

## Riverine impacts on benthic biodiversity and functional traits: A comparison of two sub-Arctic fjords

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### ARTICLE INFO

#### Keywords:

Macrobenthos  
Stable isotopes  
Biodiversity  
Riverine inputs  
Terrestrial organic matter  
Biological traits analysis  
Norway  
Troms  
Målselv fjord

### ABSTRACT

Climate change is leading to increases in freshwater discharge to coastal environments with implications for benthic community structure and functioning. Freshwater inputs create strong environmental gradients, which potentially affect the community structure of benthic infauna. In turn, changes in functional trait composition have the potential to affect the processing of terrestrially-derived nutrients and organic matter along the freshwater to marine continuum. We investigated the effects of riverine inputs on benthic community structure, functional traits, taxonomic and functional diversity, and utilization of terrestrial organic matter in two contrasting northern Norwegian fjords. Results of this study revealed extensive impacts of riverine inputs on community structure and functional traits. Communities directly affected by the river were characterized by diminished taxonomic and functional diversity, with species and trait composition indicative of an environment influenced by high sedimentation rates. Large, deep-dwelling, biodiffusors and upward conveyors dominated these communities. High community biomass at the river outlet as well as indications of terrestrial organic matter utilization evidenced by stable isotope analyses, suggest that such river-influenced communities may be important for the cycling of terrestrial carbon and nutrients in the coastal zone.

### 1. Introduction

Fjords are characterized by strong spatial gradients in salinity and stratification, resulting from a complex interplay between internal structuring factors and external forcing from both terrestrial and open ocean systems (Landaeta et al., 2012). Positioned at the land-ocean interface, fjords are potential hotspots of organic carbon burial, and may play an important role in regulating climate change on glacial to interglacial timescales (Cui et al., 2016; Gilbert et al., 2002; Smith et al., 2015; Walinsky et al., 2009; Włodarska-Kowalczyk et al., 2019). Despite their complexity, fjords may be viewed as semi-enclosed systems, an asset that makes them well suited for studies of processes along natural environmental gradients. In this manner, they can serve as models for a broader range of systems where fresh and salt waters mix, and also mimic a gradient in time for systems with predicted future changes in

freshwater influence.

Freshwater runoff is increasing due to climate change, and sediment deposition resulting from this enhanced run-off is emerging as a threat to shallow estuarine and coastal benthic communities worldwide (Edgar and Barrett, 2000; Norkko et al., 2002). Alongside the transport of inorganic particles, riverine inputs alter both the quantity and quality of organic matter in coastal waters. In recent years, an increased amount of terrestrial derived organic matter (tOM) and nutrients have been observed in fjord surface waters (Aksnes et al., 2009; Frigstad et al., 2013). Increased temperatures and precipitation, as well as greening of the terrestrial environment, are expected to further accelerate the organic matter flux to coastal waters in the future (de Wit et al., 2016; Monteith et al., 2007). The consequences of these changes, especially for benthic ecosystems, are largely unknown. Benthic communities are reliant on sedimentation of organic material, including both marine

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<https://doi.org/10.1016/j.ecss.2020.106774>

Received 14 December 2019; Received in revised form 7 April 2020; Accepted 14 April 2020

Available online 19 April 2020

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material from the water column and terrestrial material from run-off, and the relative importance and fate of tOM and nutrients for benthic communities represent a substantial knowledge gap in our understanding of coastal systems.

Sediments in coastal areas are important for OM retention, transformation and mineralization (Hellemann et al., 2017; Włodarska-Kowalczyk et al., 2019). The activities of benthic infauna, including sediment reworking, ingestion, and deposition, influence the potential turnover of carbon and nutrients in the coastal zone (Griffiths et al., 2017; Villnäs et al., 2019). Thus, processing of both terrestrial and marine derived OM is strongly dependent on the composition and functional characteristics of benthic infauna communities (Thoms et al., 2018). Species' biological traits are a useful proxy for understanding how these benthic processes may be affected by changes in community structure along environmental gradients. In this study, Biological traits analysis (BTA) was applied to describe the functional features of the infauna communities. In BTA, multiple traits are defined as variables essentially replacing species composition with a variety of functions representing, for example, morphological characteristics, life history, and role in the environment (Bremner et al., 2003, 2006). The traits may be interpreted as *response* traits (ex. mobility, degree of attachment, feeding mode, adult habit) that are related to properties that enable a species to survive in a particular habitat, or *effect* traits (ex. size, sediment reworking, fecal deposition) that reflect a species' ability to influence its surrounding environment (Suding et al., 2008). BTA has been used in several recent studies to investigate benthic community *response* to disturbance, for example, pollution in the Oslofjord (Oug et al., 2012; van Son et al., 2013), bottom trawling (de Juan et al., 2007; Tillin et al., 2006), mine tailings (Trannum et al., 2019) and king crab invasion (Oug et al., 2018). In addition, BTA has been used to predict the *effect* of changes in benthic communities on ecosystem processes, for example filtering of excessive nutrients (Villnäs et al., 2019) and biogeochemical cycling in shallow estuaries (Kristensen et al., 2014).

The overall objectives of this study are to investigate how freshwater inputs affect (1) benthic community structure and diversity and (2) functional traits and functional diversity and (3) uptake of tOM in a river influenced fjord. To address these objectives, we have chosen two contrasting fjord gradients in northern Norway. The main focus is the estuarine Målselvfjord system, which receives substantial inputs of freshwater and terrestrial organic matter from the Målselv river. In

contrast, Kaldfjord has no major river influence and was selected to assess gradients in a non-river influenced system. Biological traits (both response and effect traits) were used to determine the mechanisms underlying the response of infaunal community structure to environmental gradients (depth and river influence), and the potential effects of these compositional changes on the uptake and fate of tOM and nutrients in the coastal zone.

## 2. Methods

### 2.1. Study area

Målselvfjord and Kaldfjord are located in Troms county, northern Norway (Fig. 1). Målselvfjord is a branch of the major fjord system Malangen and is characterized by seasonally high freshwater and suspended sediment inputs from the Målselv river (Wassmann et al., 1996). The Målselv river drains a 6144 square kilometer watershed dominated by mountains and forests and has an annual discharge of  $2932 \times 10^6 \text{ m}^3/\text{year}$  (Skarbøvik et al., 2014). The fjord is narrow with rather steep sides and has a depth gradient from 20 m at the base of the shallow delta to about 130 m at the fjord mouth. Kaldfjord is a topographically similar fjord with a small watershed and scattered and limited freshwater input. The depth gradient in the inner fjord is similar to Målselvfjord. It was included in the present study for comparison with the primary purpose of disentangling the influence of depth from terrestrial inputs.

### 2.2. Field sampling

The field sampling in Målselvfjord took place in October 2017. Three stations (MA, MB, MC) were sampled along the depth gradient from the edge of the shallow delta where the Målselv river enters the fjord, to the outer fjord (Fig. 1). The samples were taken with a  $0.1 \text{ m}^2$  Van-Veen grab with 3 replicates at each station. Sediment samples for analysis of sediment fine fraction, total organic carbon (TOC), total nitrogen (TN), and stable isotopes were taken from the top 5 cm of each grab and the rest was sieved over a 1 mm sieve. Large individuals (which were identified and counted and later included in the species list) were taken for stable isotope analysis (frozen at  $-20 \text{ }^\circ\text{C}$ ), and the rest were fixed with 4% buffered formaldehyde in seawater. Sediment characteristics were noted, including color, sediment composition, stratification and remnants of terrestrial material.

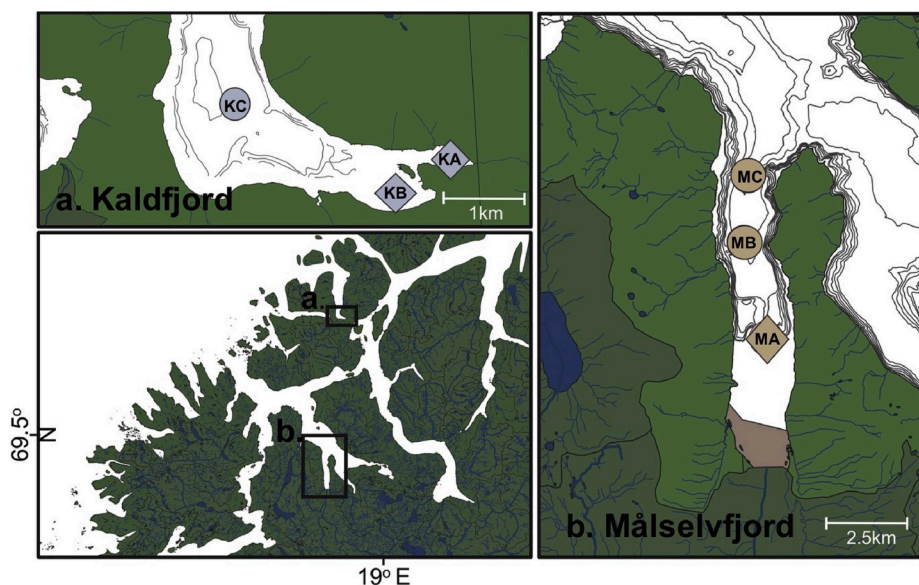


Fig. 1. Station map of sampling locations in Troms, Norway. Kaldfjord (a) had two shallow stations (27 m and 28 m) and 1 deep station (105 m). Målselvfjord (b) had one shallow station (27 m) and two deep stations (111 m and 127 m).

