



Channelling of basal resources and use of allochthonous marine carbon by soil arthropods of the Wadden Sea salt marsh

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ABSTRACT: Salt marshes are located between the marine and terrestrial systems. Because they form as sediment accumulates, they comprise a gradient of shore height with differing inundation frequencies and associated abiotic soil conditions. Along this gradient, both autochthonous vascular plant resources and allochthonous marine algal or detrital resources are available, with the availability of both varying with season and salt marsh zone. However, little is known about the importance of either resource for the soil–animal food web. We investigated both spatial and temporal resource use of soil macro- and mesofauna in a salt marsh using neutral lipid fatty acid (NLFA) analysis. Generally, irrespective of season and zone, the soil–animal food web relied on carbon originating from autochthonous vascular plants and associated bacteria and fungi, with the role of bacteria generally exceeding that of fungi. However, the channelling of fungal resources consistently peaked in October, whereas seasonal changes in the channelling of plant and bacterial resources varied among salt marsh zones. Further, variations in the channelling of resources with season and zone varied among salt marsh animal species. Allochthonous resources of marine origin provided only a minor contribution to soil food web nutrition across salt marsh zones and seasons. The contribution of algae to soil food web nutrition depended on inundation frequency and season, i.e. algal productivity. Overall, the results demonstrate that the salt marsh soil fauna predominantly relies on autochthonous vascular plant resources, with the contribution of allochthonous marine resources being minor and restricted to a few taxa.

KEY WORDS: Soil food web · Soil fauna · Spatiotemporal resource use · Resource channelling · Allochthonous resources · Autochthonous resources · Neutral lipid fatty acids

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1. INTRODUCTION

Studying trophic interactions allows insight into the channelling of energy through food webs (Terborgh & Estes 2010). This is important for identifying the basal resources food webs rely on and their channelling to higher trophic levels. In soil food webs, basal resources typically comprise dead organic matter and associated microorganisms, with the dead organic matter originating predominantly from the

local vascular plant community, i.e. autochthonous resources (Wardle & Yeates 1993, Scheu et al. 2005, Zieger et al. 2017). However, allochthonous resources may also form an important component of the nutrition of belowground food webs (Mueller et al. 2020). Allochthonous resources are defined as resources that are not produced in the habitat consumers live in, often originating from adjacent, more productive habitats (Adin & Riera 2003, Ingimarsdóttir et al. 2014, Neres-Lima et al. 2017). Habitats

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relying on allochthonous resources include glacier forelands (Ingimarsdóttir et al. 2014), streams (Neres-Lima et al. 2017) and intertidal systems (Korobushkin et al. 2016, Mueller et al. 2017). Intertidal systems receive allochthonous marine resources carried in by the tide and consequently benefit from this additional input, which is particularly important in low-productive intertidal systems such as sandy beaches.

The European Wadden Sea is one of the largest intertidal systems in the world, stretching from the Netherlands across Germany into the western coastline of Denmark (Reise et al. 2010, Kabat et al. 2012). The Wadden Sea is characterized by a high exchange between riverine, marine and terrestrial resources, and is heavily influenced by currents and waves (Lasra et al. 2008, Reise et al. 2010). The Wadden Sea mudflats owe their size to barrier islands that protect them from the open ocean (Reise et al. 2010, Balke et al. 2017). Barrier island salt marshes lie at the interface between the marine mudflats and the dunes that occur at higher elevations and towards the open marine side of the islands. Because of their location, barrier island salt marshes are subject to calm currents and a gradual build-up of soil (Chapman & Steers 1958, Pennings & Bertness 2001). The associated marine–terrestrial gradient causes changes in flooding frequency, salinity and oxygen availability in the soil (Hedges & Oades 1997, Dinter 2018). The resulting habitat forms distinct vegetation zones, depending on the shore height above the mean high water level (MHWL). In the Wadden Sea salt marshes, the upper salt marsh (USM) is located >35 cm above MHWL and is dominated by *Elymus athericus* (*Elytrigia atherica*), with a soil salinity of 5 to 20‰. However, during drought conditions, soil salinity in the USM may exceed that in saltwater (Schröder et al. 2002, Meier et al. 2020c, Pieck et al. 2021). The lower salt marsh (LSM) is situated between 0 and 35 cm above MHWL and is dominated by *Atriplex portulacoides* and *Puccinellia maritima*, with a soil salinity between 20 and 26‰. The pioneer zone (PZ) lies below the MHWL and is flooded twice a day for ca. 6 h, resulting in a soil salinity of 26 to 32‰; it is dominated by *Salicornia stricta* and *Spartina anglica* (Suchrow & Jensen 2010, Balke et al. 2017, Dinter 2018, Winter et al. 2018). In addition, macroalgae, such as *Rhizoclonium riparium*, *Fucus* sp. and *Ulva* sp., inhabit the PZ (Balke et al. 2017, Winter et al. 2018).

The tidal range of the Wadden Sea is subject to seasonal changes, related to hydrodynamic conditions and wind (Bartholomä et al. 2009). This leads to the accumulation of detrital material from the lowest

salt marsh zones and marine systems in drift lines across the USM (Bouchard et al. 1998, Bouchard & Lefeuvre 2000). The high production of phytoplankton in the shallow regions of the North Sea (Reid et al. 1990, Scholz & Liebezeit 2012) and the presence of macroalgae in shallow coastal waters cause allochthonous resources to be deposited in the salt marsh. Some studies have indicated the importance of edaphic algae for salt marsh marine invertebrates (Sullivan & Moncreiff 1990), suggesting that microalgae contribute heavily to secondary production due to their more labile structure compared to *S. anglica* and other vascular plants (Buffan-Dubau & Carman 2000). In addition, macro- and microalgae, as well as diatoms, have been shown to be used by macroinvertebrates of French salt marshes and sandy beaches (Riera et al. 1999, Adin & Riera 2003). However, these studies focused on marine invertebrates and not on the terrestrial soil fauna.

