

Variation in functional trait composition of benthic invertebrates across depths and seasons in a subarctic lake

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Abstract

Benthic invertebrate communities play a fundamental role in lake ecosystems, and the understanding of how those benthic communities are structured, particularly in terms of the identity and spatiotemporal distribution of their functional traits, is key to our understanding of how lake ecosystems work. In Takvatn, a subarctic lake in northern Norway, we identified the taxonomic and functional identity of the species characterizing benthic communities across three seasons and six different depths. Invertebrates were sampled using vacuum pump and Eckman grab and analysed using multivariate analyses. Despite the relative low species richness, we found large spatial and temporal variation in species functional composition. The upper littoral habitat shifted from a community characterized by particle gathers and algal scrapers in spring and summer, to a community largely characterized by leaf shredders in autumn. The deeper habitats showed high variation in their taxonomic composition, but a stable composition of functional traits throughout all seasons. In all seasons and habitats, gathering traits were the most common feeding traits within the benthic community. There was also high relative occurrence of predator traits towards the deeper areas of the littoral zone, as well as in the sub-littoral and profundal habitats. This result is in accordance with the low densities of other benthic top predators (e.g. fish) feeding in the deeper habitats of Takvatn. In conclusion, our study demonstrates large spatio-temporal differences in functional diversity and composition of the benthic invertebrates in Takvatn.

Key-words: lentic benthic macroinvertebrates; seasonality; bathymetry; littoral habitats; functional traits.

Introduction

Benthic invertebrates play a fundamental role in lake food webs (Vadeboncoeur et al. 2002). This diverse group of organisms is vital to the functioning of lakes by recycling autochthonous and allochthonous carbon and nutrients (Karlsson & Byström 2005, Berggren et al. 2010) and constituting an important resource pool for several aquatic top predators (Vander Zanden & Vadeboncoeur 2002, Vander Zanden et al. 2006), besides being important intermediate hosts of several parasite species present in lake food webs (Amundsen *et al.* 2003). Until recently, much focus had been given to understanding the taxonomic composition of benthic invertebrate communities, whereas knowledge about their functional composition had been more limited (e.g., Johnson & Goedkoop 2002, Tolonen et al. 2003, Heino 2008). As species primarily affect their environment through the specific functional roles they play in an ecosystem, a more accurate description of the structure and composition of functional traits within a community is key to provide an understanding of the relationship between diversity and functioning (Heino 2008, Zwart et al. 2015).

The functional role of benthic invertebrates has frequently been associated with some fixed functional feeding groups (Cummins 1973, Cummins & Klug 1979) that aim at reflecting the major feeding type of each species. These feeding groups typically classify benthic invertebrates either as leaf shredders, filter-feeders, collectors, scrapers, or predators. Although identifying benthic invertebrates by their feeding type offers a direct assessment of what species do in an ecosystem, these organisms often show more complex feeding strategies that prevent straightforward categorizations. For example, some caddisfly larvae normally identified as shredders also prey on smaller invertebrate species (Wissinger *et al.* 2004), or may scrape biofilm as an alternative food source (Carvalho & Graça 2006). This feeding plasticity, instead of being the exception, seems to be the norm for benthic

invertebrates (Friberg & Jacobsen 1994, Albariño & Díaz Villanueva 2006, Carvalho & Graça 2006, Schmidt-Kloiber & Hering 2011).

Measuring functional diversity can also be challenging due to the complexity of data needed for the analysis. Often, a matrix of species functional traits is crossed with a matrix of species abundance, with different weights given either to the trait or to the abundance matrix. Recently, several statistical indices have been proposed for handling these complex data sets (Schleuter et al. 2010, Mouchet et al. 2010). Whereas some indices quantify the amount of functionally exclusive species in a community (i.e. functional richness; see e.g. Petchey & Gaston 2002), others quantify how dispersed those functional traits are, in terms of functional evenness or dominance (Laliberté & Legendre 2010). Furthermore, it is also possible to identify which traits carry the highest ecological importance in a community following the mass ratio hypothesis (Grime 1998), which states that the most abundant traits should have the strongest effect on an ecosystem.

