MOVEMENT OF PULSED RESOURCE SUBSIDIES FROM KELP FORESTS TO DEEP FJORDS

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Abstract

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

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

Introduction

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

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

Marine resource subsidies often occur as seasonal or pulsed events that provide a temporary surplus of food inputs (Gage 2003; Yang et al. 2008; de Bettignies et al. 2013). In the deep sea, the vertical transport of particulate organic material (e.g. plankton fecal pellets, marine snow, microbial biomass) from the photic zone to the seafloor, following the spring phytoplankton bloom, strongly determines the amount and timing of organic material and nutrients reaching benthic communities (Billett et al. 1983; Platt et al. 1989; Smith et al. 1994). Extreme variations in resource supply can have individual-level effects that propagate up trophic levels, with important consequences for recipient ecosystems (reviewed by Ostfeld and Keesing 2000; Yang et al. 2008). Yang et al. (2010) conducted a meta-analysis of 189 field studies on resource pulse-consumer interactions, and found that the highest magnitude of consumer response occurred in marine systems. Field observations and manipulations have shown that the overall impact of resource pulses is strongly influenced by their timing (Durant et al. 2007; Armstrong and Bond 2013; Sato et al. 2016), duration, and frequency (e.g. Bode et al. 1997; Bologna et al. 2005; Yeager et al. 2005; Hoover et al. 2006). These trophic linkages are transmitted down to the deep seafloor, where the benthic communities are directly dependent on the seasonal pulses of organic matter produced in the sunlit surface waters (Billett et al. 2001; Smith et al. 2006, 2008).

Kelps are large brown seaweeds that have some of the highest rates of productivity on Earth (Mann 1973) and produce large amounts of particulate detritus in the form of detached and eroded organic material (sometimes termed drift kelp). Kelp detritus can range from whole plants, full blades, stipes, and blade fragments of various sizes. On average, 82% of the local primary production from kelp is estimated to enter the detrital food web where it can be exported to adjacent communities (Krumhansl and Scheibling 2012). In Norwegian kelp forests, only 3–8 % of the total kelp production is consumed directly by secondary producers within the kelp forest, while the rest is assumed to be exported (Norderhaug and Christie 2011). There are many examples of how the detrital resource subsidy from kelp forests increase secondary production in a diverse range of recipient communities across the depth gradient of marine ecosystems. In South Africa, shore cast subtidal kelp detritus can sustain large populations of limpets (Bustamante et al. 1995). In Western Australia, detrital kelp is a primary food source for sea urchins on shallow subtidal reefs with no kelps (Vanderklift and Wernberg 2008) and is heavily consumed by fish in seagrass beds 100s meters away from reefs (Wernberg et al. 2006). In eastern Canada, detrital kelp in deep subtidal habitats (30–100 m depth) subsidizes sea urchins and influences their reproduction and distribution (Filbee-Dexter and Scheibling 2014, 2017), and in California, USA, detrital kelp supports polychaete communities in 12 m deep sandy areas adjacent to reefs (Kim 1992) and shapes the abundance patterns of benthic fauna in deep canyons (150–500 m) (Vetter 1995; Vetter and Dayton 1998; Harrold et al. 1998). In deep fjord habitats in the Norwegian Arctic, isotopic measures from suspension-feeding bivalves showed that more than 50% of their carbon uptake came from kelps and rockweeds (Renaud et al. 2015), and at 431 m depth in an outer fjord in southern Norway, transplanted drift kelp quickly attracted high densities of crustaceans (Ramirez-Llodra et al. 2016). These studies indicate that deep-water communities adjacent to kelp forests partly depend on transport of food in the form of detrital kelp from the euphotic zone.

