doi: 10.1007/s10021-008-9155-y

Howard J, Sutton-Grier A, Herr D, et al (2017) Clarifying the role of coastal and marine systems in climate mitigation. Front Ecol Environ 15:42–50. doi: 10.1002/fee.1451

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva

Johnson CR, Mann KH (1986) The importance of plant defence abilities to the structure of subtidal seaweed communities: The kelp *Laminaria longicruris* de la Pylaie survives grazing by the snail *Lacuna vincta* (Montagu) at high population densities. J Exp Mar Bio Ecol 97:231–267. doi: 10.1016/0022-0981(86)90244-3

Krause-Jensen D, Duarte CM (2016) Substantial role of macroalgae in marine carbon sequestration. Nat Geosci 9:737–742. doi: 10.1038/ngeo2790

Krause-Jensen D, Lavery P, Serrano O, et al (2018) Sequestration of macroalgal carbon: the elephant in the Blue Carbon room. Biol Lett 14:20180236. doi: 10.1098/rsbl.2018.0236

Krumhansl K, Scheibling R (2012) Production and fate of kelp detritus. Mar Ecol Prog Ser 467:281–302. doi: 10.3354/meps09940

Krumhansl KA, Lauzon-Guay J-S, Scheibling RE (2014) Modeling effects of climate change and phase shifts on detrital production of a kelp bed. Ecology 95:763–74

Larson BR, Vadas RL, Keser M (1980) Feeding and nutritional ecology of the sea urchin

Strongylocentrotus drobachiensis in Maine, USA. Mar Biol 59:49–62. doi: 10.1007/BF00396982

Lauzon-Guay J-S, Scheibling RE (2007) Seasonal variation in movement, aggregation and destructive grazing of the green sea urchin (*Strongylocentrotus droebachiensis*) in relation to wave action and sea temperature. Mar Biol 151:2109–2118. doi: 10.1007/s00227-007-0668-2

Lauzon-Guay J, Scheibling R (2010) Spatial dynamics, ecological thresholds and phase shifts: modelling grazer aggregation and gap formation in kelp beds. Mar Ecol Prog Ser 403:29–41. doi: 10.3354/meps08494

Leclerc J, Riera P, Leroux C, et al (2013) Temporal variation in organic matter supply in kelp forests: linking structure to trophic functioning. Mar Ecol Prog Ser 494:87–105. doi: 10.3354/meps10564

Ling SD, Johnson CR, Ridgeway K, et al (2009) Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. Glob Chang Biol 15:719–731. doi: 10.1111/j.1365-2486.2008.01734.x

Mamelona J, Pelletier É (2005) Green urchin as a significant source of fecal particulate organic matter within nearshore benthic ecosystems. J Exp Mar Bio Ecol 314:163–174. doi: 10.1016/J.JEMBE.2004.08.026

Mann K (1973) Seaweeds: Their productivity and strategy for growth. Science 182:975–981. doi: 10.1126/science.155.3758.81

Muggeo VMR (2017) Regression Models with Break-Points / Change-Points Estimation

Norderhaug KM, Christie HC (2009) Sea urchin grazing and kelp re-vegetation in the NE Atlantic. Mar Biol Res 5:515–528. doi: 10.1080/17451000902932985

Orth RJ, Carruthers TJB, Dennison WC, et al (2006) A global crisis for seagrass e cosystems. Bioscience 56:987–996. doi: 10.1641/0006-3568(2006)56[987:agcfse]2.0.co;2

Pedersen MF, Filbee-Dexter K, Fagerli CW, et al (2019) Detrital carbon production and export in high latitude kelp forests. Oecologia in press:1–33

Peduzzi P, Herndl GJ (1986) Role of bacteria in decomposition of faecal pellets egested by the epiphyte-grazing gastropod *Gibbula umbilicaris*. Mar Biol 92:417–424. doi: 10.1007/BF00392682

Pinheiro J, Bates D, DebRoy S, et al (2018) Linear and Nonlinear Mixed Effects Models