The sampling in Kaldfjord was performed in January 2008 (Velvin et al., 2008). Three stations (KA, KB, KC) were sampled at the head of the fjord and from the inner fjord basin (Fig. 1). The samples were taken with a 0.1 m<sup>2</sup> Van-Veen grab with 3 replicates at each station, sieved on 1 mm sieves and fixed in 4% buffered formaldehyde. Sediment sub-samples for analysis of sediment fine fraction and total organic carbon (TOC) were taken from the top sediment layer.

### 2.3. Laboratory analyses

The macrofauna samples from Målselv fjord were sorted into main taxonomic groups and then identified to species or lowest possible taxon. Species names were checked according to World Register of Marine Species ([marinespecies.org](http://marinespecies.org)) to ensure valid nomenclature. Biomass was measured as wet weight for the main taxonomic groups (Polychaeta, Bivalvia, Gastropoda, Crustacea and Echinodermata). Free-living and tube-building polychaetes and large bivalves were weighed separately. A separate category was applied for unidentified material like animal parts and segments. Terrestrial material (remnants of birch leaves and twigs) was also weighed for each replicate grab (Fig. 2).

Sediment fine fraction (% < 0.063 mm; hereafter referred to as % pelite) was determined by wet sieving. Sediment total organic carbon (TOC) and total nitrogen (TN) were determined using a CHN (i.e. Carbon, Hydrogen, and Nitrogen) analyzer at the Norwegian Institute for Water Research (NIVA) after removal of inorganic carbon by acidification. Stable isotope (SI) analysis of sediments and fauna for  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  was carried out at the University of California, Davis (UC Davis Stable Isotope Facility, USA). Samples were freeze-dried, homogenized, weighed and packed in tin capsules. Subsamples of sediments and benthic organisms expected to have high calcium carbonate content (mollusks and echinoderms) were acidified to remove inorganic carbon (in order to provide robust data on  $\delta^{13}\text{C}$  and OC content) and were analyzed in parallel with unacidified samples (used for  $\delta^{15}\text{N}$  values and N content). Long-term standard deviation at UC Davis is  $\pm 0.2\%$  for  $^{13}\text{C}$  and  $0.3\%$  for  $^{15}\text{N}$ . Stable carbon and nitrogen isotope values are expressed using delta notation, relative to international standards (Vienna PeeDee Belemnite for C, and atmospheric N for nitrogen) (Peterson and Fry, 1987).

The macrofauna and sediment samples from Kaldfjord were processed by Akvaplan-niva, and were reported by Velvin et al. (2008). Biomass data for fauna and TN in sediments were not available for the Kaldfjord stations.

### 2.4. Data analyses

All data analyses were performed in R (version 3.4.2). Since species identifications from Målselv fjord and Kaldfjord transects were performed by different people, species tables were harmonized to obtain similar taxonomic resolution. Species composition and trait analyses

were computed using the vegan package (Oksanen et al., 2017). To compare species composition between stations, principal component analysis (PCA) was performed on Hellinger-transformed species abundance data. The Hellinger transformation was chosen because it allows for the use of Euclidean based ordination methods (PCA and RDA) and it gives low weight to rare species (Legendre and Gallagher, 2001), the number of which may differ between the two datasets in this study because of the different taxonomists. In addition, Shannon-Wiener diversity index ( $H_{\log(e)}$ ; Shannon and Weaver, 1963), total abundance (N) and species richness (S) were calculated.

Ecological functioning was described for the infaunal community based on the functional features (“living strategies”) of each species. Separate analyses were carried out for estimation of functional diversity and functional community composition. Before analysis, all species with total abundance < 2 individuals were removed. Biological traits analysis (BTA), where the species abundance data are combined with traits data for each species (Beauchard et al., 2017; Bremner et al., 2003, 2006; Oug et al., 2012), was used to investigate trait distribution along gradients in depth and terrestrial inputs. Eleven traits representing adult life habit, degree of attachment, fecal deposition, mobility, normal size, body form, sediment dwelling depth, feeding mode, larval type, life duration, and sediment reworking, were used. Each trait is divided into several modalities, which express different states of the trait (for details see Supplementary information, Table S1). The species traits data were extracted from a database held by the Norwegian Institute for Water Research, where information has been compiled based on literature and by consulting experts (Oug et al., 2012), except for sediment reworking which is based on the approach by Queiros et al. (2013). In cases of missing information, supplementary data were acquired from scientific literature and open databases; The Arctic Traits Database (Degen and Faulwetter, 2019) and Biotic (MarLIN, 2006), or by entering data from closely related taxa. No traits for reproduction other than larval type were defined due to insufficient information. Species traits were scored according to the “fuzzy coding” procedure (Chevenet et al., 1994) with values ranging from 0 (= no affinity) to 3 (= dominant). This implies that a species may be given values in more than one trait category.

Functional diversity was described using the Quadratic entropy index ( $FD_{\text{RAO}}$ ; Rao, 1982). Index values were calculated separately for each trait and averaged across traits for each station following procedures described by Leps et al. (2006). Functional redundancy, calculated as the ratio between  $FD_{\text{RAO}}$  and H (van der Linden et al., 2012), was used to evaluate the degree to which different species represent the same ecosystem functions. The inverted  $FD:H$  ratio ( $1-FD/H$ ; van der Linden et al., 2016) was used to obtain a regularly increasing measure. High functional redundancy would indicate that the ecosystem functions are robust to changes in species diversity (Micheli and Halpern, 2005). A Mann-Whitney  $U$  test was used to compare species and functional indices between shallow and deep stations as well as river influenced and non-river influenced stations.

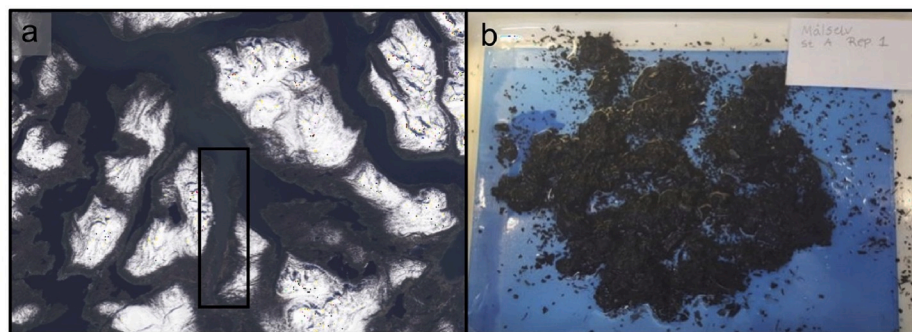


Fig. 2. (a) A satellite image of Målselv fjord during the spring flood (June 12, 2017) shows the high sediment load in the surface waters throughout the entire fjord. (b) A picture of the sieved (>1 mm) contents of the first grab from the inner station in Målselv fjord shows the high contribution of terrestrial material to the sediments.

**Table 1**

Physical and chemical characteristics of the sediments from each station. For Målselvfjord, sediment was analyzed from each grab, and the averages are presented here (+/-standard deviation).  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  are stable isotopes of carbon and nitrogen. % pelite is a grain size measurement, indicating the sediment fine fraction (% < 0.063 mm). TOC and TN are the concentrations of total organic carbon, and total nitrogen. C/N is the ratio of total organic carbon to total nitrogen. NA indicates where no data was available.