Terrestrial soil fauna is separated into meso- (0.1 to 2 mm) and macrofauna (2 to 20 mm); both are essential for the breakdown of detrital material, nutrient cycling and soil structure (Scheu et al. 2005, FAO et al. 2020). Mesofauna include mites—both predators and detritivores—as well as Collembola feeding on detritus, fungi, bacteria, algae and nematodes (Schneider et al. 2005, Heidemann et al. 2011, 2014, Ferlian et al. 2015, FAO et al. 2020). In the Wadden Sea salt marshes, mesofauna diversity declines towards the mudflats, favouring species adapted to saline environments (halobionts) such as the oribatid mite *Zachvatkinibates quadrivertex* (Polderman 1974, Weigmann 2009). Similarly, soil macrofauna diversity declines, thereby reducing their role in soil structure formation and also their interactions with soil microorganisms and plants (Scheu et al. 2005, FAO et al. 2020). Despite the importance of soil fauna, little is known about their community structure and functioning in salt marshes, and little is known about the role of allochthonous resources and the channelling of basal resources through the soil–animal food web. Earlier studies have indicated that the LSM is dominated by decomposers relying on marine input, but with increasing shore height, the food web changes towards a terrestrial plant-based system (Schrama et al. 2012, 2013, 2017). However, these studies focused on macrofauna taxa and used observations and stable isotopes to delineate trophic positions, but did not investigate how basal resources, such as bacteria, fungi and plants, are channelled through salt marsh food webs.

Analysis of the neutral lipid fatty acids (NLFAs) of consumers provides information on their diet. This

has successfully been used to trace the diet of Wadden Sea salt marsh Oribatida, indicating differential use of resources based on the zone where the species was sampled and the resulting resource availability (Winter et al. 2018). The NLFA method is based on 'dietary routing', i.e. the incorporation of fatty acids into the deposit fat of animal consumers without major structural changes of the fatty acids (Ruess et al. 2005, Pollierer et al. 2010, Ruess & Chamberlain 2010, Eitzinger et al. 2013). Using specific NLFA markers, the method allows the channelling of basal resources, such as fungi, bacteria and plant detritus, to be traced through the soil–animal food web (Pollierer et al. 2010, Traugott et al. 2013). Furthermore, specific markers for algae, including diatoms, may allow the tracing of the incorporation of resources of marine origin (Ruess & Müller-Navarra 2019).

Using NLFA analysis, we investigated the channelling of basal resources through the soil–animal food web across salt marsh zones (USM, LSM and PZ) and seasons (spring, summer and autumn); thereby examining spatial as well as temporal dynamics. We hypothesized that (1) the contribution of vascular plants, bacteria and fungi as basal resources of soil taxa increases with shore height, because of the increasing aerobic environment with shore height. Conversely, we hypothesized that the contribution of algae as a basal resource increases with decreasing shore height due to increased algal input with inundation frequency. Further, we hypothesized that (2) the NLFA marker concentrations in soil animal taxa vary with season due to changes in temperature and inundation frequency affecting resource availability and consumption, resulting in algal markers increasing in summer due to high temperature and light conditions, whereas fungi, bacteria and plant markers increase in autumn because of increased input of plant litter material.

2. MATERIALS AND METHODS

2.1. Sampling

Samples were taken along 5 transects spanning across the USM, LSM and PZ on the island of Spiekeroog (Wadden Sea National Park, Germany; 53°45'2" to 53°47'1" N, 7°40'0" to 7°49'1" E) in April (spring), July (summer) and October (autumn) 2019. Within each transect, 1 soil core of 20 cm diameter was taken per zone and separated into 2 layers (0 to 5 and 5 to 10 cm depth). Cores were stored in plastic containers and kept at ambient temperature until soil fauna ex-

traction at the University of Göttingen. Soil fauna were extracted using heat (Kempson et al. 1963) into a 1:1 mixture of ethylene glycol and water. Once extracted, the animals were filtered through 45 µm gauze, flushed with water, placed into 70% ethanol and stored at –20°C. Animals were identified under a stereomicroscope; macrofauna were identified to species, whereas mesofauna taxa were grouped into higher taxonomic units to gain sufficient material for lipid extraction. To achieve sufficient animal tissue material, soil horizons and samples were, in part, pooled. The identification followed Weigmann (2006) for oribatid mites and Schaefer (2018) for all other fauna. Sorting was done within 2 to 4 wk after extraction to minimize the loss of lipids due to placement in ethanol. Prior to storage, the ethanol was evaporated and the animals were frozen at –20°C (Zieger & Scheu 2018).

2.2. Lipid extraction

Animals were placed into 10 ml tubes and lipids extracted as described by Haubert et al. (2004). In brief, animals were shaken overnight in 5 ml extraction solution (chloroform/methanol/0.05 M phosphate buffer pH 7.4, 1:2:0.8). Then, the extract was transferred to fresh tubes with an additional 2.5 ml extraction solution and shaken for 1 h. Chloroform and distilled water were added (0.8 ml each), and the tubes were vortexed and centrifuged (Thermo Scientific Heraeus® Multifuge® 3SR Plus; $\times g = 3700$) at 1500 rpm at 7 to 10°C for 5 min. The top phase was removed, and the remaining phase was fractionated in silica columns (Chromabond® SiOH 3 ml, Machery-Nagel™) and eluted with 1.5 ml and then 2 ml chloroform. Samples were then dried at 30°C in a vacuum centrifuge before saponification with 1 ml of a sodium hydroxide-methanol solution (45 g NaOH, 150 ml CH₃OH, 150 ml distilled H₂O) at 100°C for 30 min, followed by methylation with 2 ml HCl-methanol solution (325 ml 6.0 N HCl, 275 ml CH₃OH) at 80°C for 10 min. Finally, neutral lipids were extracted into hexane-methyl tertiary butyl ether (1:1) and washed with liquid NaOH (10.8 g NaOH, 900 ml distilled H₂O). Lipids were stored in capped 1.5 ml GC-vials at –20°C until gas chromatography.