Detrital production rates and arrival in adjacent habitats have been documented previously (Wernberg et al. 2006; Britton-Simmons et al. 2012; de Bettignies et al. 2013; Filbee-Dexter and Scheibling 2016), but the actual movement of this material from the kelp forests into adjacent marine habitats has rarely been quantified. Detrital kelp is produced throughout the year from distal erosion, breakage, and mortality, with shorter periods of high detrital production during peak breakage or dislodgement (reviewed by Krumhansl and Scheibling 2012). Some studies have quantified its export. Filbee-Dexter and Scheibling (Filbee-Dexter and Scheibling 2012) documented a pulse of detrital kelp moving from kelp forests to deep subtidal habitats in the weeks following a strong storm event. Vanderklift & Wernberg (2008) used site-specific morphological markers to identify the source of detrital kelp delivered to urchins at a subtidal temperate reef with no kelp, and found that 10–38% of the kelp originated 6–8 km away. Hobday (2000) used data from ARGOS satellite-tracked drifters in California, USA to mimic the transport of floating rafts of *Macrocystis pyrifera* kelps, and estimated that floating kelps moved an average of 8.5 km d^{-1}, ending up as far as 448 km offshore.

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

Here, we aimed to track the pulse of old kelp blades as they moved through habitats and to uncover the extent that shallow and deep marine systems are coupled by the flow of this resource. We tested two competing hypotheses: either 1) the pulsed production of kelp detritus would be retained within the shallow kelp forests until it slowly fragmented and entered deeper habitats in a somewhat steady supply, or 2) it would be flushed into adjacent deep habitats as a short-term pulse of whole blades. To determine the dominant transport processes our study had three main objectives: 1) to quantify seasonal abundance of kelp detritus in shallow and deep-sea habitats, 2) to track the pulse of old blades from shallows to deep-subtidal and deep-fjord habitats, and 3) to determine key biotic and abiotic drivers of the transport of detritus during this pulse.

Materials and methods

Study area

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

Video surveys in shallow and deep habitats

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

Deep subtidal surveys (<85 m depth) were conducted using an underwater drop camera (Tronitech UVS5080 with VR overlay) towed at an average speed of 0.5 m s^{-1} from a 4 m research vessel and maintained ca. 1 m off the seafloor (field of view ~1 m^2). All video transects began at 65 to 85 m depth, extended perpendicularly to shore, and ended at the lower margin of the kelp forest where the seafloor beneath the canopy could not be reliably observed (typically 12–25 m). The depth of the camera and position of the vessel were recorded during each transect using a depth sensor mounted on the camera and a GPS receiver connected to the surface console unit. In total, 10 transects were conducted in March, 8 repeated in May and 10 repeated in August 2017. No transects could be recorded in October 2016 as the camera flooded.

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

Video analysis

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

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

Biomass estimates

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

Collections

To quantify how the size of detrital kelp pieces varied with season and depth, detritus was collected from shallow habitats (4–12 m depth) by divers and from deep habitats (400–450 m depth) using benthic trawls. In the shallow subtidal, kelp detritus was bagged on encounter from accumulations within or along the margin of the kelp forest during dive surveys in March, May, and August 2017. Detrital kelp was collected from the deep basin in Malangen fjord using otter or beam trawls in March, May, and October 2017. All collected pieces were laid out flat beside a scale and photographed from above. Detritus size was determined from the photographs by measuring the total area of each piece using ImageJ (National Institute of Health). To visually compare between these measures and observations of blades of kelp from video transects, large pieces of collected detritus were separated using a cut-off of >300 cm^2, which captured all full blades and the majority of partial blades, and were plotted.

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

Field measures of export

To quantify the movement of detached kelp out of kelp forests and into adjacent habitats, we released tagged kelp detritus at 6 of the 10 dive sites and tracked its displacement after a ~2-week period. Kelps were collected and cut into blades, stipes, and fragments (~10 cm long digits), and tagged in 2 places with uniquely numbered high-visibility flagging tape. At each site, kelps were bundled together with a line, lowered directly from a small boat over the subsurface float (suspended 0.5 m off the seafloor) used for dive surveys, and released when level with the canopy. Following release, the unbundled kelp sank to the seafloor. A total of 390 kelp fragments were released during calm conditions at low tide: 10 stipes, 30 fragments, and 15 blades at two sites on 9-May-2017; and 10 stipes, 30 fragments, and 30 blades at four sites on 10-May-2017. Divers revisited the sites between 11 to 17 days after the release to measure the displacement of kelp fragments. Divers located the tagged kelps by searching the immediate area surrounding the float for ~20 minutes and recording any tagged kelp encountered along the four 50-m video transects (see above). For each recovered kelp, the divers recorded the tag number, the type of detritus (blade, stipe, or fragment), the distance and bearing from the release point, the habitat type (kelp forest, kelp forest margin, barren or sand), and whether it was trapped by one or more sea urchins (*Echinus esculentus* or *Strongylocentrotus droebachiensis*). To estimate export velocity, the total displacement from the float was divided by number of days since release.