	Depth	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	% pelite	TOC (mg/g)	TN (mg/g)	C/N
MA	27	-25.4 ( $\pm 1.1$ )	4.6 ( $\pm 1.3$ )	47 ( $\pm 24$ )	8.2 ( $\pm 2.3$ )	0.6 ( $\pm 0.1$ )	15.3 ( $\pm 3.7$ )
MB	111	-23.4 ( $\pm 0.3$ )	5.7 ( $\pm 0.03$ )	86 ( $\pm 3$ )	12.6 ( $\pm 0.5$ )	1.2 ( $\pm 0.1$ )	10.2 ( $\pm 0.5$ )
MC	127	-23.6 ( $\pm 0.3$ )	6.1 ( $\pm 0.5$ )	92 ( $\pm 2$ )	12.3 ( $\pm 1.7$ )	1.2 ( $\pm 0.2$ )	10. ( $\pm 0.4$ )
KA	28	NA	NA	14	7.6	NA	NA
KB	27	NA	NA	43	24.8	NA	NA
KC	105	NA	NA	74	22.8	NA	NA

Functional community composition was described by calculating community weighted means (CWMs: [Beauchard et al., 2017](#)). Patterns among traits and relationships to environmental gradients were analyzed by multivariate ordination using PCA. The traits adult habit, mobility, degree of attachment, body form and larval type were considered as *response* traits reflecting the functional adaptations to the environmental conditions, whereas size, life duration, feeding habit, sediment dwelling depth, fecal deposition, and sediment reworking were considered as *effect* traits reflecting the influence on the environment and the processing of terrestrial organic matter. In order to find the species and functional traits that were most strongly associated with groups of stations, indicator values (IndVal, 'labdsv' package ([Roberts, 2016](#)) using 9999 permutations) were calculated from the Hellinger-transformed abundance data, and the community-weighted mean traits data to find the species and functional traits that were most strongly associated with each group of stations ([Dufrêne and Legendre, 1997](#)). An IndVal index value of 100% indicates a species or trait that is observed at all stations of one cluster and not in any other cluster.

To identify the importance of individual environmental parameters in structuring the benthic community and functional traits, the variation explained by each environmental parameter was partitioned using redundancy analyses (RDA; [Borcard et al., 1992](#)) for Målselvfjord alone, and both fjords together. To obtain parsimonious RDA models, variables were selected using a forward selection procedure (9999 permutations of residuals) based on a double-stopping criterion ([Blanchet et al., 2008](#)). Variation partitioning was then computed on these RDA models using the *varpart* function in *vegan*, which uses adjusted R-squared to estimate variation explained by the environmental variables ([Peres-Neto et al., 2006](#)). The significance of each variable was obtained by 9999 permutations. Environmental variables were log transformed where necessary.

Benthic fauna analyzed for stable isotopes were grouped based on dominant feeding habit (based on the BTA matrix) in order to determine the effect of feeding habit on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. These groups included sub-surface deposit feeders (0.5–5 cm sediment depth), deep deposit feeders (>5 cm sediment depth), filter feeders/surface deposit feeders, and scavengers/carnivores. Filter feeders/surface deposit feeders and scavengers/carnivores were grouped into single categories since for many taxa, the BTA matrix assigned equal weighting to these feeding habits. We tested for significant differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of benthos both between stations and between dominant feeding habits (excluding deep deposit feeders since there was only one sample representing this feeding habit) using Kruskal-Wallis rank sum tests followed by pairwise comparisons with the Dunn's test ([Dunn, 1964](#)). These non-parametric approaches were used because they are robust to the uneven sample sizes present in the current study.

### 3. Results

#### 3.1. Gradient in environmental variables

In both fjords, changes in depth were accompanied by changes in sediment chemistry ([Table 1](#)), including total organic carbon (TOC) and percent fine fraction (% pelite), which were comparable between fjords and were both higher at the deeper stations ([Table 1](#)). The C/N ratio, or more precisely the TOC/TN ratio, is commonly used to reflect the origin and quality of organic matter in marine sediments ([Oug, 1998](#); [Koziorowska et al., 2016](#)). In Målselvfjord, the C/N ratio was highest at the innermost station MA ( $15.3 \pm 3.7$ ) and lowest at the outermost station (MC;  $10.0 \pm 0.4$ ), reflecting the gradient from terrestrial to marine-impacted sediments. This is further confirmed by surface sediment  $\delta^{13}\text{C}$  values, which were lowest at the innermost station (MA;  $-25.4 \pm 1.1\%$ ) compared to the outer stations (MB and MC;  $-23.4 \pm 0.3\%$  and  $-23.6 \pm 0.3\%$ ). Terrestrial debris (mulch made up of leaves and twigs) collected from station MA had  $\delta^{13}\text{C}$  values of  $-30.9\%$ .

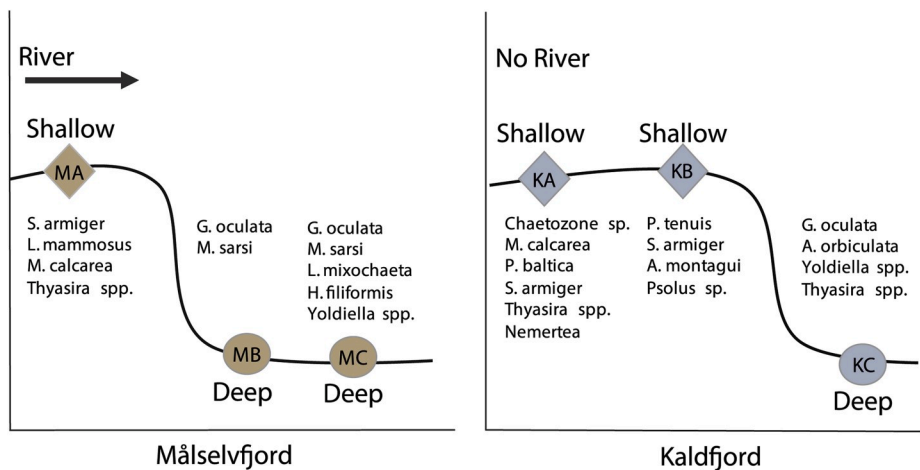
#### 3.2. Gradient in species composition and diversity patterns

Species composition differed between shallow and deep stations in both fjords ([Fig. 3](#)). Shallow stations in both fjords were characterized by high abundances of the polychaete *Scoloplos armiger* and the bivalve *Macoma calcarea*. Deep stations in both fjords had high abundances of *Galathowenia oculata* and *Yoldiella* spp. The IndVal analyses selected polychaetes *Lumbrineris mixochaeta*, *Glycera capitata*, *Leitoscoloplos mammosus*, *Heteromastus filiformis* and the caudofoveate *Chaetoderma nitidulum* as indicative of river-influenced stations and the polychaetes *Cirratulus cirratus*, *Mediomastus fragilis*, *Oxydromus flexuosus* and *Glycera alba* for the non-river influenced stations ([Table 2](#)). The main community differences are illustrated in the PCA on species abundances where stations were grouped by depth and fjord ([Fig. 4](#)).

Diversity statistics varied between fjords. Målselvfjord had higher total abundance while Kaldfjord had higher Shannon-Wiener diversity (T-influence; [Fig. 5](#)). Results of Mann-Whitney U tests demonstrate that both depth and degree of river influence may be related to the diversity patterns ([Fig. 5](#)). Shallow stations in both fjords were significantly higher in Shannon-Wiener diversity compared to deeper stations, whereas river stations (Målselvfjord) had significantly higher total abundance and significantly lower Shannon-Weiner diversity compared to stations with no river influence (Kaldfjord; [Fig. 5](#)). Biomass, which was only available for Målselvfjord samples, was by far the highest at the innermost station (MA; [Table S2](#)), and then decreased to station MB and MC. The finding of higher biomass at the innermost station was driven by the high abundance of very large individuals of the polychaetes *Scoloplos armiger* and *Glycera capitata* at the innermost station in Målselvfjord.

#### 3.3. Community traits and functional diversity

Traits data displayed in a PCA using community-weighted means also



**Fig. 3.** Graphic visualization of each fjord with a list of the most abundant species at each sampling site (listed species make up 5% or more of the total abundance). Colors (brown for river and blue for no river) and shapes (diamond for shallow (27–28 m) and circle for deep (105–127 m)) represent groupings that are used in figures throughout the rest of the manuscript. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

demonstrate the importance of depth and fjord for grouping of the stations (Fig. 4d). Individual trait groups varied in their relationship to the two gradients (Fig. 6). For response traits, river inputs were related to high mobility, burrowers, and semi-permanent tube buildings and negatively related to surface crawling, and low and no mobility. When considering effect traits, river stations were associated with subsurface deposit feeding, deep dwelling habit (1 cm to >15 cm), biodiffusers and upward conveyors, while non-river stations were associated with surface dwelling filter/suspension and scraper/grazers, epifauna, and downward conveyors. Deep stations were correlated with smaller individuals (<0.5–1 cm) and lecithotrophic larvae while larger individuals (1 cm to >10 cm) and planktotrophic species were related to the shallow stations.