Povero P, Misic C, Ossola C, et al (2003) The trophic role and ecological implications of oval faecal pellets in Terra Nova Bay (Ross Sea). Polar Biol 26:302–310. doi: 10.1007/s00300-003-0485-0

Queirós AM, Stephens N, Widdicombe S, et al (2019) Connected macroalgal-sediment systems: blue carbon and food webs in the deep coastal ocean. Ecol Monogr. doi: 10.1002/ecm.1366

Renaud PE, Løkken TS, Jørgensen LL, et al (2015) Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. Front Mar Sci 2:31. doi: 10.3389/fmars.2015.00031

Rogers-Bennett L, Catton CA (2019) Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. Sci Rep 9:15050. doi: 10.1038/s41598-019-51114-y

Sauchyn L, Scheibling R (2009) Degradation of sea urchin feces in a rocky subtidal ecosystem: implications for nutrient cycling and energy flow. Aquat Biol 6:99–108. doi: 10.3354/ab00171

Schram JB, Kobelt JN, Dethier MN, Galloway AWE (2018) Trophic transfer of macroalgal fatty acids in two urchin species: digestion, egestion, and tissue building. Front Ecol Evol 6:83. doi: 10.3389/fevo.2018.00083

Shchepetkin AF, McWilliams JC (2005) The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. Ocean

Model 9:347–404. doi: 10.1016/J.OCEMOD.2004.08.002

Smale DA, Moore PJ, Queirós AM, et al (2018) Appreciating interconnectivity between habitats is key to blue carbon management. Front Ecol Environ 16:71–73. doi: 10.1002/fee.1765

Smith RW, Bianchi TS, Allison M, et al (2015) High rates of organic carbon burial in fjord sediments globally. Nat Geosci 8:450–453. doi: 10.1038/ngeo2421

Steneck RS, Graham MH, Bourque BJ, et al (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ Conserv 29:436–459. doi: 10.1017/S0376892902000322

Thor P, Dam H, Rogers D (2003) Fate of organic carbon released from decomposing copepod fecal pellets in relation to bacterial production and ectoenzymatic activity. Aquat Microb Ecol 33:279–288. doi: 10.3354/ame033279

Vanderklift MA, Wernberg T (2008) Detached kelps from distant sources are a food subsidy for sea urchins. Oecologia 157:327–335. doi: 10.1007/s00442-008-1061-7

Vetter EW, Dayton PK (1998) Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. Deep Sea Res Part II Top Stud Oceanogr 45:25–54. doi: 10.1016/S0967-0645(97)00048-9

Wernberg T, Filbee-Dexter K (2018) Grazers extend blue carbon transfer by slowing sinking speeds of kelp detritus. Sci Rep 8:17180

Wernberg T, Krumhansl KA, Filbee-Dexter K, Pedersen MF (2019) Status and trends for the world's kelp forests. In: Sheppard C (ed) World Seas: An Environmental Evaluation, Vol III: Ecological Issues and Environmental Impacts. Academic Press

Wotton RS, Malmqvist B (2001) Feces in aquatic ecosystems: feeding animals transform organic matter into fecal pellets, which sink or are transported horizontally by currents; these fluxes relocate organic matter in aquatic ecosystems. Bioscience 51:537–544. doi:

10.1641/0006-3568(2001)051[0537:fiae]2.0.co;2
Yorke CE, Page HM, Miller RJ (2019) Sea urchins mediate the availability of kelp detritus to benthic consumers. Proc R Soc B Biol Sci 286:20190846. doi: 10.1098/rspb.2019.0846

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

Site	Detritus production (g FW d^{-1} m^{-2})		Sea urchin density (m^{-2})	Capture in kelp forest (%)		Grazed detritus (g FW m^{-2} d^{-1})
	Blades and fragments	Stipes	Kelp forest	Blade and fragments	Stipes	Blades, fragments, and 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%)