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

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

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

Results

Observations of detritus from shallow and deep video surveys

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

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

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

In the deep fjord (400–450 m), each of the four Yo-Yo Camera transects conducted in May encountered kelp detritus. This detritus was observed at least once in each of the Yo-Yo Camera transects, and in a total of 5 images of the 328 taken (1.5%). However, considering the small field of view of the camera (0.36 m^2) and the vast area of the deep fjord (9,998,363 m^2), these numbers are fairly large (Table 1). All observations were of full or partial blades, with little evidence of degradation (Fig. 2d).

Collections of kelp detritus

Further evidence that old blades enter deep habitats as a pulsed resource subsidy comes from collections of kelp detritus, which indicate that most export to deep-fjord habitats occurred during the short period between late March and early May, coinciding with the timing of old blade loss. A total of 2580 drift fragments were collected before, during, and after the pulsed loss of old blades: 1948 from accumulations at the kelp forest margin and 634 from the middle of the deep fjord. The average area of all fragments was 66 cm^2 ± 201 SD (61 ± 208 in shallows and 84 ± 178 in the deep). Small fragments of *Laminaria hyperborea* were found in all shallow collections from all 3 periods, and in all deep trawl collections from May. Whole and partial old blades were mainly present in shallow and deep collections in May (Fig. 5). MANOVA comparisons of size frequency parameters from collections showed that detritus size was significantly higher during the period comprising the detritus pulse (May) compared to before (March) and after the pulse (August/October) in both deep and shallow habitats. There was no significant difference in the size composition of detritus between deep and shallow collections in any season (Table 2), indicating a short time-span between detritus leaving the kelp forest and reaching the deep fjord.

Recovery of tagged kelp detritus

We recovered 53% of all tagged kelp pieces released at the sites. At most sites the recovered kelps were found in a narrow line or bundle offshore of the release point (Fig. 6a). Displacement ranged between 4 and 50 m (mean 11.8 m ± 8.5 SD) over the 11–17-day period since release. These represent minimum estimates of displacement as the kelp pieces that were not recovered most likely moved farther from the release point. Of the total recovered kelp, 79% were trapped by sea urchins (Fig. 6b). Kelp found the farthest from the release point were more likely to be trapped by sea urchins.

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

Discussion

Understanding the ways in which resource subsidies are transported among habitats is critical to understand how this energy is delivered and incorporated into recipient communities. Evidence from surveys and collections throughout our study area indicated that large quantities of kelp detritus entered adjacent deep subtidal habitats beyond the kelp forests, underscoring the importance of kelp as a substantial source of carbon inputs to nearby marine communities.

The detrital export during the short period between late March and early May coincided with the timing of old blade loss in *L. hyperborea* (>99% of kelps collected at study sites had old blades in mid-March, compared to <35% of kelps in early May; M. F. Pedersen, unpublished data). The spring timing of this pulse differs from other kelp ecosystems. In Western Australia and Atlantic Canada, De Bettignies et al. (2013) and Krumhansl and Scheibling (2012) measured highest production of kelp detritus in autumn, during periods of strong storm activity and/or when kelp tissue was the weakest. In our study, the peak in the number of stipes and fragments observed in March indicate high rates of dislodgement, breakage and fragmentation also occur during winter, however this mechanism was less important than the loss of old blades in the overall export of detritus. Interestingly, the occurrence of fragments of detritus in the deep subtidal transects did not show as strong of a temporal signal. This may indicate a consistent background supply of detritus in these areas due to erosion or fragmentation of kelp throughout the year. Alternatively, it could be the result of a 'conveyor belt effect', where detrital blades or fragments are continually transported through the deep subtidal region and into the deeper fjord at a constant rate, making its occurrence independent of the amount of detritus in shallow accumulations.