Results of IndVal analysis (Table 2) show that indicator traits of river stations include biodiffusers and upward conveyors, which have long, thin and threadlike body forms and dwell deep in the sediment (5–15 cm), depositing their feces in the sub-surface of the sediment (0–5 cm). Meanwhile, non-river stations have indicator traits including downward conveyors, temporary attachment, scavengers and feeding on dissolved matter/symbionts.

Diversity statistics were related to fjord type and depth. Functional diversity ( $FD_{Rao}$ ) was significantly higher in Kaldfjord than in Målselv (Fig. 5). Functional redundancy ( $1 - (FD_{Rao}/H')$ ) was relatively high both in Kaldfjord compared to Målselv and for shallow stations compared to deep stations. Shannon-Wiener diversity and functional diversity had a positive linear relationship for all data ( $R^2 = 0.71$ ,  $p < 0.01$ ). The fjords were somewhat different, however, with rather little increase in functional diversity compared to species diversity from deep to shallow stations in Kaldfjord, illustrating the relatively high functional redundancy at the shallow stations.

### 3.4. Relationship to environmental variables

Variation partitioning was used to determine which environmental variables explained the greatest amount of variation in the community and trait datasets. Using categorical variables for depth (shallow vs. deep) and terrestrial influence (river vs. no river), significant amounts of variation were explained both in the combined community (0.32 and 0.11) as well as trait matrices (0.37 and 0.23; Fig. 4). Meanwhile, using continuous environmental variables only, depth, TOC and % pelite were found significant (Table 3). For Målselv taken alone, only depth (as a continuous variable) was significant for the community matrix (explaining 0.32 of the variation) while station (categorical; MA, MB, MC) and % pelite were significant for the traits matrix (explaining 0.20 of the variation individually and another 0.38 together).

### 3.5. Stable isotopes of benthic infauna

Stable C and N isotope analysis of selected benthic organisms ( $n = 41$ , from 25 taxa) revealed a high degree of spatial and taxonomic variability in  $\delta^{13}C$  and  $\delta^{15}N$ , with  $\delta^{13}C$  ranging from  $-25.9$  to  $-17.3$ ‰ and  $\delta^{15}N$  ranging from 0.7 to 14.7‰ (Fig. 7a). There was a strong positive relationship between  $\delta^{13}C$  and  $\delta^{15}N$  across all sampled organisms ( $r^2_{adj} = 0.54$ ,  $p < 0.0001$ ). This relationship was largely driven by changes in  $\delta^{13}C$  and  $\delta^{15}N$  along the fjord transect, with increasing values from the inner to outer fjord (Fig. 7a). There were significant between-station differences in both  $\delta^{13}C$  and  $\delta^{15}N$  of collected organisms (Kruskal-Wallis rank sum test,  $p = 0.00017$  for  $\delta^{13}C$  and  $p = 0.0036$  for  $\delta^{15}N$ ). Post-hoc pairwise comparisons (Dunn's test) revealed that organisms from the innermost station (MA) had significantly lower  $\delta^{13}C$  and  $\delta^{15}N$  values than those from the outer stations (MB and MC;  $P < 0.001$ ), while stations MB and MC did not differ.

Although much of the variability in  $\delta^{13}C$  and  $\delta^{15}N$  was driven by spatial changes along the fjord transect, there was considerable within station variability in  $\delta^{13}C$  and  $\delta^{15}N$  among species. When species were classified by dominant feeding habit, spatial changes in  $\delta^{13}C$  and  $\delta^{15}N$  were still apparent within these groups, with organisms from station MA consistently having lower  $\delta^{13}C$  and  $\delta^{15}N$  than organisms with the same feeding habit collected at stations B and C. There were also differences between feeding habits, with significantly higher  $\delta^{13}C$  values for scavengers/carnivores than for subsurface deposit feeders ( $p = 0.0050$ ) (Kruskal-Wallis rank sum/Dunn's pairwise comparisons test:  $p = 0.0013$ ).  $\delta^{15}N$  values were significantly higher for scavengers/carnivores than for subsurface deposit feeders ( $p < 0.0001$ ) and filter feeders/surface deposit feeders ( $p = 0.012$ ), and were higher for filter feeders/surface deposit feeders than for subsurface deposit feeders ( $p = 0.013$ ) (Kruskal-Wallis rank sum/Dunn's pairwise comparisons test:  $p = 0.0001$ ). Deep deposit feeders were omitted since there were data only for one individual.

The range of variation in  $\delta^{13}C$  and  $\delta^{15}N$  among taxa was substantial both across stations and feeding habits. At the one extreme, the bivalve *Thyasira* spp. collected from station MA had much lower  $\delta^{13}C$  ( $-25.9$ ‰) and  $\delta^{15}N$  (0.7‰) than any other organism sampled, followed by the polychaete *Scoloplos armiger* ( $n = 2$ ), with  $\delta^{13}C$  of  $-25.6$  to  $-25.0$ ‰ and  $\delta^{15}N$  of 4.0–4.2‰. At the other end of the scale, the predatory priapulid, *Priapulid caudatus*, had the highest  $\delta^{15}N$  values of the sampled organisms (14.7‰).

## 4. Discussion

The combined influence of terrestrial inputs and riverine disturbance is evident in taxonomic and functional composition of the communities.

**Table 2**

Results of indicator value analysis show the species, and traits (response and effect) most indicative of each station group, including Shallow (MA, KA, KB), Deep (MB, MC, KC), River (MA, MB, MC), and No River (KA, KB, KC). Each group is represented by nine grab samples. An IndVal index of 100% indicates a species or trait that is observed at all stations of one group and not in any other group. Significant IndVal indices were determined using 9999 random permutations, and only significant indicators are displayed ( $p < 0.05$ ). AH = adult habit, AM = adult mobility, BF = body form, DA = degree of attachment, FD = fecal deposition, FH = feeding habit, LD = life duration, LT = larval type, NS = normal size, SD = sediment dwelling depth, SR = sediment reworking.

Indicator Species	IndVal (%)	Indicator Response Traits	IndVal (%)	Indicator Effect Traits	IndVal (%)
<b>Shallow</b>					
<i>Pholoe baltica</i>	99	LT: Planktotroph	70	NS: 3–6 cm	64
<i>Scoloplos armiger</i>	96	BF: Short cylindrical	67	FH: Carnivore/omnivore	64
<i>Glycera alba</i>	89	BF: Flattened dorsally	65	FH: Scraper/grazer	62
<i>Macoma calcarea</i>	73	AH: Semi-permanent tube	62	NS: 1–3 cm	56
<i>Cirratulus cirratus</i>	67	AM: High	62		
<b>Deep</b>					
<i>Yoldiella</i> spp	98	AH: Swimmer	88	FD: Deep subsurface (>5 cm)	77
<i>Ceratocephale loveni</i>	89	BF: Ball shaped	77	NS: < 0.5 cm	70
<i>Nephtys ciliata</i>	89	AH: None-tube sessile	71	FH: Deep deposit feeder	65
<i>Galatowenia oculata</i>	87	AM: None	69	SR: Epifauna	65
<i>Paramphionome jeffreysii</i>	78	AH: Permanent tube	63	NS: 0.5–1 cm	61
<b>River</b>					
<i>Lumbrineris mixochaeta</i>	96	BF: Long, thin threadlike	64	SR: Biodiffusor	66
<i>Glycera capitata</i>	89			SD: 5–15 cm	61
<i>Leitoscoloplos mammosus</i>	89			SR: Upward conveyor	60
<i>Heteromastus filiformis</i>	77			FD: Subsurface (0–5 cm)	59
<i>Chaetoderma nitidulum</i>	68			FH: Subsurface deposit feeder	57
<b>No River</b>					
Nemertea	67	DA: Temporary	72	FH: Dissolved matter/symbionts	75
<i>Cirratulus cirratus</i>	67	BF: Irregular	66	SR: Downward conveyor	70
<i>Mediomastus fragilis</i>	67	LT: Planktotrophic	64	FH: Scavenger	65
<i>Oxydromus flexuosus</i>	67	AH: Surface crawler	61	LD: > 5 yrs	56
<i>Glycera alba</i>	62	BF: Short cylindrical	60	SD: 0–1 cm	56