Lipids were separated using a gas chromatograph (Clarus 500, PerkinElmer) equipped with an Elite-5 capillary column (30 m × 0.32 mm i.d., film thickness 0.25 µm, PerkinElmer). The analysis started at 60°C for 1 min, and the temperature was increased by 30°C min⁻¹ to 160°C, followed by 3°C min⁻¹ to 260°C. Injection temperature was 250°C, with helium as car-

rier gas. Lipids were identified by retention time based on standard mixtures composed of 37 FAMES (fatty acid methyl esters) ranging between chain lengths of C11 to C24 as well as 26 BAMES (bacterial acid methyl esters, Sigma-Aldrich) and algal standards for 16:2 ω 6,9 and 16:3 ω 3,6,9 (Larodan) (Buse et al. 2013). Lipid concentration was calculated as percentages. Only lipids contributing >1% of the total were included in the analysis. Lipids were aggregated into 6 NLFA marker groups including algae (14:0; 16:2 ω 6,9; 16:3 ω 3,6,9 and 20:5 ω 3,6,9,12,15), animals (20:1 ω 9), bacteria (a15:0; i15:0; i16:0; 16:1 ω 7; i17:0 and 18:1 ω 7), fungi (18:2 ω 6,9), vascular plants (18:1 ω 9 and 24:0) and unspecific (13:0; 14:1; 15:0; 16:0; 17:0; 17:1; 18:0; 20:0; 20:2; 20:3 ω 6,9,12; 20:4 ω 6,9,12,15).

2.3. Statistical analyses

The NLFA percentage data were arcsine transformed and analysed by principal component analysis (PCA) in CANOCO 5 (ter Braak & Šmilauer 2018) with Zone (USM, LSM, PZ), Season (April, July, October) and Species as passive (supplementary) variables not affecting the ordination. Linear mixed-effects models were used to assess the influence of Zone and Season on lipid marker concentrations. First, variations in each marker with the fixed factors Zone and Season were analysed; Core ID nested within transect as well as the species were included as random factors to control for non-independency of species from the same soil core. This model included *Amischa* sp., *Archisotoma besselsi*, Mesostigmata, Staphylinidae larvae and *Talitrus saltator*. These taxa/species were selected because they were present across multiple zones and seasons, and covered multiple trophic levels; they comprised 54% of the total individuals. Subsequently, to assess changes within taxa/species across zone and season, linear mixed-effects models were run for each taxon with the factors Zone, Season and Marker (type of NLFA marker group) with CoreID nested within transect to account for multiple samplings within

the same transect. Linear mixed-effects models were run in R (4.1.0) (R Core Team 2021) using the packages emmeans (Version 1.6.2-1), lme4 (Version 1.1-27.1), car (Version 3.0-11), lmerTest (Version 3.1-3) and dplyr (Version 1.0.7).

3. RESULTS

Generally, fatty acids contributing most to total NLFAs (including unspecific NLFAs) declined in the order plant marker 18:1 ω 9 (30.62 \pm 13.92%) > unspecific marker 16:0 (19.17 \pm 9.33%) > unspecific marker 18:0 (13.90 \pm 10.53%) > fungal marker 18:2 ω 6,9 (11.05 \pm 10.90%) > bacterial marker 18:1 ω 7 (8.99 \pm 11.20%) > bacterial marker 16:1 ω 7 (8.32 \pm 11.22%). None of the taxa contained NLFA markers for Gram-negative bacteria. The PCA of the NLFA data explained 55.1% of the variation in the dataset and separated the USM from the LSM and PZ along the first 2 axes, whereas seasons contributed little to the separation (Fig. 1). The LSM and PZ were closely

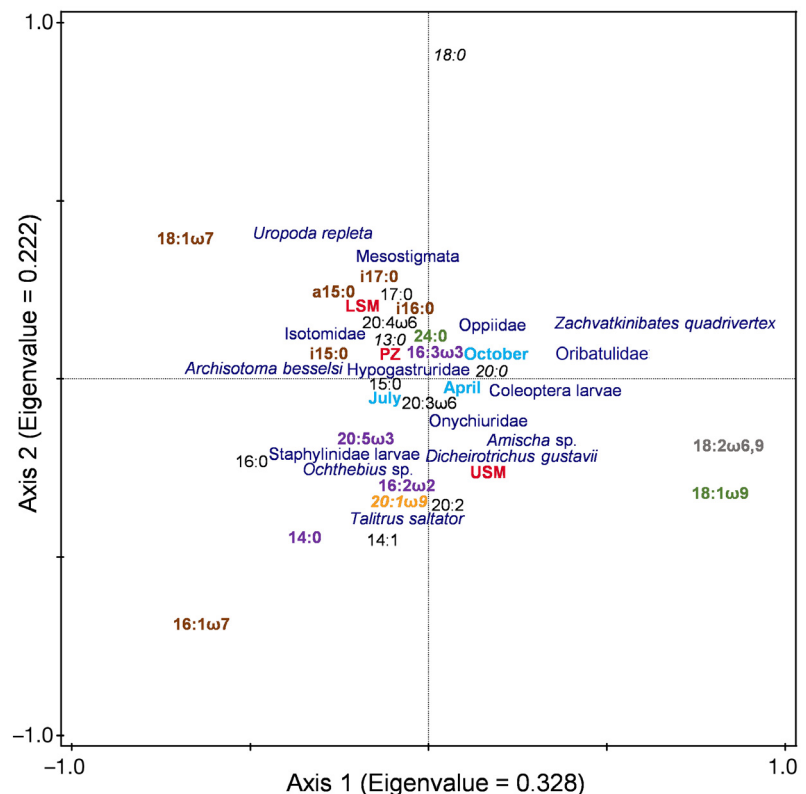


Fig. 1. Principle component analysis (PCA) of arcsine-transformed concentrations of neutral lipid fatty acids (NLFAs) including zone (USM: upper salt marsh; LSM: lower salt marsh; PZ: pioneer zone) and season (April: spring; July: summer; October: autumn), with species as passive variables. NLFAs are colour coded corresponding to their marker group: brown—bacteria; grey—fungi; orange—animal; purple—algae; green—plant; black—unspecific