Figure legends

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

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

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

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

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

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

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

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

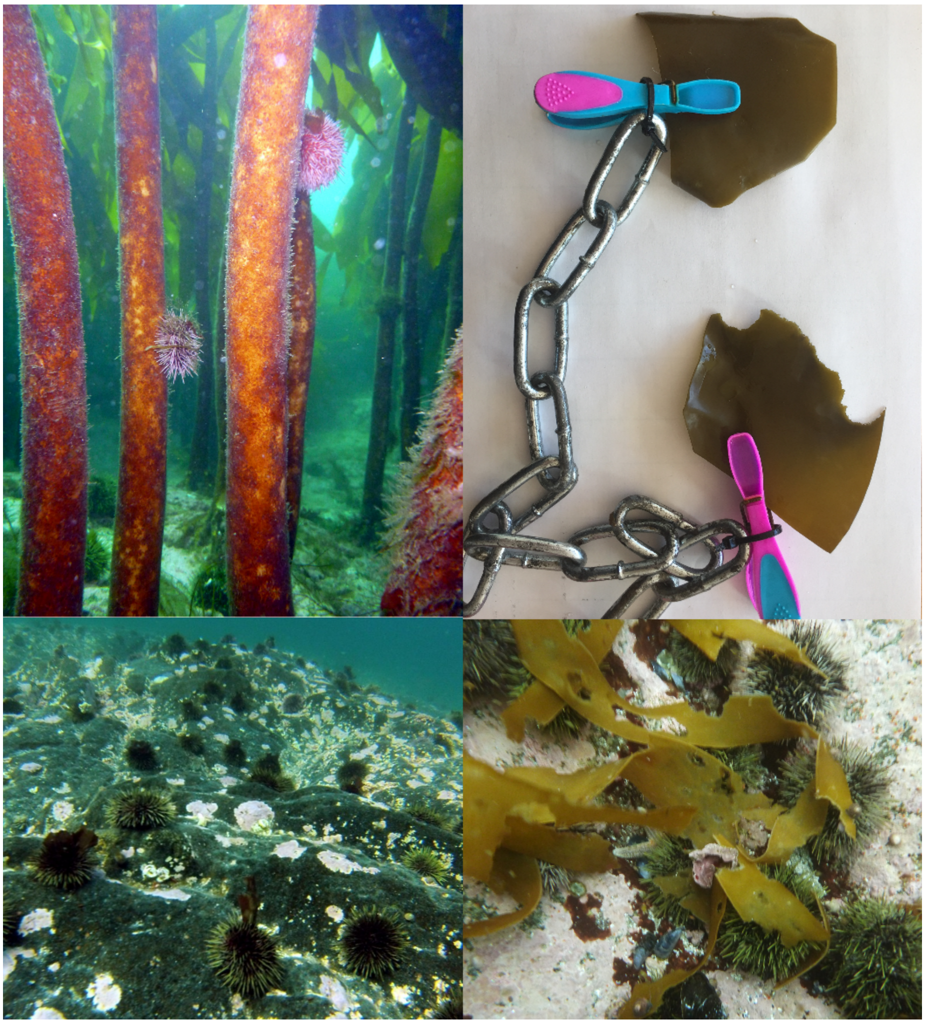
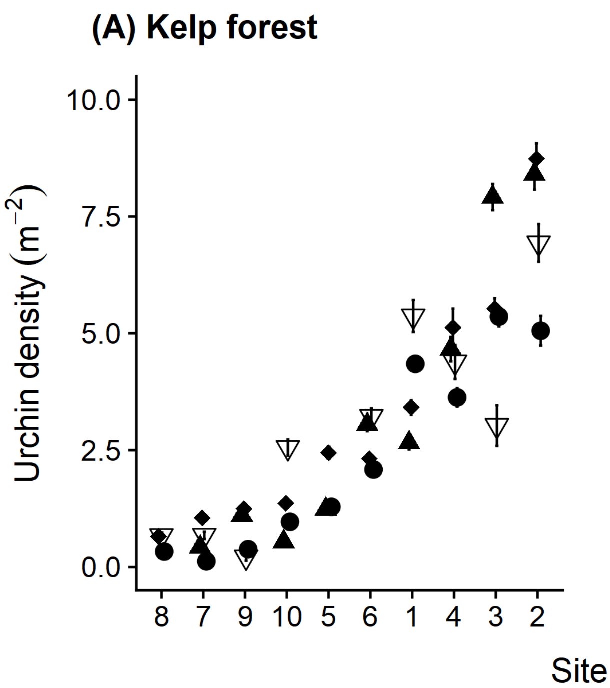