In addition, there is strong evidence of uptake and assimilation of terrestrial organic matter in the river-influenced fjord. Målselv fjord is heavily impacted by the Målselv river (Figs. 1 and 2), which, due to strong currents and inorganic sedimentation, is a source of chronic disturbance at the inner fjord, and seasonal disturbance to the entire fjord during the spring flood and after intense rainfall or melting events. Concentrations of suspended particulate matter in the Målselv river can reach levels exceeding 60 mg/L during the spring flood in June (A. Poste pers. comm., based on frequent samples collected throughout the spring 2019 freshet). The sedimentation of these particles influences the sediment grain size in Målselv fjord, with the highest percentage of finer particles at the outermost stations (% pelite; Table 1). The composition of biological traits was strongly related to % pelite in Målselv fjord (Table 3). However, the freshwater to marine gradient in Målselv fjord coincided with a steep depth gradient (Fig. 3), which was also a significant factor in explaining variation in community composition in our study (Table 3). This was unsurprising, as many previous studies have demonstrated the importance of depth (and associated changes in environmental variables including grain size, oxygen and organic matter) in structuring benthic communities in northern Norwegian fjords (Holte et al., 2005; Holte, 1998; Jorda Molina et al., 2019; Larsen, 1997; Oug, 2000). In order to differentiate between the influence of river inputs and depth gradients on benthic community structure and functioning, we included Kald fjord, a northern Norwegian fjord with comparable station depths, but no major source of terrestrial influence. While northern Norwegian fjords are subject to several environmental forcing factors that cause differences within and between fjords (Jorda Molina, 2019; Wassmann, 1996), in the present case, it is assumed that the differences between Målselv fjord and Kald fjord can largely be attributed to the degree of river influence.

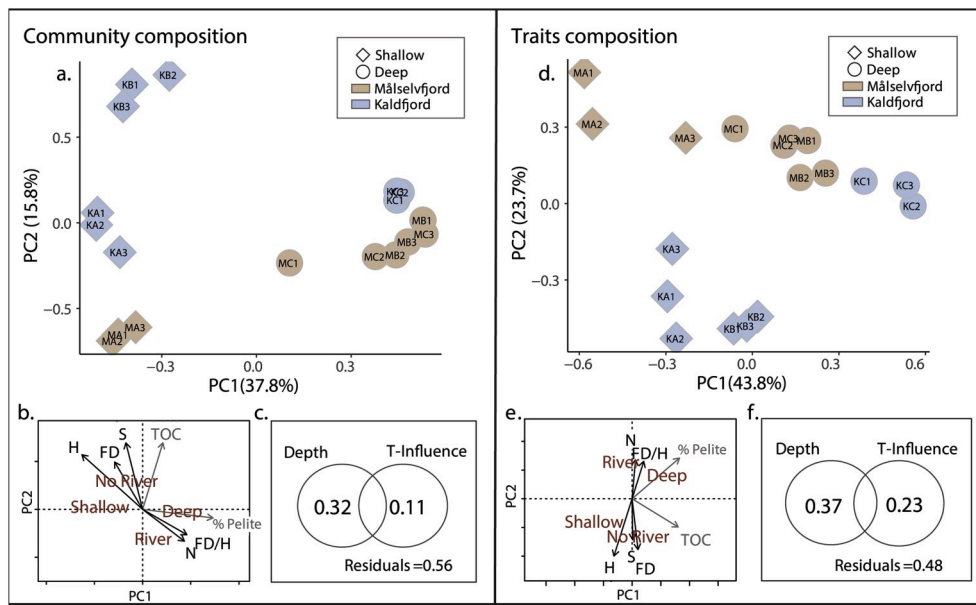
#### 4.1. River influence as a driver of taxonomic and functional diversity

In river-influenced Målselv fjord, both taxonomic ( $H'$ ) and functional diversity ( $FD_{Rao}$ ) were lower than in non-river influenced Kald fjord (Fig. 5). Similar trends have been found in the Arctic where inner fjord

glacial-basins, with their high rates of sedimentation of inorganic particles, are characterized by decreased taxonomic diversity compared to the outer fjord and shelf (Holte and Gulliksen, 1998; Włodarska-Kowalczyk et al., 2012). Decreases in functional diversity have also been documented in response to hydrodynamic disturbance (van der Linden et al., 2017), sewage discharge (Gusmao et al., 2016), land use (Bierschenk et al., 2017) and deposition of mine tailings (Trannum et al., 2019).

Stations with diminished taxonomic and functional diversity, and the innermost station in Målselv fjord in particular, were characterized by high abundances of subsurface deposit feeding polychaetes *Scoloplos armiger*, *Leitoscoloplos mammosus*, and *Heteromastus filiformis* (Fig. 3 and Table 2), which have been found frequently occurring in glacier-impacted sediments (Holte and Gulliksen, 1998; Renaud et al., 2007). These species are not limited to shallow depths, and can be found up to 200 m deep in nearby fjords (Holte et al., 2004; Holte & Gulliksen, 1998). The deeper stations in Målselv fjord were also characterized by high abundances of species that are considered to be typical for northern Norwegian fjords influenced by high sedimentation rates. These include *Lumbrineris mixochaeta*, *Heteromastus filiformis* and *Yoldiella* (= *Portlandia*) spp, which have been recorded in glacial-impacted fjords in northern Norway and on Svalbard where they tolerate very high levels of disturbance from glaciers at the fjord-head (Holte and Gulliksen, 1998; Włodarska-Kowalczyk et al., 2012). These stations, while they are less affected by the chronic disturbance at the river mouth, likely experience sedimentation events throughout the year.

The river-influenced communities may be expected to demonstrate opportunistic traits associated with environmental stress (small, short lived species), as described by classic ecological disturbance theory (Pearson and Rosenberg, 1978). The response we observed differs slightly from the classic paradigm in that communities had larger size, but agreed in other characteristic features such as mobility, no attachment and subsurface deposit feeding (Fig. 6). These traits are well-suited for surviving the conditions at the river mouth where high sedimentation rates may bury the sediment-dwelling fauna and make it difficult for the organisms to maintain their position in the sediment (Aller and



**Fig. 4.** (a) PCA of species community data (using the Hellinger transformed abundance data). (b) Environmental variables and community and diversity metrics are placed passively on top of the community PCA ordination. (c) Results of variation partitioning indicate the proportion of the variation in the community dataset explained by the main grouping categorical variables for depth (shallow vs. deep) and terrestrial influence (river vs. no river). (d) PCA of community weighted means (CWM) trait composition. (e) Environmental variables and community and diversity metrics are placed passively on top of the traits PCA ordination. (f) Results of variation partitioning indicate the proportion of the variation explained by the main grouping categorical variables for depth (shallow vs. deep) and terrestrial influence (river vs. no river). Colors indicate fjord (brown for river and blue for no river) and shapes indicate depth (diamond for shallow and circle for deep). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Stupakoff, 1996; Rhoads et al., 1985). Increased size toward the river mouth has also been observed in other delta environments (Akoumi-naki et al., 2006). The increase in mobility and lack of attachment at stations with a high river load likely reflects an advantage to moving in and out of patches influenced by the high sedimentation. This would allow for feeding on newly sedimented particles while also avoiding the most heavily disturbed areas. Furthermore, larvae and juveniles of sessile species may have difficulties in settling in a physically unstable sediment due to burying or interference with feeding processes (Holte, 1998; Renaud et al., 2007). The trait for lecithotrophic larvae was more abundant in Målselvford than in Kaldfjord (Fig. 6), perhaps as a strategy to reduce time in the water column under high flow regimes. Larval retention may also act to maintain the distinctness of benthic fauna within fjord basins (Renaud et al., 2007). Stations with low river impact, including deeper stations, were characterized by no or low mobility and increased occurrence of stationary epifauna and filter/suspension feeding. This reflects a more stable environment with regard to physical stress and food inputs. The lack of filter/suspension feeders close to the river outlet (Fig. 6) is not surprising, since such species may experience clogging of their feeding apparatus when exposed to high rates of sedimentation (Topçu et al., 2019). The same trend has been observed in sediments receiving high loads of e.g. glacier-derived inorganic sedimentation and mine tailings (Holte, 1998; Trannum and Vøgele, 2001; Trannum et al., 2019; Włodarska-Kowalczyk, 2007; Włodarska-Kowalczyk et al., 2012).