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

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

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

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

Once detritus deposits in deep sediment habitats, there are a number of possible fates; it can be consumed by benthic fauna, undergo decomposition, become buried and sequestered in the sediment, or exported to another area (Krumhansl and Scheibling 2012). The reduction in number of old blades found in deep and shallow habitats in August and October compared to May suggests that the supply becomes reduced and/or that the turnover of detritus increases during this period (the material could be either fragmented, consumed, or exported). Deep-sea benthic communities rely on the input of organic matter advected down the slope or through the water column, in the form of small particles (marine snow) or large parcels of organic matter (e.g. fish, cetaceans, wood and macroalgae) (Gage 2003). Although evidence of macroalgal detritus input to deep-sea ecosystem and the response of the benthic fauna is well documented (Wolff 1979; Vetter and Dayton 1998; Harrold et al. 1998; Bernardino et al. 2010; Ramirez-Llodra et al. 2016; Krause-Jensen and Duarte 2016), the overall significance of macroalgal input to the energetic budget of deep benthic communities remains uncertain (Gage 2003). The deep basin at the mouth of the Malangen fjord is not that deep and surrounded by highly productive shallow water systems, and thus the benthic communities in the deep fjord are unlikely to be food limited. However, all observations and collections in the Malangen fjord provided evidence of kelp detritus on the deep seafloor, from large blades to small particles collected in sediment grabs (K. Filbee-Dexter, personal observation), and it is arguable that the biomass, and potentially the diversity, of benthic communities supported by the system are influenced by this kelp subsidy.

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

Kelp forests are among the most extensive coastal marine habitats, but their role as a source of carbon for other marine ecosystems is not well explored. Most research on detrital kelp subsidies has focused on measuring the amount of detrital production or quantifying its impact on recipient communities (Krumhansl and Scheibling 2012), and studies on the transport and fate of kelp and other macroalgal detritus are generally limited to the export of detritus from marine to terrestrial systems (Polis et al. 1997; Krumhansl and Scheibling 2012). Our results showed that kelp forests and deep fjord habitats appeared to be closely linked by the seasonal production of detritus, challenging the common approach of treating them as closed ecosystems. As a consequence, human activities (e.g. harvesting, pollution, anthropogenic climate change) that reduce or alter timing of resource pulses (e.g. global declines in kelp overviewed by Krumhansl et al. 2016) will have immediate impacts on subsidy reaching deep fjords. In Norway, *L. hyperborea* is increasing along the west coast due to increased crab predation on, and temperature-driven recruitment failure of, sea urchins (Fagerli et al. 2013, 2014), while *S. latissima* is declining in abundance along the southwest and Skagerrak coast, possibly due to heat stress or eutrophication (Moy and Christie 2012). Research on the export of detrital kelp will provide a better understanding of the broader consequences of these changes in kelp detritus abundance. We suggest that maintaining the connectivity between kelp forests and deep fjords may be essential to conserve biodiversity and services (e.g. biomass of commercial species such as the shrimp *Pandalus borealis*) provided by these ecosystems, but additional studies to quantify this link are necessary.

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

Table 2. MANOVA comparing detritus size frequencies parameters (mean, standard deviation, coefficient of variation, and size at 95th quartile) among period (before, during, and 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

95th quartile: During ≠ (Before = After)

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

Figure legends

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

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

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

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

Fig 5. Size of detrital kelp fragments from shallow collections (a, b) and deep trawls (c, d) before (March, N = 443, 205), during (May, N = 441, 374), and after (August, N = 1064; October, N = 55) the loss of old blades. Left panels show all collections and all sizes, right panels show fragments > 300 cm^2 pooled by collection times. Boxplots show median (thick line), first and third quartiles.

Fig 6. Velocity ($m\ d^{-1}$) of tagged kelps in relation to (a) detritus type, (b) association with sea urchins (2 species: Ee = *Echinus esculenta*, Sd = *Strongylocentrotus droebachiensis*), and (c) habitat it was found in. Velocities are minimum estimates based on tagged kelps recovered during a calm period. Number of pieces recovered shown above boxplots