Fig 1

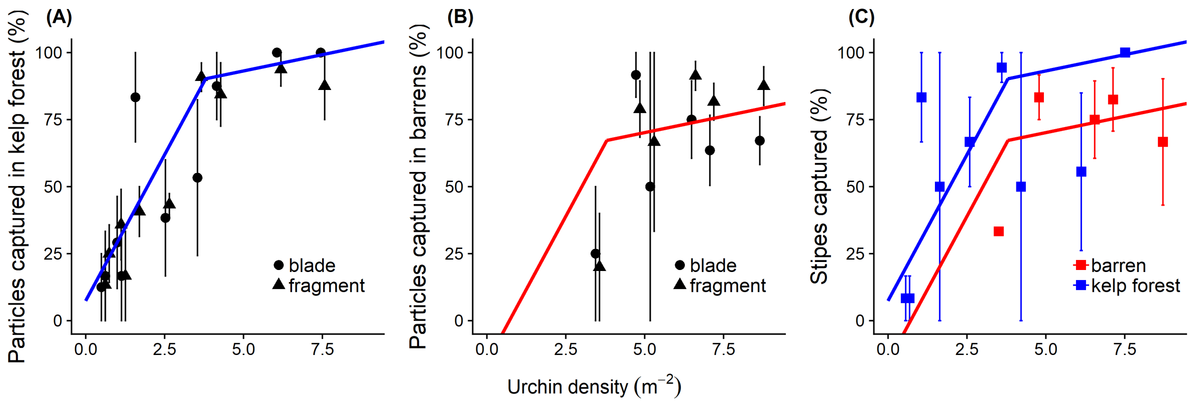


(A) Kelp forest
(B) Barrens
Urchin density (m−2)
10.0
7.5
5.0
2.5
0.0
8 7 9 10 5 6 1 4 3 2
8 7 5 6 10 1 4 3 2 9
Aug 2016
Oct 2016
Mar 2017
May 2017
Site

666

667 Fig 2

668



(A)
Particles captured in kelp forest (%)
100
75
50
25
0
0.0
2.5
5.0
7.5
blade
fragment
(B)
Particles captured in barrens (%)
Urchin density (m^{-2})
(C)
Stipes captured (%)
barren
kelp forest