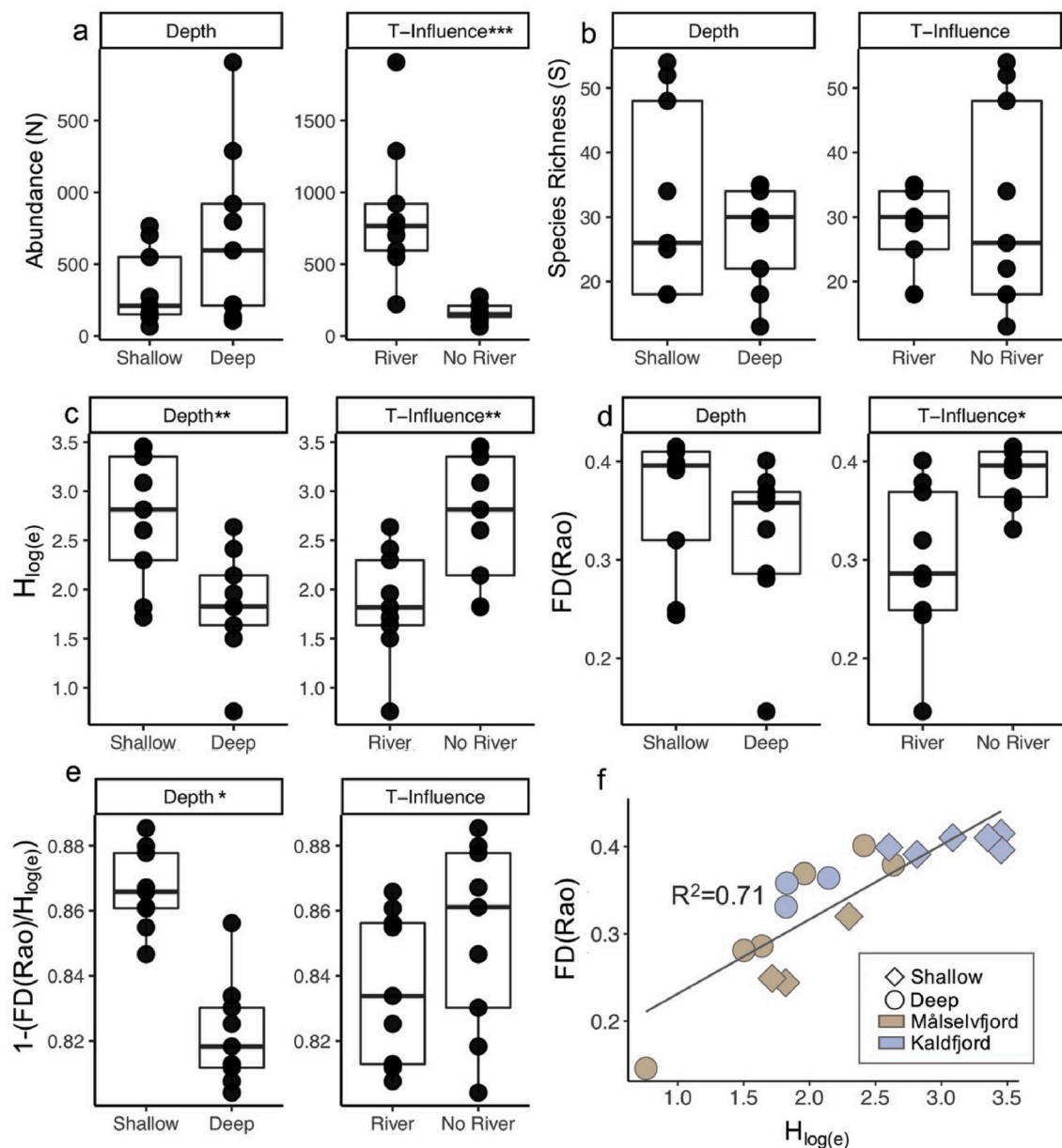
The significant trend toward lower functional diversity in Målselvford was mirrored in the functional redundancy, but wasn't statistically significant in the latter (Fig. 5). Functional redundancy showed a down-fjord gradient in both fjords, decreasing with distance from the fjord head. Higher levels of disturbance may result in higher functional redundancy if sensitive taxa are removed and the remaining taxa have more similar traits (Sasaki et al., 2009; van der Linden et al., 2016). In other cases, functional redundancy is expected to be reduced simultaneously with functional diversity if no particular trait features are affected (see Micheli and Halpern, 2005). Thus, interpretation of functional redundancy as an ecosystem quality is difficult because it may vary differently depending on the species richness and the identity and specificity of the traits considered (Micheli and Halpern, 2005; van der Linden et al., 2016).

#### 4.2. Depth-associated environmental variables as drivers of taxonomic and functional diversity

Environmental variables including % pelite and TOC explained a considerable proportion of the variance in the community composition in both fjords (Table 3). Generally, sediment composition (here only measured as the pelite-content) is one of the most important structuring variables for soft bottom communities (Ellingsen, 2002; Gray and Elliott, 2009; Oug, 1998) because it encompasses a wide range of sediment properties. While % pelite was strongly correlated with depth, it was also likely influenced by the river in Målselvford. Due to down-fjord advection in low-salinity surface-waters, smaller particles are likely transported farther from the river mouth, leading to coarser sediment in the shallow areas, as demonstrated in other river estuaries (Vonk et al., 2015).

Shallow stations in both fjords were largely composed of large, surface-crawling, motile and carnivore/scavenging taxa, which have been reported previously for sandy near-shore sediments (Liu et al., 2019). Meanwhile, the deep stations, which had higher pelite content, were largely composed of small, immobile taxa (Fig. 6) like the oweniid *Galathowenia oculata*, which had an abundance as high as 16 000 ind.  $m^{-2}$  in one of the samples from station MB and was also dominant at the deep station in Kaldfjord (Fig. 3). While many of the traits correlated with the river vs no river contrast, two traits were strongly related to depth. These included larval type and normal size (Fig. 6). Lecithotrophic larvae were associated with deeper stations, and planktotrophic with shallower (non river influenced) stations. This has also been observed in an analysis of nearshore coastal stations in Skagerrak, and was interpreted as reflecting differences in food availability (Trannum et al., 2018). For the normal size of species, smaller individuals were associated with deeper stations while larger individuals were associated with shallow stations, which again may be related to food availability (Fig. 6).

TOC also explained a significant proportion of the variation in the community and traits dataset in this study (Table 3). TOC, which was positively correlated with % pelite, was higher in deeper waters of both fjords (Table 1). However, while bulk TOC is a proxy for the total amount of organic matter in the sediment, it consists of material of various origins and stages of decomposition (Oug, 1998) and does not indicate the origin or bioavailability of the OM to the benthic community. In Målselvford, stable isotope values of the sediment indicate that