associated with Gram-positive bacterial NLFA markers, whereas the USM clustered with the vascular plant (18:1 ω 9) and the fungal NLFA markers (18:2 ω 6,9). Unspecific NLFAs, including some algal markers (14:0, 16:2 ω 6,9 and 20:5 ω 3,6,9,12,15), clustered separately. Mesostigmata clustered with Gram-positive bacterial NLFA markers of the PZ and LSM, together with Isotomidae and *Archisotoma besselsi*, whereas *Uropoda repleta* clustered with the general bacterial NLFA marker 18:1 ω 7. Staphylinidae larvae, *Ochthebius* sp. and *Talitrus saltator* clustered with the algal NLFA markers 20:5 ω 3, 16:2 ω 2 and 14:0, as well as the animal marker 20:1 ω 9 and unspecific NLFAs 14:1 and 20:2. Onychiuridae, *Dicheirotrichus gustavii* and *Amischa* sp. showed little association with any marker lipid, but clustered with the USM and the fungal marker 18:2 ω 6,9 and the plant marker 18:1 ω 9. Oppiidae, *Zachvatkinibates quadrivertex* and Oribatulidae did not cluster with any marker lipids, but e.g., with the unspecific NLFA 20:0 separate from the other animal taxa.

3.1. Variations in individual NLFA markers across taxa between zones and seasons

The plant NLFA marker concentration across the 5 animal taxa that occurred in each of the 3 seasons varied with Zone and Season (significant Zone \times Season interaction; $F_{4,63} = 3.63$, $p = 0.010$). In the USM, it was highest in July and lower in April and October; in the LSM, it was lowest in July and higher in April and October; whereas in the PZ, it increased from April to October (Fig. 2a). However, averaged across seasons, the concentration declined from the USM ($34.81 \pm 12.17\%$) to the LSM ($29.29 \pm 14.73\%$) and to the PZ ($26.96 \pm 8.59\%$). Similarly, the bacterial NLFA marker concentration varied with Zone and Season (significant Zone \times Season interaction; $F_{2,73} = 3.42$, $p = 0.013$). Unlike the plant marker, bacterial NLFA marker in the USM was lowest in July and higher in April and October; in the LSM, it was highest in July and lower in April and October; in the PZ, it declined from April to October (Fig. 2b). The fungal NLFA marker concentration did not vary significantly with Zone but only with Season ($F_{2,69} = 3.32$, $p = 0.042$): it was highest in October ($12.12 \pm 12.86\%$ of total), lower in April ($7.55 \pm 8.90\%$) and lowest in July ($6.33 \pm 4.83\%$). Further, unspecific NLFA markers also significantly varied with Season ($F_{2,62} = 6.82$, $p = 0.002$): they were highest in July ($41.74 \pm 13.39\%$ of total), lower in April ($36.88 \pm 11.28\%$) and lowest in October ($30.60 \pm 12.59\%$). Neither algal nor animal

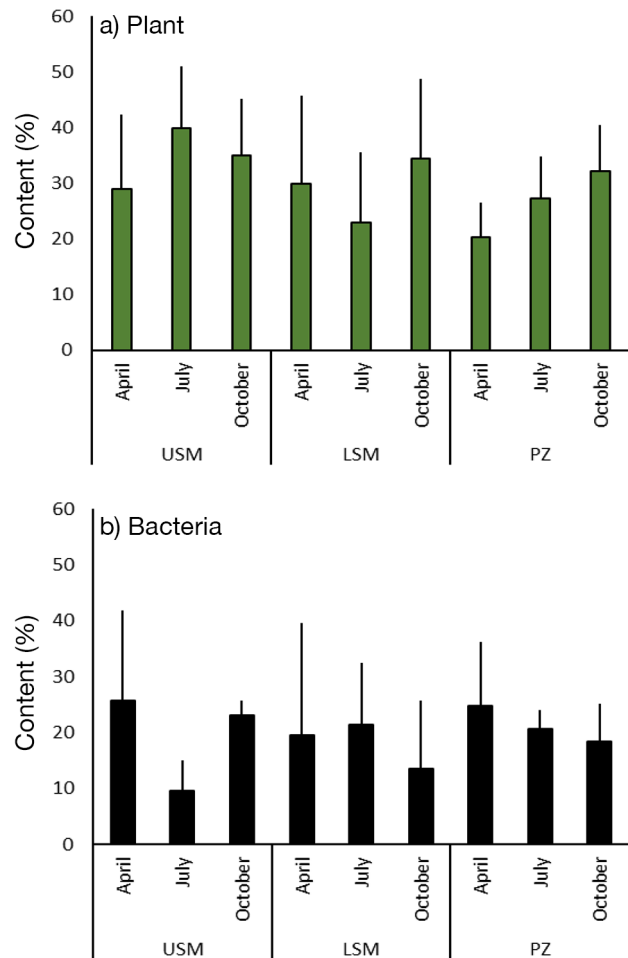


Fig. 2. Variations in neutral lipid fatty acid (NLFA) marker concentrations for (a) vascular plants and (b) bacteria in animal consumers averaged across consumer species with zone (USM: upper salt marsh; LSM: lower salt marsh; PZ: pioneer zone) and season (April: spring; July: summer; October: autumn). Error bars denote SD

NLFA marker concentrations varied significantly with Zone or Season and were on average $3.65 \pm 3.92\%$ and $0.21 \pm 0.71\%$, respectively.

3.2. Variations in NLFA markers of individual taxa

Of the taxa which were present at each of the 3 seasons, the NLFA marker concentration only varied significantly among markers but not with Season in Coleoptera larvae, *T. saltator*, Isotomidae and Onychiuridae (Table 1). NLFA marker concentrations also did not vary with Zone in Isotomidae, Onychiuridae and *T. saltator*, which were present in at least 2 zones and all seasons (Table 1). Excluding unspecific markers, NLFA marker concentrations in *T. saltator*

and Onychiuridae declined in the order plant marker > bacterial marker > fungal marker > algal marker (Table 2). Similarly, in Coleoptera larvae, the plant marker dominated, but concentrations of the fungal marker exceeded those of the bacterial marker. Bacterial markers only dominated in Isotomidae, followed by plant marker, algal marker and fungal marker. Animal NLFA markers were very low or not present.