669 Fig 3

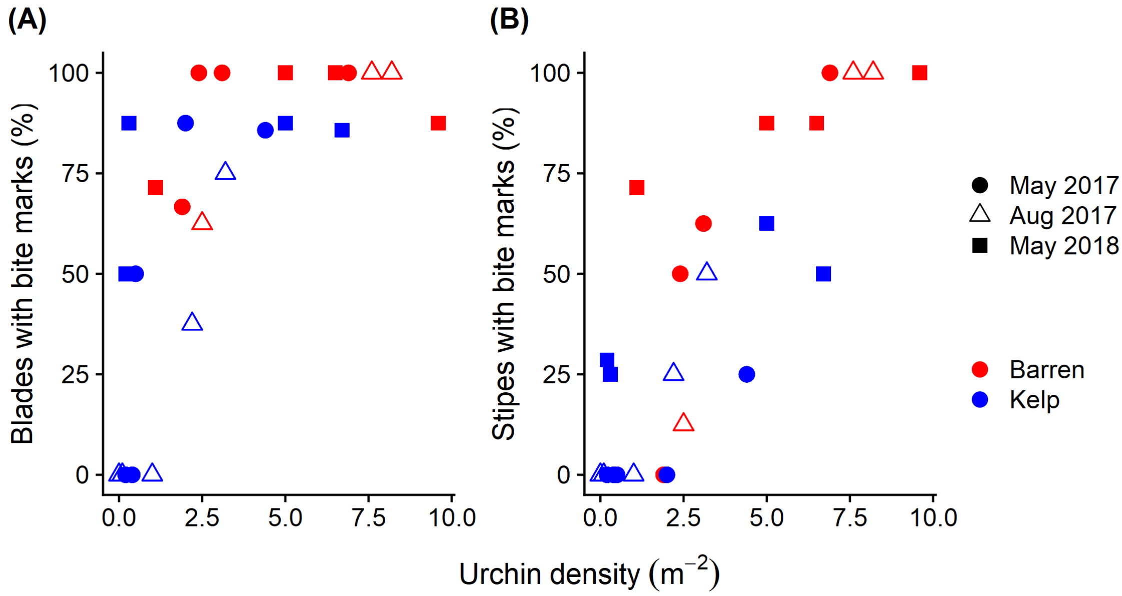

(A)
(B)
Blades with bite marks (%)
Stipes with bite marks (%)
100
75
50
25
0
0.0
2.5
5.0
7.5
10.0
Urchin density (m⁻²)
May 2017
Aug 2017
May 2018
Barren
Kelp

Fig 4

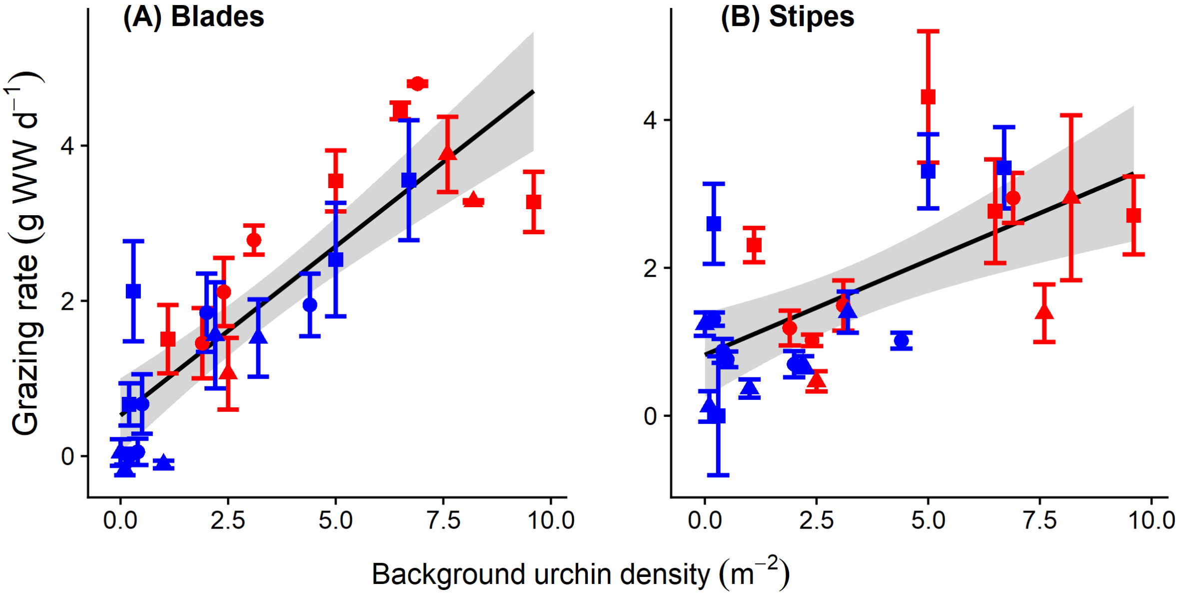

(A) Blades
(B) Stipes
Grazing rate (g WW d^{-1})
Background urchin density (m^{-2})
0
2
4
0.0
2.5
5.0
7.5
10.0