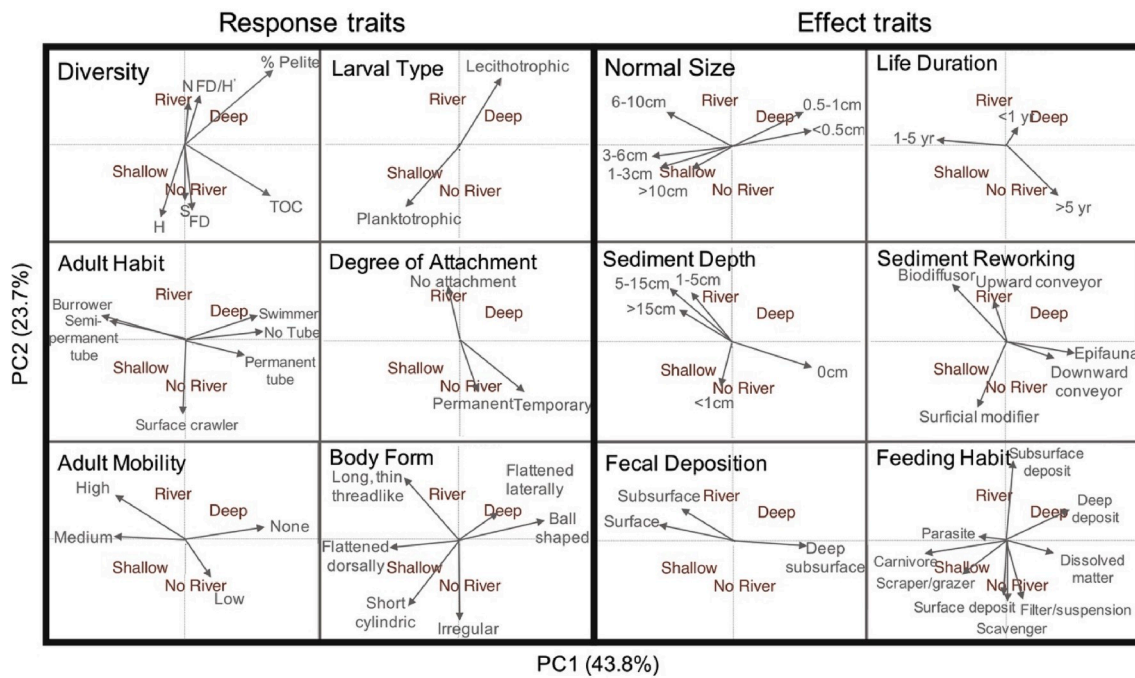


**Fig. 5.** Boxplots (the crossbar indicates the median value, the top and bottom of the box indicate the first and third quartiles, and the black points represent each individual grab sample) for each group of stations organized by depth (Shallow vs Deep) and terrestrial influence (River vs No River). Boxplots depict (a) total abundance per station (N), (b) species richness (S), (c) Shannon-Wiener's diversity index ( $H_{\log(e)}$ ), (d) functional diversity as calculated by Rao's quadratic entropy (FD(Rao)), (e) Functional redundancy ( $1 - (FD(Rao)/H_{\log(e)})$ ), (f) the relationship between taxonomic diversity ( $H_{\log(e)}$ ) and functional diversity (FD(Rao)). Mann-Whitney *U* Tests were performed for each of the boxplot pairs. Significant results are indicated by an asterisk (p-values adjusted for multiple comparisons,  $* = < 0.05$ ,  $** = < 0.01$ ,  $*** = < 0.001$ ). Colors indicate fjord (brown for river and blue for no river) and shapes indicate depth (diamond for shallow and circle for deep). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

the relative contribution of marine carbon to the sediments increased along the fjord gradient from the inner to the outer fjord (Fig. 7). Stable C and N isotope values for sediments from inner Målselv fjord were similar to values for particulate organic matter (POM) samples previously collected from the Målselv river ( $\delta^{13}\text{C}$  of  $-27.7 \pm 1.2\text{‰}$ ,  $\delta^{15}\text{N}$  of  $2.0 \pm 1.6\text{‰}$ ; based on  $n = 5$  samples collected in 2015/2016 covering all seasons; A. Poste pers. Comm.). Meanwhile, values for sediments in the outer fjord had higher  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, likely reflecting increased contributions of marine-derived OM, which for Målselv fjord, has been found to range from  $-22.7$  to  $-23.6\text{‰}$  for  $\delta^{13}\text{C}$ , and from  $4.9$  to  $6.7\text{‰}$  for  $\delta^{15}\text{N}$  ( $n = 6$ , data from 2015/2016 spring bloom; A. Poste pers. Comm.). The terrestrial  $\delta^{13}\text{C}$  values for the inner fjord sediments corresponded fairly well with data from other Arctic fjords sediments (Koziorowska

et al., 2016; Zaborska et al., 2018), and were unsurprising considering the substantial amount of large terrestrial material in the sieved grab samples (see Fig. 2), which looked like a thick mulch of birch leaves (M. McGovern, pers. obs.). The large pieces of terrestrial material were analyzed separately ( $\delta^{13}\text{C} = -30.9\text{‰}$ ), but the sediments still had distinctly terrestrial values of  $\delta^{13}\text{C}$  (as low as  $-26.4\text{‰}$ ). Thus, results of TOC and stable isotope analysis suggest that inner fjord sediments both had lower concentrations of TOC (likely due to dilution by high sediment load from the river in Målselv fjord) and lower bioavailability compared to outer fjord sediments.





**Fig. 6.** PCA of the traits matrix based on community weighted means with both fjord transects showing trait modalities for response and effect traits. Diversity statistics and environmental variables are included as passive vectors. Main station groups are in red (Shallow, Deep, River and No river). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

**Table 3**

Results of variation partitioning using RDA functions and adjusted R-squared for both the Hellinger-transformed community matrix and the community-weighted means (CWM) traits matrix for both fjords together, and Målselv fjord alone. Environmental variables were chosen via a forward selection procedure and all were significant ( $p < 0.01$ ). Values indicate the proportion of the total variation explained by each variable alone, as well as overlapping variation of two or more variables.

Environmental variable	Community	Traits
<b>Both Fjords</b>		
Depth (m)	0.15	0.12
TOC (mg/g)	0.13	0.24
% pelite	0.06	0.08
Depth + % pelite	0.16	0.11
Depth + % pelite + TOC	0.02	0.10
Residual	0.51	0.47
<b>Målselv fjord</b>		
Depth (m)	0.32	
Station (MA, MB, MC)		0.20
% pelite		0.20
Station + % pelite		0.38
Residual	NA	0.22

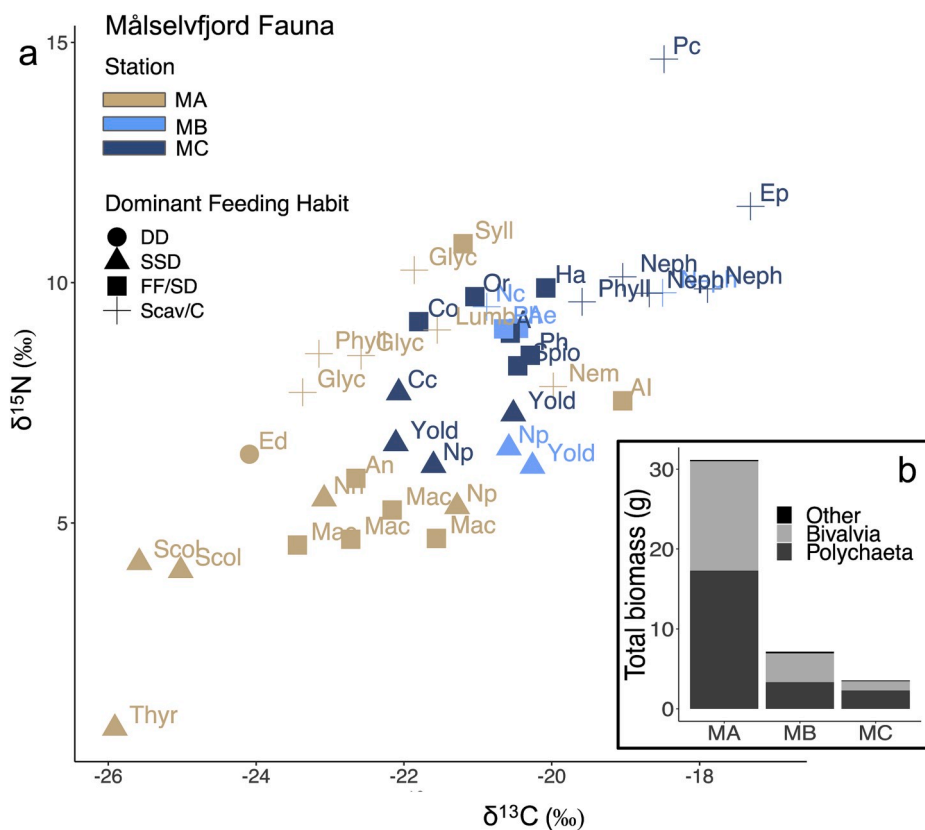
**4.3. Utilization of terrestrial carbon close to the river outlet**

Terrestrial material has generally been considered of little benefit as a carbon source to marine systems due to the high content of refractory compounds like cellulose, lignin, as well as phenols, phenolic acids and xylose (Antonio et al., 2010; Jednacak-Biscan and Juracic, 1987). Despite this, our results indicate that much of the benthic community in the inner fjord have stable isotope values indicative of terrestrial organic carbon assimilation (Fig. 7a). Studies in the Canadian Arctic have found terrestrial material to be a significant source of carbon to hyperbenthic organisms at the mouth of the Mackenzie river (Connelly et al., 2014; McTigue and Dunton, 2013), as well as to benthos in the Beaufort Sea (Bell et al., 2016; Stasko et al., 2018) and coastal lagoons (Harris et al., 2018). The utilization of terrestrial carbon by benthic infauna has significant implications for the cycling of terrestrially derived OM and

nutrients. In our study, the utilization of terrestrial carbon was associated with specific feeding habits of the sampled benthic community (Fig. 7a). We observed higher reliance on terrestrial OM for subsurface deposit feeders (which feed directly on sediments) than for more selective feeders (such as scavengers/carnivores), a finding mirroring that of Harris et al., (2018) in the Beaufort Sea. The species showing the most depleted  $\delta^{13}C$  was *Thyasira* sp., but many of the species of *Thyasira* have symbiotic sulfur-oxidizing bacteria (Keuning et al., 2011), and it is therefore likely that the depleted signal is due to the utilization of sulfides in reducing sediments rather than tOM. The most abundant species at the inner station in Målselv fjord, however, was a deposit-feeding polychaete (*Scoloplos armiger*; Ballerstedt, 2005) which exhibited particularly depleted  $\delta^{13}C$  values indicating terrestrial resource utilization. This finding is noteworthy since this species, which can reach up to 12 cm in length (Hartmann-Schröder, 1996) contributed considerably to the high biomass at this station (Fig. 7b). Large, long-lived species retain greater nutrient pools relative to smaller, shorter-lived species, and therefore *Scoloplos armiger*, which lives 3–5 years (MarLIN, 2006), could be an important species for retaining terrestrial carbon and nutrients within the fjord ecosystem. Furthermore, since *Scoloplos armiger* is also a key prey species for the polychaete *Nephtys* spp. (Schubert and Reise, 1986), which is a vital food source for crabs and fish (Blegvad, 1914; de Vlas, 1979), it may also serve as an avenue for tOM to sustain higher trophic levels.