Shifts in the diversity and composition of functional traits can also serve as early warning signals for detecting environmental disturbances at the ecosystem level (Williams et al. 2010, Mouillot et al. 2013). Lake benthic communities are particularly vulnerable to environmental degradation. Sediment loading (Donohue & Molinos 2009), nutrient enrichment (Kronvang et al. 2005, Donohue et al. 2009), and water level fluctuations (Wantzen et al. 2008, Petrin et al. 2013) can have large effects on the lake benthic fauna, affecting the identity and structure of those communities. Another growing threat to lake ecosystems, especially in Arctic and subarctic regions, is the expected increase in temperature during the next century (Wrona & Reist 2013). Specifically, climate predictions indicate that higher latitudes will suffer the highest increases in temperature and precipitation (IPCC 2013), potentially reducing the duration of ice-cover. A decrease in ice cover will likely increase primary and secondary production in lakes, and in turn facilitate successful invasion

of fish species from warmer and more productive lakes (Primicerio *et al.* 2007), which are currently limited due to winter starvation (Shuter & Post 1990). Shifts in invertebrate community composition and structure, either caused by environmental alterations or by shifts in the fish community, can have strong impacts on ecosystem functioning. For example, a reduced functional diversity of invertebrate detritivores may result in reduced processing efficiency of allochthonous organic matter (Frainer *et al.* 2014), an important source of carbon and nutrients for freshwater ecosystems (Gessner *et al.* 2010), or may affect the recycling of dead organic matter deposited on the bottom of the lake.

Compared to boreal and temperate systems, subarctic lakes show a less diverse and less abundant benthic community (e.g., Klemetsen & Elliott 2010). Nonetheless, shifts in invertebrate species composition and in the structure and function of benthic communities will impact higher trophic levels and the functioning of these ecosystems. In the present study, we aimed at documenting the spatial and temporal variation in the functional diversity of benthic invertebrates in a subarctic lake, alongside with analyses on their taxonomic diversity. We hypothesized that (1) benthic communities in the upper littoral zones vary more both in terms of functional and taxonomic identity across seasons, with functional traits reflecting seasonal alterations in resource availability, from algal scrapers during summer to leaf shredders during autumn. As a consequence, we hypothesized that (2) the identity of invertebrate functional traits is more similar throughout all seasons in the profundal zone, reflecting the stable, but low productive environment in those habitats.

Material and Methods

Study site

This study was conducted in Takvatn, a subarctic lake located in northern Norway (69°07' N, 19°05' E), at 214 m altitude. Takvatn is a well-oxygenated, circumneutral, oligotrophic lake,

with phosphorus concentrations normally below $5 \mu\text{g L}^{-1}$. Secchi disc transparency varies between 12 and 17 m. The lake surface area is 14.2 km^2 , and the maximum depth is 80 m. The lake catchment is small and is surrounded by birch (*Betula pubescens*) forest presenting scattered willow (*Salix* sp.) and alder (*Alnus incana*).

Takvatn is normally ice-covered from December to June. After ice break in June, the lake goes through the three remaining seasons in a relatively short time, from spring in June, to summer in July and August, and finally to autumn in September and October. Takvatn is located 300 km north of the Arctic Circle, which means that sunlight is reduced from a few hours per day in mid-October to zero in mid-November, when the polar night begins. The period of 24h sunlight starts in late May and lasts until late July. Average monthly air temperatures normally range between -10°C in January and 13°C in July. Takvatn is a dimictic lake with short thermal stratification, usually from July to early September, and with epilimnion temperatures usually not exceeding 12°C (Primicerio 2000, Amundsen et al. 2007). Accordingly, phytoplankton production peaks in late July and is considerably less both in June and in September (Primicerio 2000). Takvatn is in general characterised by a gentle slope from the upper shallow littoral to the lower deeper littoral, at $\sim 15\text{m}$ depth. Beyond the littoral area lie the sub-littoral and profundal aphotic zones.

Sampling areas and invertebrate sampling

In 2012, we assessed the benthic community structure of Takvatn from the shallow littoral area to the profundal zone, covering six distinct depths, classified as (1) upper littoral (0.5 m depth), (2) intermediate littoral (1-2 m), (3) *Nitella* belt (6-9 m), (4) lower littoral (12-14 m), (5) sub-littoral (*ca* 20 m), and (6) profundal (*ca* 30 m). All samples were taken across one transect located in the SE end of the lake (Hauglibukta), which constitutes a typical near-shore habitat of Takvatn. The site is exposed to frequent winds and a wave action due to large

fetch (>2 km), which results in a wave-washed, hard-bottom shoreline area with no vegetation (Klemetsen & Elliott 2010). The upper littoral habitat extends to about five meters from the shoreline and is characterized by large presence of boulders and pebbles. The intermediate littoral habitat extends from 5 to c. 15 m from the shore, has mean depth between one and two meters, and is characterized by fine sand substratum. The *Nitella* belt, characterised by the tall-growing alga *Nitella* sp, and the presence of other aquatic plants, as *Myriophyllum* sp. and *Isoetes lacustris*, forms a vegetated zone around the lake between c. 4-10 m depth on a substratum characterized by sand and silt. At about 12 m depth, the lower littoral habitat is at the edge of the photic zone, and is also characterized by sand and silt substratum. Finally, the two deeper sub-littoral and profundal sites, at 20 and 30 m depth, respectively, are characterized by fine sand and silt substratum and are below the photic zone.