3.3. Zone

In 6 of the 9 taxa that occurred in at least 2 zones and seasons, NLFA marker concentrations varied with both Markers and Zone (significant Marker × Zone interaction; Table 1, Fig. 3). In *Amischa* sp., which was present in the LSM and USM, plant NLFA marker concentrations generally dominated, and algae and animal NLFA markers were very low or absent (Fig. 3a). By contrast, bacterial and fungal marker concentrations varied between zones, with the bacterial marker increasing and the fungal marker decreasing from the LSM to the USM. In *A. besselsi*, which was present in the PZ and LSM, the unspecific markers were generally dominant. The plant NLFA marker was also high but similar in both zones, whereas animal and fungal markers were low or absent (Fig. 3b). By contrast, algal and bacterial marker concentrations were higher in the PZ than in the LSM. In Mesostigmata, which were present in each of the 3 zones, unspecific and plant markers were dominant. Bacterial markers were also high but similar among zones, whereas animal and algal markers were low or absent in each of the 3 zones (Fig. 3c). By contrast, the fungal NLFA marker increased from the PZ to the LSM and to the USM. In *Ochthebius* sp., which was present in the LSM and USM, the concentrations of unspecific, plant and bacterial markers were high, with the bacterial marker differing strongly between zones, being higher in

the USM than in the LSM (Fig. 3d). Although concentrations of the algal and fungal NLFA markers were generally low, the concentration of the algal marker in the USM exceeded that in the LSM, whereas the opposite was true for the fungal marker. In Staphylinidae larvae, which were present in the LSM and USM, the unspecific and bacterial NLFA markers were dominant but concentrations did not vary across zones. By contrast, plant and algal NLFA marker concentrations in the USM exceeded those in the LSM, whereas the opposite was true for the fungal marker (Fig. 3e). In *Z. quadrivertex*, which was present in the PZ and LSM, plant NLFA marker concentration was highest, but declined from the PZ to the LSM (Fig. 3f). Concentrations of the fungal marker were similar in the PZ and LSM, whereas the unspecific marker and the bacterial marker, although being generally low, increased from the PZ to the LSM. Concentrations of algal and animal markers were low or absent.

3.4. Season

In 8 of the 15 taxa, NLFA marker concentrations varied with Marker and Season (significant Marker × Season interaction; Table 1, Fig. 4); in 2 of them (*A. besselsi* and *Amischa* sp.), this depended on Zone (significant Marker × Season × Zone interaction). In *Amischa* sp., the plant marker was high throughout the seasons, whereas the bacterial marker peaked in July and the fungal marker in October (Fig. 4a); this was more pronounced in the LSM than in the USM (data not shown). The algal NLFA marker of the USM peaked in April and July, whereas in the LSM, it peaked in July and October. In *A. besselsi*, the plant marker peaked in April and October (Fig. 4b) and this was most pronounced in the LSM (data not shown). The algal marker was similar across seasons, whereas the bacterial marker peaked in April (Fig. 4b). In *D. gustavii*, the plant marker dominated

Table 2. Average concentration (%) of neutral lipid fatty acid (NLFA) markers in salt marsh taxa/species present in each of the 3 seasons (April, July and October), but not varying significantly with season (data pooled for season); for statistical analysis see Table 1

Taxa/species	Plant marker (%)	Bacterial marker (%)	Fungal marker (%)	Algal marker (%)	Animal marker (%)	Unspecific marker (%)
Coleoptera larvae	28.13 ± 19.66	10.31 ± 9.26	25.84 ± 9.64	4.06 ± 4.02	–	31.66 ± 17.00
<i>Talitrus saltator</i>	28.66 ± 5.30	17.48 ± 6.91	11.62 ± 2.69	5.30 ± 3.25	1.57 ± 1.21	35.36 ± 8.11
Isotomidae	23.02 ± 12.53	37.01 ± 13.20	2.63 ± 3.29	3.36 ± 2.74	–	33.97 ± 5.68
Onychiuridae	32.23 ± 10.26	17.24 ± 8.57	9.32 ± 6.28	5.56 ± 7.59	–	35.65 ± 12.07