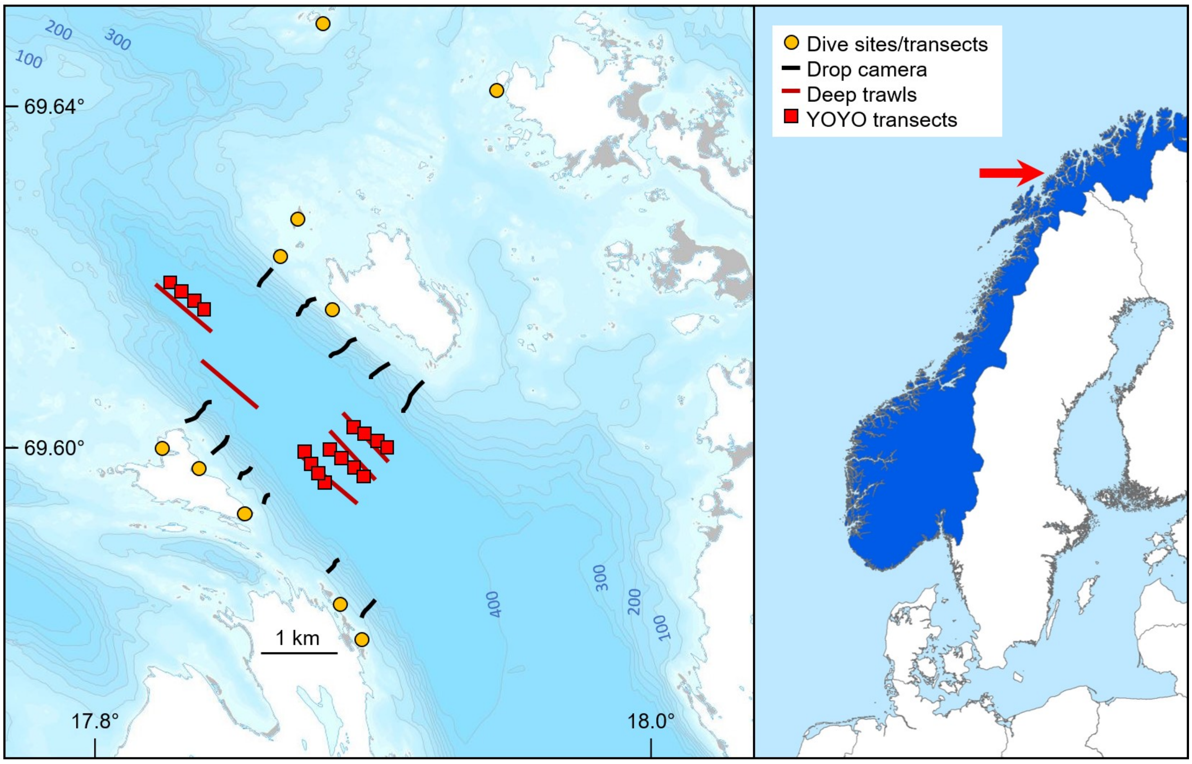

Dive sites/transects
Drop camera
Deep trawls
YOYO transects
69.64°
69.60°
17.8°
18.0°
1 km
100
200
300
400

Fig 1.