At each depth, 15 samples were taken once every season during the ice-free period (June = spring, August = summer, and October = autumn), with the exception of the sub-littoral and profundal habitats, which had reduced sampling effort (n = 5), and were assessed only in August and October.

The upper littoral benthos were sampled using a vacuum pump for 1 min inside a circular tray ($\varnothing = 60$ cm) that is surrounded by 10 cm of nylon mesh (mesh opening = 0.45 mm) (see pump description in Klemetsen & Elliott 2010). All other sites were sampled using an Ekman grab (area 16 x 16 cm). We converted densities to m^2 by applying the following conversion factors: 3.54 for the vacuum pump and 39.06 for the Ekman grab. Depth was measured using an echo-sounder.

Invertebrate taxonomic and functional diversity

All invertebrate species were identified to the lowest possible taxonomic level, and counted. To estimate the identity of the dominant functional trait present, we assessed the composition

of functional feeding traits among the benthic invertebrates. Feeding strategies of benthic invertebrates were classified as: (1) shredders, (2) scrapers, (3) gatherers, (4) filter-feeders, and (4) predators. Shredders feed on leaf-litter (e.g., several caddisfly and stonefly species), while scrapers feed on algae or biofilm by grazing on leaf or rock surfaces (e.g., several mayfly and snail species). Gatherers normally feed on deposited particulate organic matter (e.g., many aquatic beetle and mayfly species) and filter-feeders feed on suspended particulate organic matter (e.g., mussels). Finally, predators are species that can feed on living animal tissue during some stage of their development. However, as several of our species show more than one specific feeding strategy (i.e., they may be generalist consumers), we used fuzzy coding (Greenacre 2013), that allows the proportional quantification of diet preferences, to assess variation in diet (e.g., Frainer *et al.* 2014). All information on feeding traits was collected from the Freshwater Ecology database (Schmidt-Kloiber & Hering 2011).

Based on the functional feeding groups we calculated the functional identity of each invertebrate community. Functional identity was calculate as the Community-Weighted Mean trait values (CWM), following the mass-ratio hypothesis (Grime 1998), where the functional traits are weighted by the abundance of all species sharing it in a given community.

Functional identity was assessed using the R package *FD* (Laliberté & Shipley 2011).

Due to absence of detailed information on species taxonomy and functional feeding traits, Nematoda (corresponding to 0.25% of all individuals sampled in our study) were removed from our analyses on functional diversity. Chironomidae that were not identified at least to genus level (or tribe level, in the case of Tanytarsini) were also removed from the analyses on functional diversity. The removed unidentified Chironomidae corresponded to 5.0% of all invertebrates found in our study.

Data analysis

We investigated variation in community taxonomic composition across seasons and depths using non-metric multidimensional scaling (NMDS), following Bray-Curtis standardization. Analyses were done on a site \times abundance data matrix using the R package *vegan* (Oksanen *et al.* 2011). Variation in functional trait composition was analysed using Detrended Correspondence Analyses with the R package *vegan* (Oksanen *et al.* 2011). Depth data was then fit onto the multivariate plots using generalized additive models with the package *vegan*.

The relationship between our response variables (invertebrate richness and density) and the predictors depth, season, and the interaction between the two were analysed using individual linear regressions. Seasons were treated as categorical variables and depth was treated as continuous variable. For these analyses we used mean values pooled across the 15 sampling units at each depth.

Results

Invertebrate taxonomic and functional diversity

From a total of 9530 invertebrate specimens that were sampled and sorted, we identified 55 species or morphospecies (an operating taxonomic unit given when family or genus were known, but not the species identity) belonging to the groups Annelida, Crustacea, Insecta, Mollusca, and Nematoda. Insecta, with 36 species, was the most abundant group, corresponding to 70% of the sampled individual invertebrates. Some of the individuals belonging to the subclass Oligochaeta, to the phylum Nematoda, and to the Chironomidae sub-family Tanypodinae and tribe Tanytarsini were not identified to lower taxonomic levels.