Fig 5

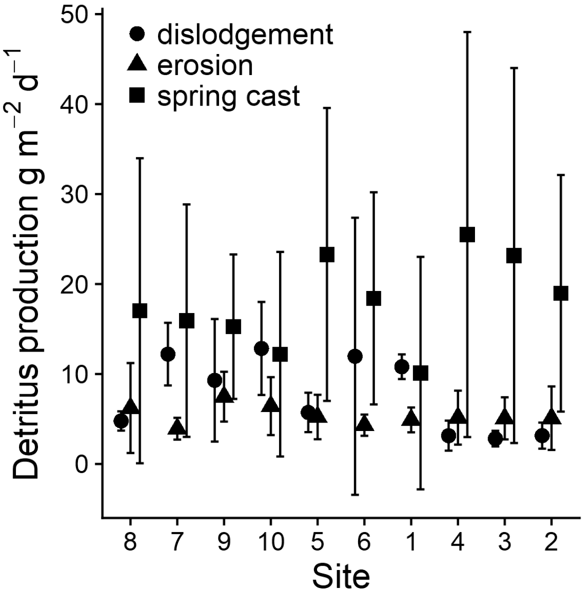

dislodgement
erosion
spring cast
Detritus production g m^{-2} d^{-1}
50
40
30
20
10
0
8
7
9
10
5
6
1
4
3
2
Site

Fig 6

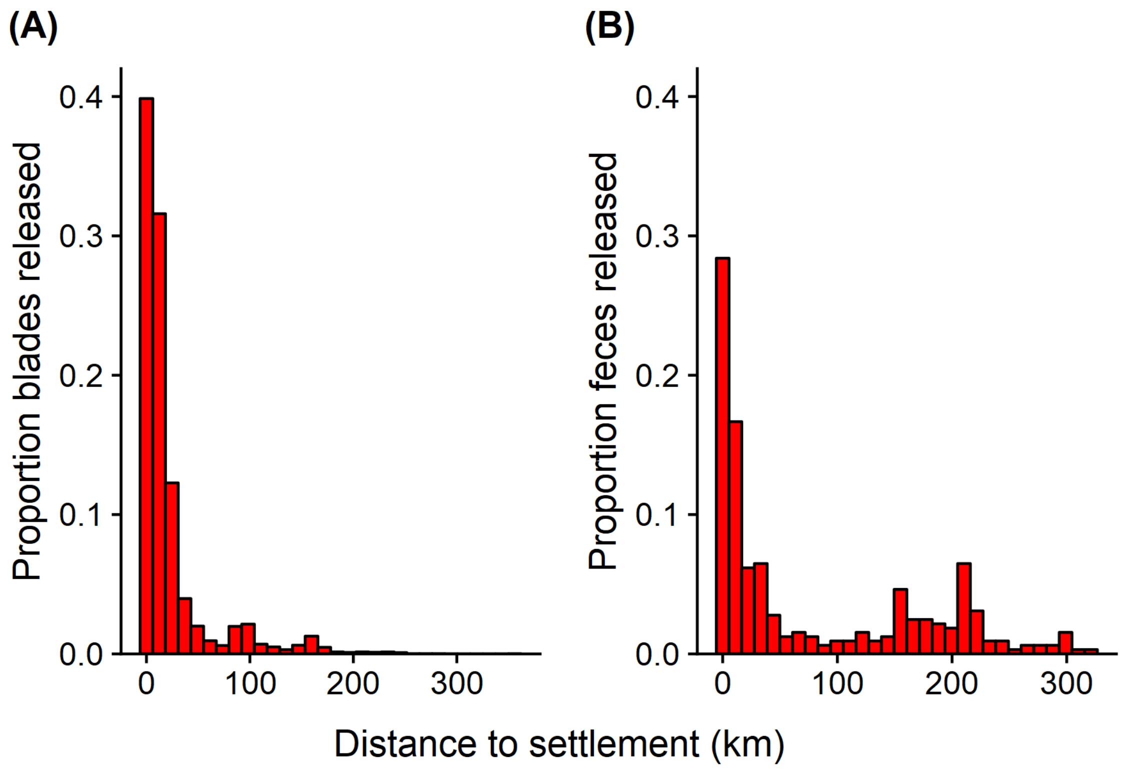

(A)
Proportion blades released
0.4
0.3
0.2
0.1
0.0
0
100
200
300
(B)
Proportion feces released
0.4
0.3
0.2
0.1
0.0
0
100
200
300
Distance to settlement (km)