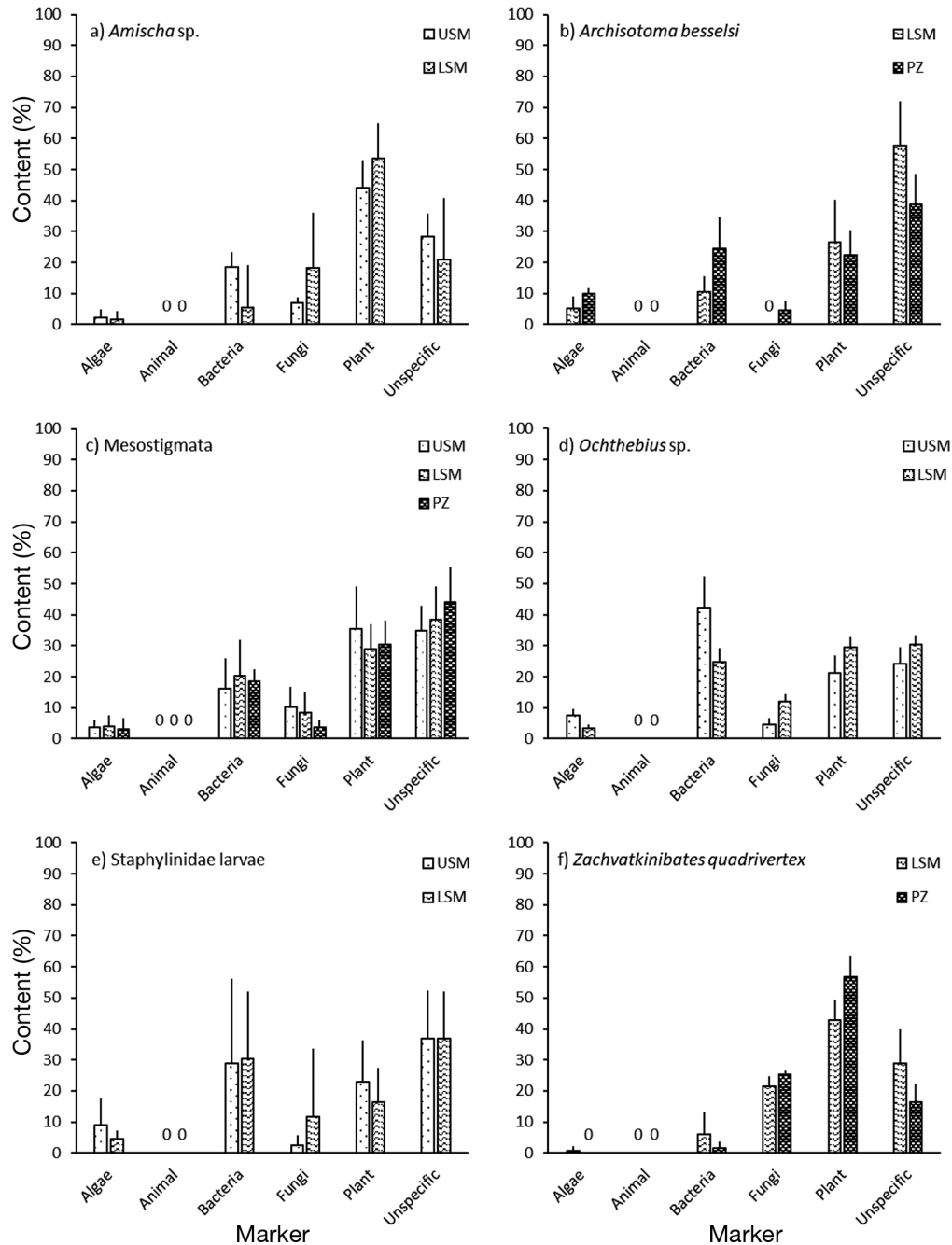


Fig. 3. Variations in neutral lipid fatty acid (NLFA) marker concentrations (%) across zone (USM: upper salt marsh; LSM: lower salt marsh; PZ: pioneer zone) of (a) *Amischa* sp., (b) *Archisotoma besselsi*, (c) *Mesostigmata*, (d) *Ochthebius* sp., (e) *Staphylinidae* larvae and (f) *Zachvatkinibates quadrivertex*. Zones where taxa/species originated are indicated; error bars denote SD. Zeros indicate absence of the marker in the consumer (0%)

and peaked in October (Fig. 4c). Although less abundant, the bacterial marker also peaked in October, whereas the fungal marker peaked in July. The algal marker was generally low. In *Hypogastruridae*, plant, bacterial, fungal and unspecific marker concentrations were at a similar level, whereas algal and

animal marker concentrations were low (Fig. 4d). The plant and fungal NLFA markers declined in October, whereas the bacterial NLFA marker increased. In *Oppiidae*, plant fungal and unspecific marker concentrations dominated, whereas concentrations of algal, animal and bacterial markers were