Species richness was highest in the *Nittela* belt and lower in the littoral habitats in spring, but was higher towards the littoral habitats in summer and autumn (season \times habitat interaction: $F_{2,19} = 7.4$, $p = 0.01$). The sub-littoral and profundal habitats, presented the lowest species richness in summer and autumn (Fig. 2).

Invertebrate density was not related to habitat depth, season, nor by the interaction between the two (all $F < 2.3$, $p > 0.16$). However, some trends are worth noting (Fig. 3). Invertebrate density was ~100-fold lower in the upper littoral habitat (mean \pm s.d.: 26 ± 11 individuals m^{-2}) compared to the intermediate littoral, *Nitella* belt and lower littoral habitats (2367 ± 1359 , pooled across the three other littoral depths). A similar difference was observed in August. The sub-littoral and profundal habitats were also characterized by overall low densities of benthic invertebrates (234 ± 131 and 238 ± 106 , respectively. Values pooled across August and October).

Taxonomic and functional composition

Our NMDS indicated differences in community composition across the four littoral depths and the three seasons (Fig. 4). The upper littoral habitat varied more in species composition across the three seasons, ranging from a dominance of *Ameletus inopinatus* (Ephemeroptera) in spring, to *Heptagenia dalecarlica*, *Metretopus borealis* (both Ephemeroptera), and *Diura bicaudata* (Plecoptera) in summer, and to *Capnia atra* (Plecoptera) in autumn. The intermediate littoral habitat had high abundances of the clam *Pisidium* sp., and Oligochaeta, whereas the *Nitella* belt was characterized by higher abundance of *Pisidium* sp. and the amphipod *Gammarus lacustris*. The lower littoral habitat was characterized by a higher presence of Chironomidae, represented by the Tanypodinae taxon *Procladius* sp. and the Orthocladinae species *Heterotrissocladius maeari* and *H. marcidus*. Both the sub-littoral and the profundal habitats were mostly characterized by the presence of Oligochaeta and Chironomidae species.

The principal component analysis describing variation in trait identity in our sampling sites was characterized by 56% of the variation in functional identity along axis 1, and 24% along axis 2. The upper littoral habitat was characterized by different sets of traits across the

seasons, with scraper and gatherer traits more strongly associated with this habitat during spring and summer, and shredders more strongly associated with it in autumn (Fig. 5). The deeper littoral habitats were characterized by higher presence of particle gatherers and filter-feeders and the sub-littoral and the profundal habitats were characterized by higher incidence of predator and particle-gathering traits throughout all three seasons (Fig. 5).

Discussion

The total number of species identified (55) places Takvatn at the middle range of species richness for similar lakes across the arctic and sub-arctic regions (Brittain & Lillehammer 1978, Lindegaard 1992, Namayandeh & Quinlan 2011). However, most studies do not identify Oligochaete and Chironomidae to species level. Without considering these two groups, the number of benthic species in Takvatn decreased to about 60% (i.e., reduced to 34 species). Despite the low species richness observed, we identified strong temporal and seasonal variation in species taxonomic and functional composition, reflecting strong links to natural fluctuations in the lake environment and holding implications for lake food-web structure and ecosystem functioning.

Confirming our first hypothesis, the invertebrate community in the upper littoral habitat shifted from being dominated by organic particle gatherers and algal scrapers in spring and summer (mostly mayflies), to a community represented by almost 50% leaf shredders in autumn (mostly caddisflies and stoneflies). Seasonal changes in littoral species composition were also expected based on previous studies (Klemetsen & Elliott 2010) and are in agreement with expectations over the tight linkages between the lake littoral benthic community and the riparian zone (Johnson & Goedkoop 2002). This is particularly important in lakes with low autochthonous production on account of low temperatures, a short ice-free season, and low nutrient levels (Larsson *et al.* 1978), such as subarctic and arctic lakes.

Higher light incidence during spring and summer promote higher algal growth and positively affect the abundance of algal-scrapers (Liboriussen et al. 2005, Tarkowska-Kukuryk 2013). In turn, leaf litter fall in autumn fuels the detritivore food web in lakes (Bjelke et al. 2005).