Fig 7

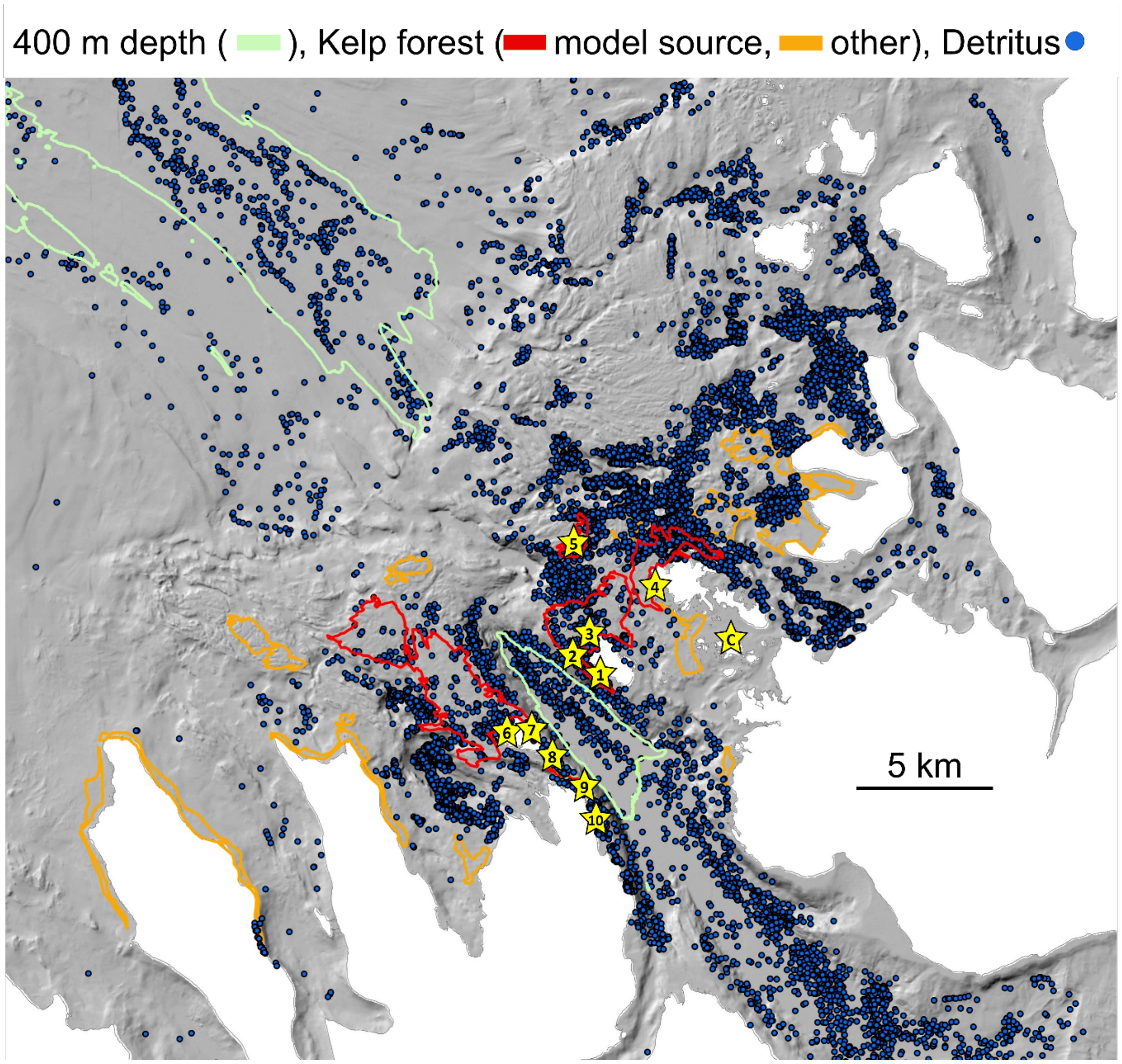

400 m depth ( ), Kelp forest (model source, other), Detritus
5 km
1
2
3
4
5
6
7
8
9
10
C

Fig 8