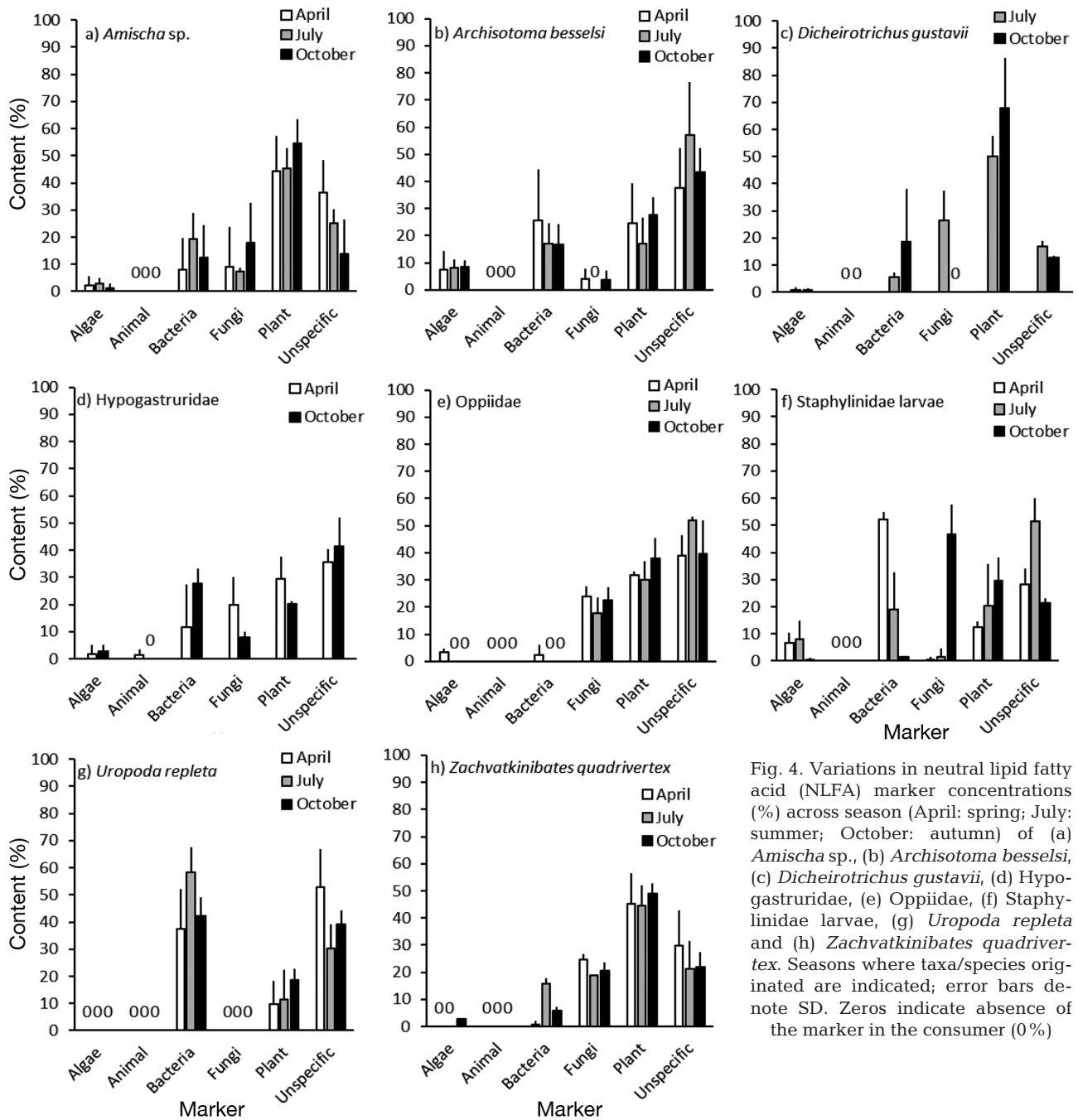


Fig. 4. Variations in neutral lipid fatty acid (NLFA) marker concentrations (%) across season (April: spring; July: summer; October: autumn) of (a) *Amischa* sp., (b) *Archisotoma besselsi*, (c) *Dicheirotrichus gustavii*, (d) Hypogastruridae, (e) Oppiidae, (f) Staphylinidae larvae, (g) *Uropoda repleta* and (h) *Zachvatkinibates quadrivertex*. Seasons where taxa/species originated are indicated; error bars denote SD. Zeros indicate absence of the marker in the consumer (0%)

low or absent (Fig. 4e). Although marker concentrations varied significantly with season, their relative proportions generally stayed rather constant across the 3 seasons. In Staphylinidae larvae, plant NLFA marker increased from April to October (Fig. 4f). Bacterial and fungal marker concentrations varied strongly and in opposite directions among seasons: the bacterial marker peaked in April and was virtually absent in October, whereas the fungal marker

peaked in October and was virtually absent in April and July. In *U. repleta*, the plant marker was generally low, whereas bacterial and unspecific markers dominated. Although marker concentrations varied significantly with season, their relative proportions were similar across seasons. Algal, animal and fungal NLFA markers were absent. In *Z. quadrivertex*, the plant marker dominated throughout the seasons, whereas concentrations of the bacterial marker were

low but peaked in July (Fig. 4h). The fungal marker varied little among seasons, but generally ranked second after the plant marker. The algal and animal markers were very low or absent.

4. DISCUSSION

The aim of this study was to determine spatial and temporal dynamics in the channelling of basal resources and marine carbon through the soil food web of the Wadden Sea salt marsh by using NLFA markers. Overall, NLFA markers pointed towards the dominant use of plant and bacterial resources across the studied animal taxa/species, indicating the predominant use of autochthonous resources channelled to higher trophic levels via consumption of plant detritus and bacteria. Although less important, autochthonous plant resources were also channelled to higher trophic levels via fungi.

4.1. Changes in energy channelling with season and salt marsh zones across taxa

Generally, the plant NLFA marker dominated across salt marsh zones and seasons, averaging 46.9% of total NLFA markers (excluding unspecific NLFAs). However, it declined from the USM to the LSM and to the PZ, suggesting that the use of plant-associated resources decreases with decreasing shore height, supporting our first hypothesis. These findings are in line with the decline in plant phospholipid FA (PLFA) markers in soil with decreasing shore height (Rinke et al. 2022) and vascular plant resource use by soil invertebrates (Schrama et al. 2012, 2013, 2017). However, plant biomarker NLFA concentrations in consumers also varied with season. They were generally high in autumn, but were also high in summer in the USM and PZ, partially supporting our second hypothesis. These patterns coincide with the seasonal biomass production of the dominant vascular plant species (Bouchard et al. 1998, Morris & Jensen 1998, Bouchard & Lefeuvre 2000), indicating a corresponding increase in the channelling of plant-based resources through the salt marsh food web. However, seasonal patterns depended on the salt marsh zone, and minimum values in the LSM in July suggest that, in this zone, little plant detritus enters the below-ground system in summer. In the LSM and PZ, plant litter material is likely displaced by tides, limiting its availability for animal consumers (Bouchard et al. 1998, Bouchard & Lefeuvre 2000).

Although generally high across salt marsh zones and seasons, averaging 30.7% of total NLFA markers (excluding unspecific NLFAs), the bacterial NLFA marker concentration of soil animals was highest in the PZ. This is in contrast to the results of Mueller et al. (2020), who did not find changes in bacterial density with shore height, but it confirms earlier findings that bacteria generally dominate the decomposer system in salt marsh soils, particularly in the PZ (Benner et al. 1984, Calado & Barata 2012, Calabon et al. 2021, Leadbeater et al. 2021, Rinke et al. 2022). Although high, bacterial NLFA marker concentrations in each zone varied with season, indicating changes in consumption of bacteria with season. Notably, these changes were most pronounced in the USM, where bacterial NLFA markers dropped in July, indicating reduced presence of bacteria in diets during summer. This decline coincided with high temperature, salinity and reduced water content at our study site (Meier et al. 2020a,c, Pieck et al. 2021). Presumably, these factors limited the accessibility of bacteria for consumers in the USM. By contrast, in the LSM, bacterial NLFA marker concentration remained at a similar high level in April and July but declined in autumn. This suggests that the accessibility and consumption of bacteria in summer in the LSM benefited from more frequent inundation (Meier et al. 2020b), whereas reduced channelling of bacterial resources in autumn might be related to increased anoxia (Meier et al. 2020b, Pieck et al. 2021) as well as displacement of litter material by frequent tides (Bouchard et al. 1998). In the PZ, bacterial NLFA marker concentrations peaked in April and then continuously declined until October. The factors responsible were likely the same as in the LSM. High channelling of bacteria in spring might reflect that the colonization of litter by bacteria increases during decomposition and this coincides with more intensive grazing by bacterivorous nematodes as shown e.g. for *Spartina anglica* litter (Alkemade et al. 1994, de Mesel et al. 2003). This may generally explain the high channelling of bacterial resources in spring in each of the salt marsh zones. Displacement of bacterial grazers by tides, as shown for nematodes (Alkemade et al. 1994, de Mesel et al. 2003), may also have contributed to the low channelling of bacterial resources in autumn.