Substrate composition is a key factor explaining the presence of crawling insect invertebrates (Lenat et al. 1981, Cobb et al. 1992) in the upper littoral habitat. This habitat is mostly composed of larger cobbles and some smaller boulders that allow mayflies, stoneflies, and caddisflies to adhere to the substrate, preventing their displacement by wave actions. Despite these potentially positive substrate effects, the upper littoral habitat had the lowest invertebrate density across all sampled depths. This reduced invertebrate density may be partly explained by the effect of ice cover from early winter to spring as the upper littoral habitat is either frozen to the bottom during this period or has a shallow layer of water between the substrate and the ice layer, with water temperatures below 0.5°C (Brittain 1983). Invertebrate larvae from boreal and subarctic regions typically show adaptations for overwintering and include migration to more suitable habitats or ability to freeze solid in the ice (Danell 1981, Danks 2007). Despite these potential adaptations, the invertebrate community in the upper littoral habitat is highly affected by the ice conditions (Koskenniemi 1994), with invertebrate abundances reduced by 90% from autumn to the following spring (Danell 1981).

Both shredder and scraper traits, which dominated the upper littoral habitat (0.5 m depth), were mostly absent from the neighboring 1- to 2-meter-deep intermediate littoral habitat during all three seasons. Instead, the intermediate littoral habitat was mostly populated by gatherers and filter-feeders – particularly burrowing oligochaetes and clams – across all three seasons, and at much higher invertebrate densities. This difference in invertebrate composition and density between the two shallow littoral habitats occurred despite the spatial proximity between the two, and the fact that both habitats are equally frequently wave-

disturbed, although the intermediate littoral habitat is not affected by ice formation during winter. The soft substrate mostly composed of sand and absent of major habitat structures, as those found in the upper littoral and *Nitella* belt (see below), allowed a greater occurrence of burrowing clams and worms, which explains the higher occurrences of filter-feeders (clams) or gatherers (worms) in this habitat.

The tall-growing alga *Nitella* offered a more suitable protective habitat for invertebrates in opposition to the constantly wave-disturbed upper and intermediate littoral habitats. Indeed, this habitat was characterized by the highest invertebrate densities across all depths, mostly due to the high abundance of the generalist consumer *G. lacustris*. Besides being a stable habitat, the *Nitella* alga is also potentially consumed by generalist invertebrates, as some *Gammarus* species (Willoughby 1983). *G. lacustris* is key to several food-web linkages in lake ecosystems, as it is a common prey to several fish species and intermediate host of ecologically significant parasite species in Takvatn and other nearby lakes (Knudsen et al. 2001, Amundsen et al. 2003). The presence of functional traits related to leaf-shredding in this habitat is mostly a consequence of the generalist feeding behaviour of *G. lacustris*, which is characterized by feeding traits including leaf shredding, algal grazing, and particle gathering, besides potential for predation. Nonetheless, the *Nitella* belt may also trap some of the allochthonous material that is not retained in the upper littoral area and is washed down over the sand-dominated intermediate littoral area, promoting the occurrence of leaf shredders in this habitat.

The invertebrate communities of the deeper habitats of the littoral zone, and also the sub-littoral and profundal habitats, were characterized by high incidence of predator traits. Despite Takvatn being populated by three fish species that prey on benthic invertebrates, brown trout (*Salmo trutta*), arctic charr (*Salvelinus alpinus*), and three-spined stickleback (*Gasterosteus aculeatus*) (Jørgensen & Klemetsen 1995, Klemetsen et al. 2003, Amundsen &

Knudsen 2009), these species mostly have diets composed of littoral benthic species. Furthermore, of the three fish species, only arctic charr utilizes the deep water habitats (Knudsen et al. 2006, Amundsen et al. 2008), but there it has a diet mostly composed of pelagic prey (Eloranta et al. 2012). This reduced top-down control by fish might explain the higher presence of invertebrate predator traits in the profundal habitats of Takvatn, particularly represented by the Chironomidae genus *Monodiamesa* (subfamily Prodiamesinae) and other Chironomidae species of the subfamily Tanypodinae, in contrast to the shallower littoral habitats, where predacious invertebrates were not abundant.

Alongside predator traits, all habitats below the *Nitella* belt, including the profundal and sub-littoral habitats, were also characterized by the higher presence of particle gatherers and filter-feeders. These traits are common in profundal lake habitats, where primary production and the role of allochthonous input are reduced, and the major source of carbon and nutrients is the sinking of organic matter from the more productive epilimnion. In our work, invertebrate density decreased from spring to autumn in all habitats below the *Nitella* belt, although we do not have data from spring to confirm that the same decrease in species density occurred in the sub-littoral and profundal habitats. The observed seasonal decrease in density in the deeper littoral habitats is possibly a consequence of reduced phytoplankton and zooplankton production after the summer (Primicerio & Klemetsen 1999, Primicerio 2000), which reduces the supply of sinking organic particles to the benthic communities (but see Mousavi & Amundsen 2012). The combination of insect emergence throughout summer and the late oviposition in autumn may also have contributed to the autumnal decrease in insect densities observed in this study.