**4.4. Implications for cycling of OM and nutrients**

Coastal sediments may act as a sink for organic and inorganic material that sediments from the surrounding water masses (Burt et al., 2013), but benthic fauna may aid in the regeneration of nutrients from deposited organic matter (Hall et al., 1996; van Nugteren et al., 2009). Benthic macrofauna can drive the retention and turnover of tOM and nutrients through uptake, respiration and movement in the sediments (Thoms et al., 2018; Villnäs et al., 2019). Traits with direct effects on the turnover vs. retention of organic matter and nutrients are size and life duration, while traits that have indirect effects are related to



**Fig. 7.** (a) Biplot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for benthic organisms sampled in Målselv fjord. Stations are indicated by color, dominant feeding habit of organisms are indicated by shape (DD = Deep deposit feeder, SSD = Subsurface deposit feeder, FF/SD = Filter feeder/surface deposit feeder, Scav/C = Scavenger/carnivore). Labels indicate taxon as follows: An: *Abra nitida*, Ae: *Acanthocardia echinata*, Al: *Arctica islandica*, Cc: *Ctenodiscus crispatus*, Co: *Cuspidaria obesa*, Ed: *Euclymene droebachiensis*, Ep: *Euspira pallida*, Glyc: *Glycera capitata*, Ha: *Hiatella arctica*, Lumb: *Lumbrineris mixochaeta*, Mac: *Macoma calcarea*, Nem: *Nemertea*, Neph: *Nephtys* sp., Nc: *Nothria conchylega*, Nn: *Nucula nucleus*, Np: *Nuculana pernula*, Or: *Ophiura robusta*, Ph: *Pectinaria hyperborea*, Phyll: *Phyllodoce groenlandica*, Pc: *Priapulius caudatus*, Scolop: *Scoloplos armiger*, Spio: *Spionidae* indet, Syll: *Syllidae* indet, Thyr: *Thyasira* sp., Yold: *Yoldiella* sp. (b) Total biomass across all three stations in Målselv fjord by taxonomic group ("Other" includes crustaceans, echinoderms and gastropods). Note that mollusks were weighed with shells. One individual of *Arctica islandica* (72 g) at station MA and one individual of *Ctenodiscus crispatus* (4 g) at station MC were not included. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

bioturbation (size, sediment dwelling depth, sediment reworking), which indicate how a species can influence the transport of carbon, nutrients and elements through the sediments with its movements (Queiros et al., 2013).

River inputs were associated with high abundances of biodiffusers and upward conveyor species that indirectly affect organic matter mineralization and nutrient fluxes through oxygenation and ventilation of the sediments (Kristensen et al., 2012). Upward conveyors (including *Heteromastus filiformis*) have been found in high abundances in sediments affected by high sedimentation (Holte and Gulliksen, 1998; Ols-gard and Hasle, 1993; Schaanning et al., 2019), and are functionally important for benthic communities as they facilitate the transfer of carbon between the deeper layers of sediment and the surface (Holte, 1998) while also irrigating the sediments and enhancing microbial activity. In contrast, the outer fjord stations and non-river-impacted sites were characterized by surface-dwelling, stationary downward conveyors, which may be better at efficiently retaining and burying carbon (Middelburg, 2018). However, body size, which is important for ecosystem functioning (Norkko et al., 2013) because of its role in bioturbation and carbon and nutrient utilization, varied dramatically along the Målselv fjord gradient and could have the opposite implications for carbon and nutrient turnover. The innermost Målselv fjord station was characterized by higher 'normal size' of individuals (Fig. 6) compared to the outer stations, which was further confirmed by the high total biomass at this site (Fig. 7b). Since  $\delta^{13}\text{C}$  evidence suggests that tOM is utilized by organisms at the river mouth, these large individuals may be important for carbon and nutrient retention at the land-ocean interface.

While taxonomic and trait composition of macrofauna are important for benthic processing of OM and for carbon burial (Middelburg, 2018), the spatial, temporal, and compositional variations in OM inputs and deposition are also important for understanding the fate of terrestrially-derived organic carbon (Moodley et al., 2002). As discussed,  $\delta^{13}\text{C}$  data from surface sediments in Målselv fjord suggested strong contribution of terrestrial material, even at the outer fjord. This

likely arises from high river flow events (including the spring freshet) when the Målselv river plume extends throughout the entire fjord and beyond (Fig. 2). The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for the terrestrial debris from inner Målselv fjord were much lower than for riverine POM, and were consistent with values typical of foliar and woody material from trees, suggesting two isotopically distinct main sources of terrestrial OM to the fjord: finer suspended particles, and larger terrestrial debris. These terrestrial OM pools are also likely to differ in their cycling, availability as food for benthos, and eventual fate. The higher quality tOM at the outer stations is likely to be efficiently consumed and remineralized by the faunal communities. However, during larger run-off events, when more refractory terrestrial material is transported to the deeper stations, the tOM may be more effectively buried by these communities than the chronically-impacted communities close to the river mouth. These findings may be important with regard to predictions of responses of future global warming. Nevertheless, variability between fjords must be taken into account both for the present-day global estimates of fjords' role as carbon sequestration hot spots and for predicting this future role in blue carbon storage (Włodarska-Kowalczyk et al., 2019).

## 5. Summary and conclusions

Benthic communities contribute to ecosystem functioning by decomposing organic matter, burying carbon, regenerating nutrients, and providing higher trophic levels with food (Middelburg, 2018). Changes in these communities due to natural or anthropogenic influences can alter the functioning of the fjord ecosystem, including carbon pathways. Results of this study suggest that environmental filtering of the benthic community, driven by river influence on sediment grain size and high rates of sediment deposition, leads to decreased taxonomic and functional diversity in the river-impacted fjord. This includes the loss of functional traits (ex. downward conveyors, epifauna) with potential implications for benthic ecosystem functioning, including carbon sequestration. However, while the river in Målselv fjord is clearly

a source of disturbance to the local benthic communities, it also supplies terrestrial organic matter and nutrients to the fjord. The species able to survive in this disturbed environment, including mobile deposit feeders, also had tissues depleted in  $\delta^{13}\text{C}$ , suggesting a diet rich in terrestrial carbon. The uptake of tOM and high biomass of this river-estuary community indicate that river-influenced benthic communities may be important for incorporation of terrestrial carbon and nutrients into the fjord food-web. Expected increases in terrestrial inputs with climate change can be expected to lead to changes in the inorganic and organic loadings to coastal areas, with implications for the local benthic biodiversity and ecological functioning.

#### Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

#### CRediT authorship contribution statement

**Maeve McGovern:** Data curation, Formal analysis, Conceptualization, Writing - original draft, Writing - review & editing. **Amanda E. Poste:** Formal analysis, Conceptualization, Writing - review & editing. **Eivind Oug:** Data curation, Conceptualization, Writing - review & editing. **Paul E. Renaud:** Conceptualization, Writing - review & editing. **Hilde Cecilie Trannum:** Funding acquisition, Conceptualization, Project administration, Writing - review & editing.

#### Acknowledgements

The authors thank Hector Andrade and Katherine Dunlop for their help with fieldwork and Charlotte Pedersen Ugelstad for sorting the macrofauna. We also thank Gunhild Borgersen of NIVA for extracting traits from the NIVA traits database, and Sabine Cochrane and Rune Palerud for useful discussions and extraction of the Kaldfjord community dataset. This project was supported by NIVA's Land-Ocean Interactions Strategic Institute programme, and the Centre for Coastal Research, University of Agder, as well as the Norwegian Research Council (TerrACE; project number 268458).

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2020.106774>.

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