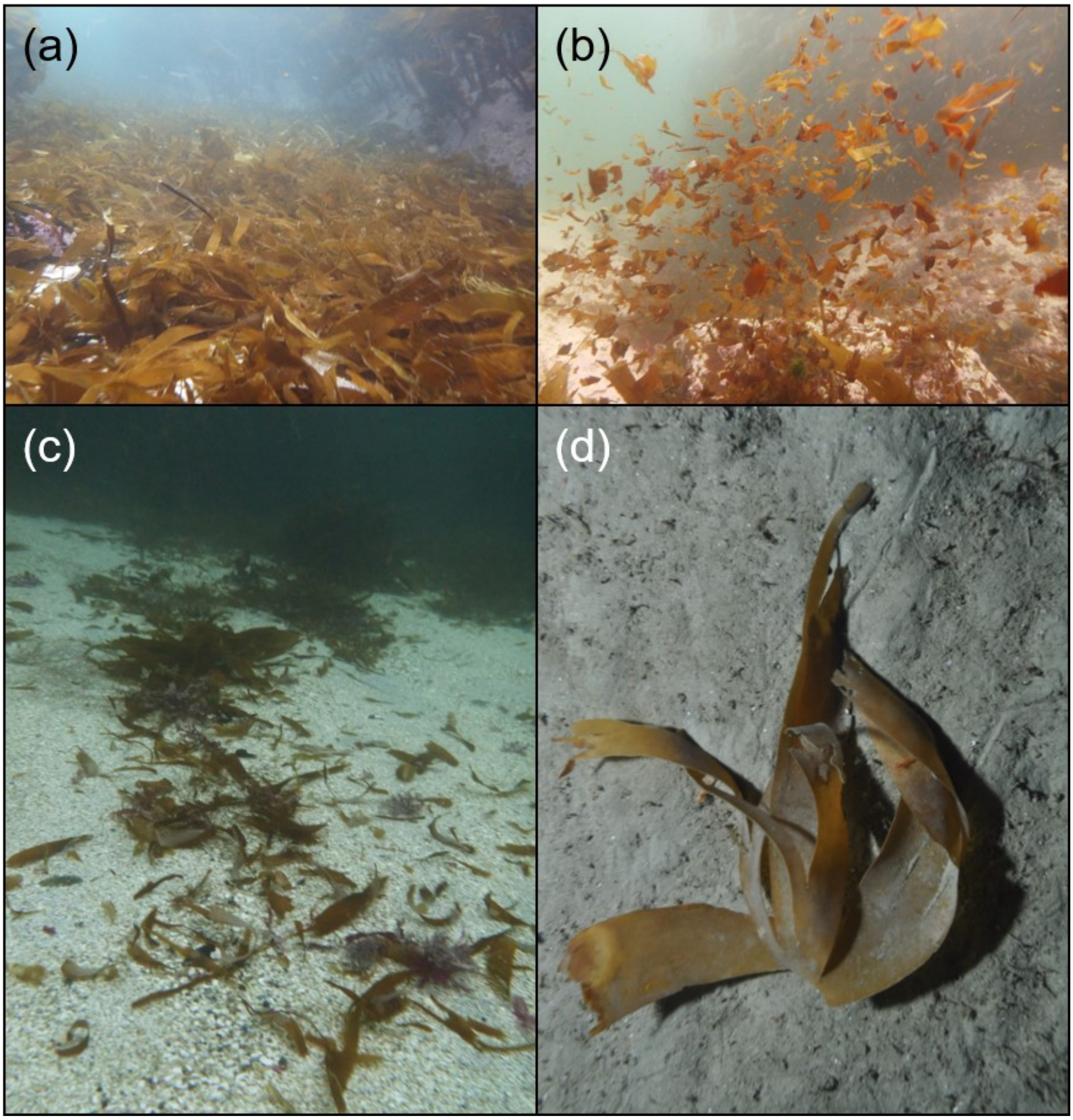
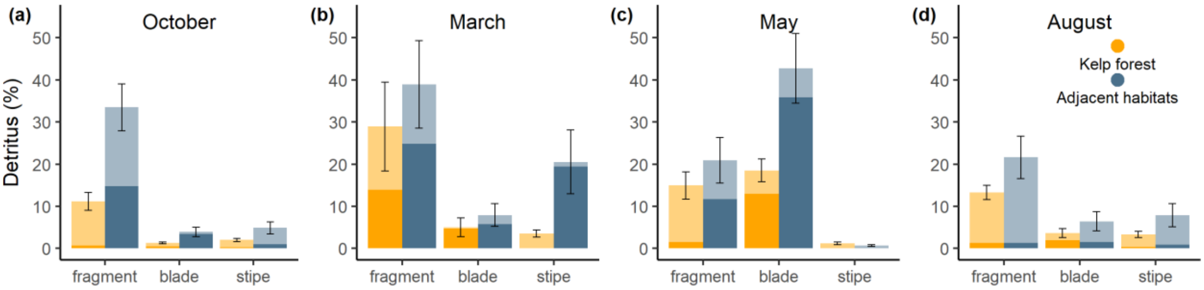