Gathering traits were the most common feeding traits within the benthic communities across all seasons and habitats, excepting the littoral habitat. In particular, supporting our second hypothesis, the sub-littoral and profundal habitats had the most similar trait

composition across all seasons. This finding indicates that gathering traits are always the most abundant trait in the profundal habitats, despite seasonal variations in species taxonomic identity (Mousavi & Amundsen 2012). Most insect species, and nearly all Oligochaeta found in our study are characterized by some level of particle-gathering as feeding trait (Schmidt-Kloiber & Hering 2011). Despite the variation in species composition seen especially between the upper littoral and the deeper habitats, the wide and temporally constant distribution of this trait further confirms the role of benthic invertebrates in recycling dead organic matter in lakes, potentially originating from both terrestrial and aquatic sources (Vadeboncoeur et al. 2002, Telöken et al. 2011).

We found that species taxonomic dominance varied little across depths and seasons, whereas functional dominance varied much more. Throughout the three seasons, the upper littoral habitat presented the lowest functional evenness (low $F_{\text{Dispersion}}$), whereas the deeper littoral habitats had higher functional dispersion, indicating that the latter had a community composed of more evenly distributed, dissimilar functional traits. Although this finding partially supports our third hypothesis, the sub-littoral and profundal habitats, on the contrary, had a high dominance of few functional traits (predator and particle-gathering traits) in both summer and autumn, which indicates higher homogeneity in the functional composition of the benthic invertebrate community in these habitats.

The seasonal shift in species functional composition and the low density of invertebrates observed throughout the three seasons indicate a potential vulnerability for the upper littoral habitat and for the lake ecosystem as a whole. Littoral benthic communities are particularly susceptible to water level alterations (Aroviita & Hämäläinen 2008, Baumgärtner et al. 2008, Petrin et al. 2013), alterations in ice conditions (Koskeniemi 1994), or to changes in the feeding preference of top-predators after the introduction of new fish species with distinct feeding preferences (Naestad & Brittain 2010, Jeppesen et al. 2012). These potential

disturbances are predicted to increase in frequency under projected climate change scenarios (Primicerio et al. 2007, Wantzen et al. 2008, Hayden et al. 2013), and can largely impact the structure of benthic invertebrate communities. Thus, the marked seasonal composition of functional traits in the upper littoral habitat points to potential ecosystem-level disruptions if the benthic community is disturbed. If the occurrence of specific functional traits are altered, their effect on the processing of organic matter (Frainer *et al.* 2014) or the consumption of primary production (Cattaneo & Mousseau 1995) will also be affected. In conclusion, assessing the structure and composition of functional traits of benthic invertebrates allows for a better understanding of how lake ecosystems function and can also help in detecting early stressor signals and indicate areas that are more sensitive to environmental alterations.

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Figure 1. Mean density of feeding traits at six different habitats, ranging from littoral to profundal sites, and in three different seasons: spring (June), summer (August), and autumn (October). Densities of feeding traits are calculated as the Community-Weighted Mean trait values (CWM) of each feeding trait multiplied by the density of individual invertebrates in each sample.

Figure 2. Benthic invertebrate species richness across six depths, spanning from littoral (~0.5 m depth) to profundal (~30 m depth) habitats, and three seasons in Lake Takvatn, northern Norway.

Figure 3. Density of benthic invertebrates across six depths, spanning from littoral (~0.5 m depth) to profundal (~30 m depth) habitats, and three seasons in Lake Takvatn, northern Norway.

Figure 4. Principal Component Analysis on functional trait composition across six lake habitats and three seasons. Habitats range from Upper littoral (0-1 m depth), Intermediate littoral (1 – 2 m depth), Nitella belt (4 – 5 m depth), lower littoral (12 m depth), sub-littoral (20 m depth), and profundal (30 m depth).

Figure 5. Non-metric multidimensional scaling (NMDS) following Bray-Curtis transformation on a species \times abundance data, showing mean values of each habitat *per* season. Habitats range from Upper littoral (0-1 m depth), Intermediate littoral (1 – 2 m depth), Nitella belt (4 – 5 m depth), lower littoral (12 m depth), sub-littoral (20 m depth), and profundal (30 m depth). All species/groups with total relative abundance above 1% are shown.

Figure 1.

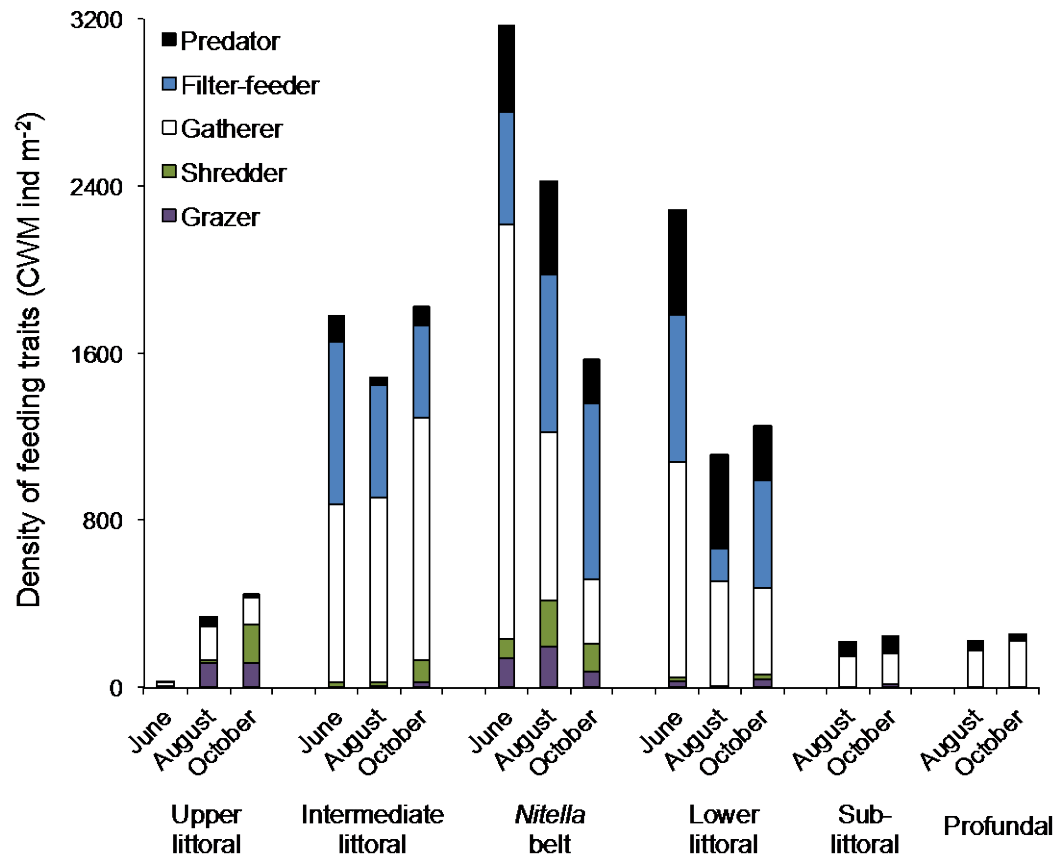


Figure 2.

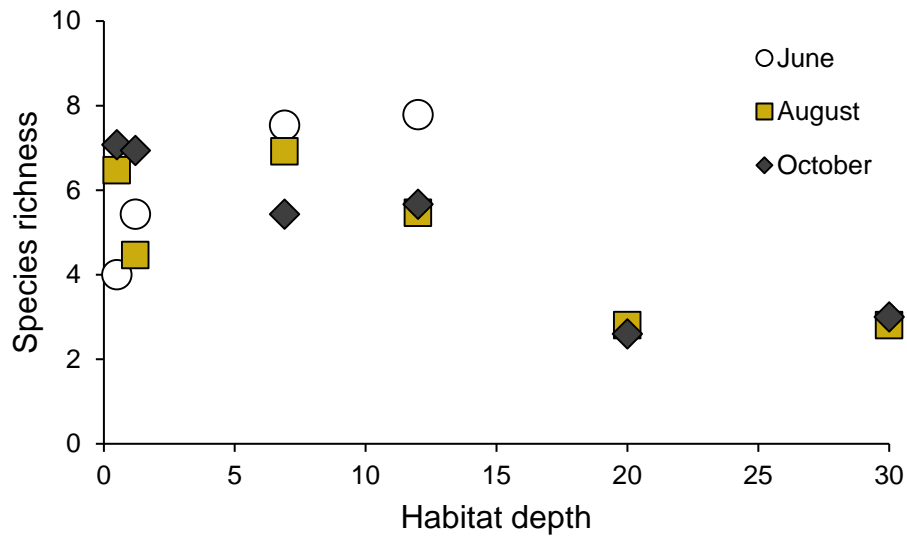


Figure 3.