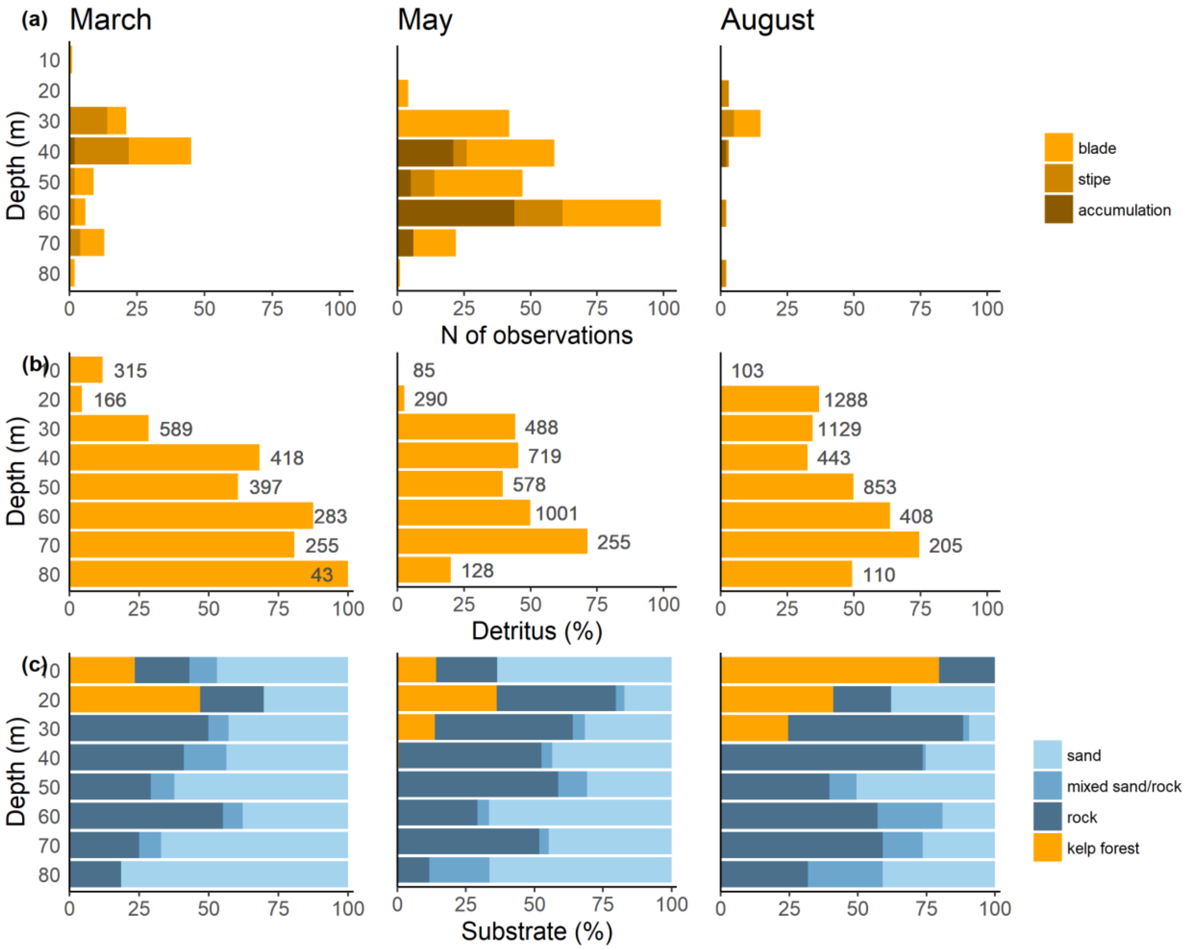