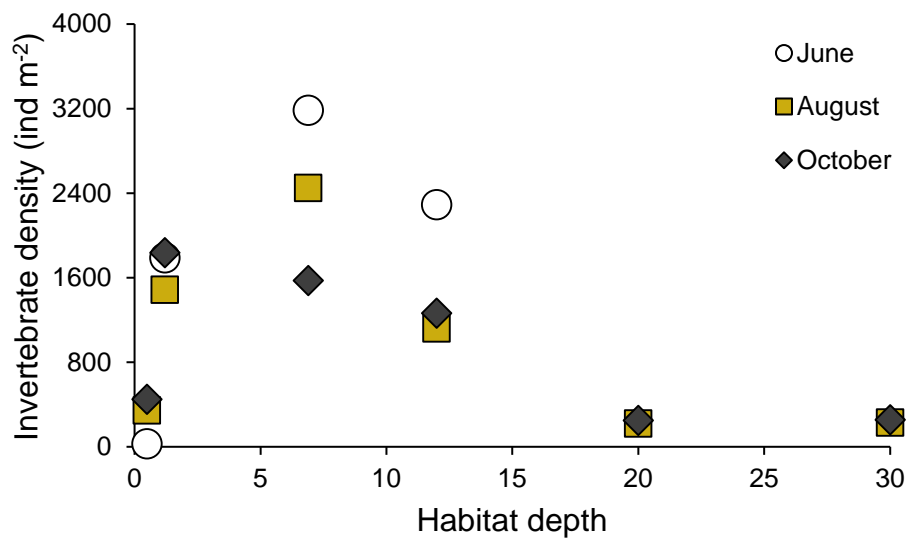


Figure 4.

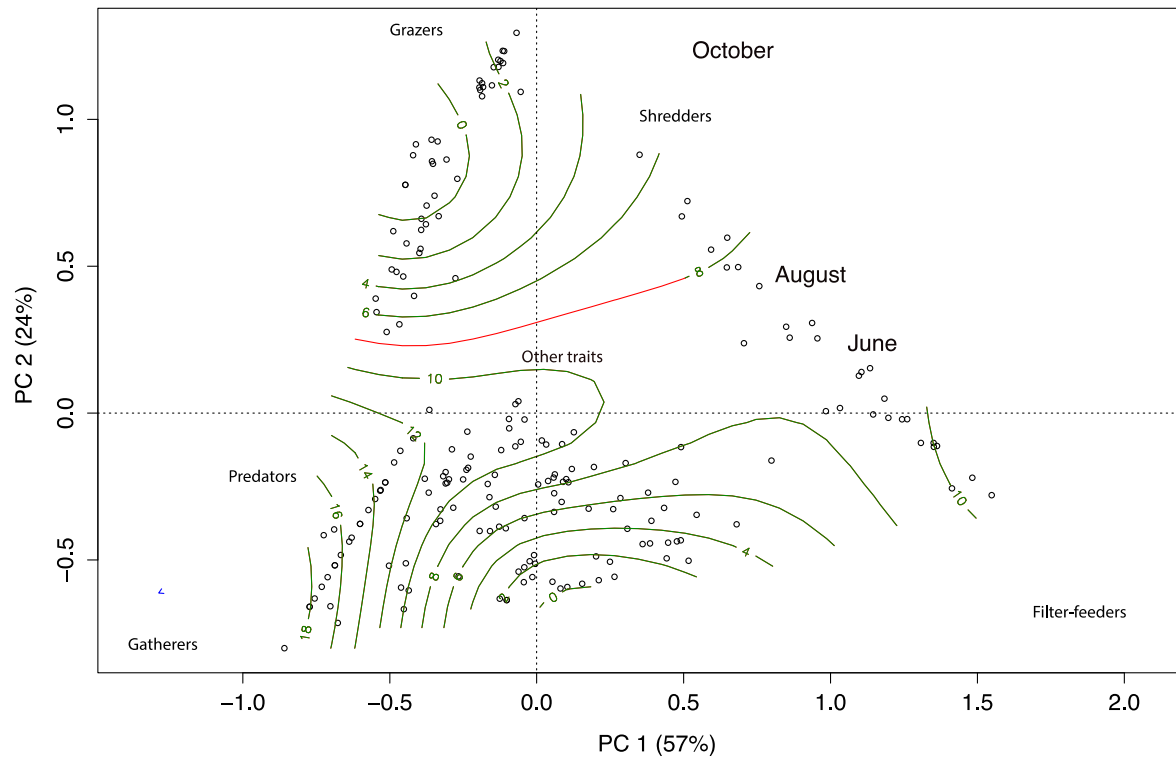


Figure 5.