Fig 2.


(a)
October
(b)
March
(c)
May
(d)
August
Detritus (%)
50
40
30
20
10
0
fragment
blade
stipe
Kelp forest
Adjacent habitats

722

723 Fig 3.



(a)
March
May
August
Depth (m)
N of observations
blade
stipe
accumulation
(b)
Detritus (%)
315
166
589
418
397
283
255
43
85
290
488
719
578
1001
255
128
103
1288
1129
443
853
408
205
110
(c)
Substrate (%)
sand
mixed sand/rock
rock
kelp forest

724

725 Fig 4.

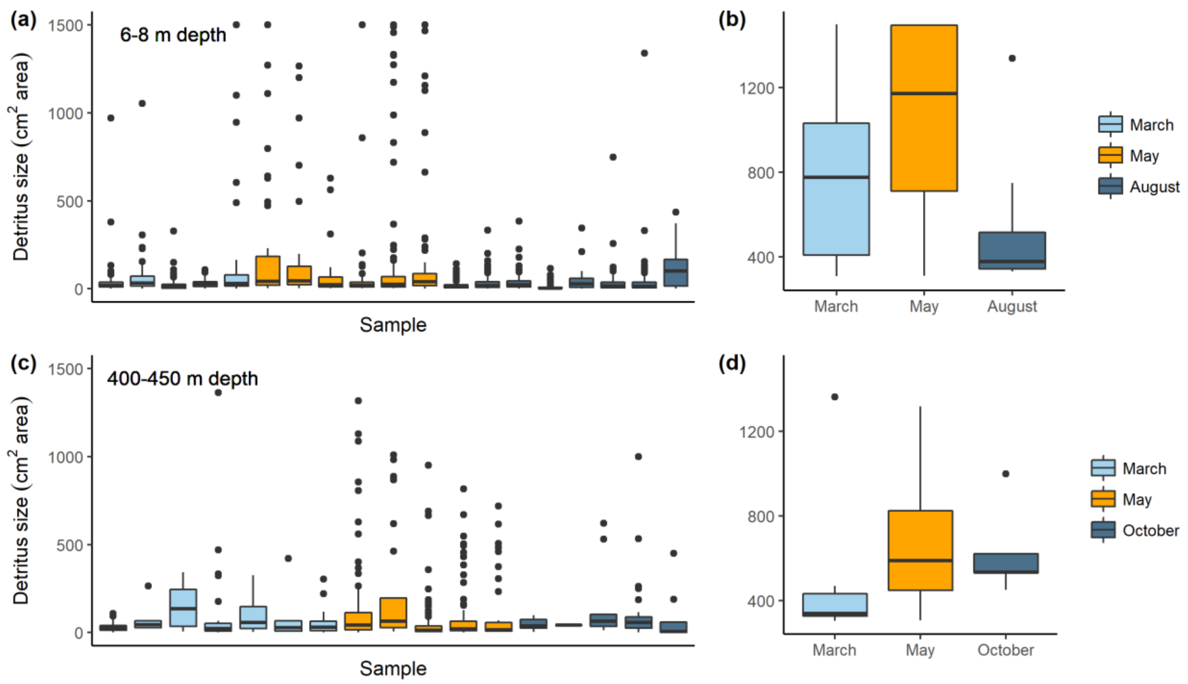

(a)
6-8 m depth
Detritus size (cm^2 area)
1500
1000
500
0
Sample
(b)
1200
800
400
March
May
August
March
May
August
(c)
400-450 m depth
Detritus size (cm^2 area)
1500
1000
500
0
Sample
(d)
1200
800
400
March
May
October
March
May
October

Fig 5.

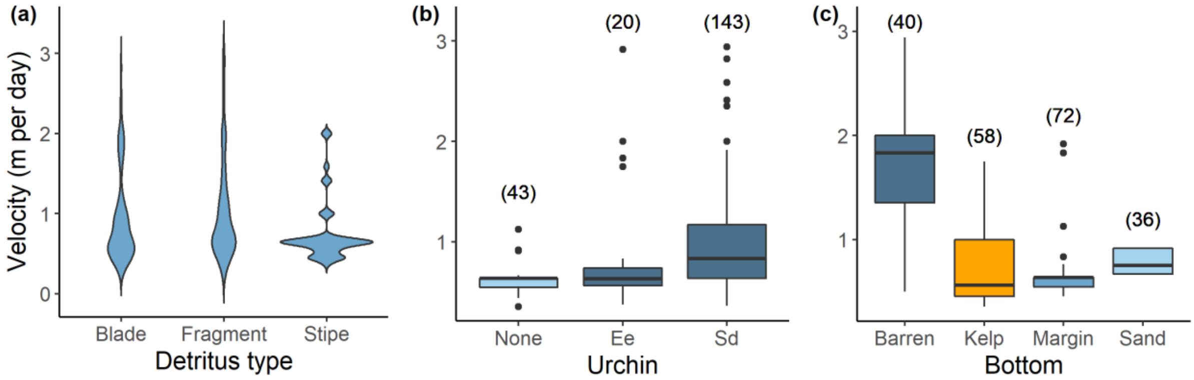

(a)
Velocity (m per day)
0
1
2
3
Blade
Fragment
Stipe
Detritus type
(b)
(43)
(20)
(143)
None
Ee
Sd
Urchin
(c)
(40)
(58)
(72)
(36)
Barren
Kelp
Margin
Sand
Bottom

Fig 6.