The fungal NLFA marker concentration was generally low and averaged 16.2% of the total NLFA markers (excluding unspecific NLFAs). Contrasting with the plant and bacterial NLFA markers, and earlier findings by Mueller et al. (2017, 2020), it did not vary significantly between salt marsh zones but did

among seasons. Across seasons, the fungal marker concentration was highest in October and about 50% lower in April and July, suggesting maximum channelling of fungi to higher trophic levels in autumn. This contrasts with the low fungal PLFA markers in the soil of the USM and LSM in autumn reported by Rinke et al. (2022), but coincides with the peak of dead organic matter from salt marsh plants in autumn (Morris & Jensen 1998, Bouchard & Lefeuvre 2000), likely boosting saprotrophic fungi (Calado & Barata 2012, Calado et al. 2019). Supporting this conclusion, Mueller et al. (2017) found fungi to be closely associated with vascular plant litter in salt marshes. Therefore, increased channelling of fungi in autumn likely reflects the input of plant litter material with associated saprotrophic fungi contributing to the predominant use of autochthonous resources by the salt marsh food web.

Algal and animal NLFA marker concentrations were generally low and accounted for only 5.9 and 0.34% of total marker concentration (excluding unspecific NLFAs), respectively, suggesting that allochthonous and animal-based resources do not contribute substantially to the basal resources for the salt marsh soil fauna. This is in contrast to the results of Schrama et al. (2012, 2013), which indicated greater consumption of marine input at lower shore height.

Overall, the results indicate that autochthonous vascular plant material forms the basis of the salt marsh soil food web. Furthermore, bacteria are the dominant decomposers in the salt marsh soil, whereas fungi become more important with the input of plant litter. This suggests that plant resources are either channelled directly to animal consumers via primary decomposers feeding on plant litter or via bacteria colonizing plant organic matter and being consumed by secondary decomposers, as well as to a lesser degree by fungi associated with plant litter at early stages of decay, again being channelled to higher trophic levels by secondary decomposers.

4.2. Spatial changes in energy channelling through salt marsh taxa

The channelling of energy from basal resources into animal consumers varied strongly among the taxa/species studied. Conforming to the general pattern discussed in Section 4.1., the plant NLFA marker dominated in most taxa/species, but the bacterial marker exceeded the plant marker concentration in a number of taxa/species, including *Ochthebius* sp.,

Staphylinidae larvae and *Uropoda repleta*. Although the general pattern of energy channelling within taxa/species remained consistent across seasons and salt marsh zones, i.e. the dominant NLFA marker and the association of species to energy channels typically remained the same, NLFA marker composition varied significantly with season, saltmarsh zone or their interaction in each of the 15 taxa/species studied, except Coleoptera larvae, Isotomidae, Onychiuridae, Oribatulidae and *Talitrus saltator*.

Conforming to the pattern across animal taxa/species, the plant NLFA marker declined with decreasing shore height in *Archisotoma besselsi*, Staphylinidae larvae and Mesostigmata, again pointing to the decline in vascular plant resources with increased inundation frequency (see Section 4.1.). This agrees with the results of Schrama et al. (2012, 2013), which indicated greater vascular plant consumption in salt marsh soil invertebrates at higher elevations.

Contrasting the general pattern of increased channelling of bacterial resources with decreasing shore height, the bacterial NLFA marker declined at lower elevations in *Amischa* sp. and *Ochthebius* sp. This suggests that the access to bacterial resources in these species declines with inundation frequency, which is consistent with changes in bacterial PLFAs across salt marsh zones (Rinke et al. 2022). Presumably, these comparatively large species are more sensitive to the removal of litter due to frequent inundations, which detrimentally affects their access to bacterial resources.

Fungal NLFA patterns were not consistent among taxa/species, but in agreement with the general pattern they were uniformly low. In contrast to the overall uniform use of fungal resources across salt marsh zones, fungal NLFA marker concentrations declined with decreasing shore height in Mesostigmata, whereas they increased in *Amischa* sp., Staphylinidae larvae and *Ochthebius* sp. in the LSM, matching soil fungal PLFA patterns (Rinke et al. 2022).

The algal NLFA marker did not change in a consistent way with shore height in the studied taxa/species, in contrast to the results of Schrama et al. (2012, 2013), which indicated higher consumption of marine input at lower shore height. Presumably, the lack of a pattern is related to the fact that its concentration was generally low across the taxa studied. The same applies to animal NLFA markers.

Overall, changes in NLFA patterns among the taxa/species studied reflect species-specific trophic niches linked to changes in the availability of autochthonous litter resources and their predominant processing by bacteria in the soil.

4.3. Temporal changes in energy channelling through salt marsh taxa

In 8 of the 15 taxa/species studied, NLFA marker concentrations varied with season. The dominant channel of 6 of these taxa/species was the plant and bacterial channel, whereas the fungal channel predominated in Oppiidae and *Zachvatkinibates quadrivertex*. Conforming to the general pattern, plant NLFA marker concentrations peaked in October in *Amischa* sp., *A. besselsi*, *Dicheirotrichus gustavii*, Staphylinidae larvae and *U. repleta*, suggesting that these taxa/species benefit from the increased input of vascular plant litter in autumn (see Section 4.1.) (Morris & Jensen 1998, Bouchard & Lefeuvre 2000).

Bacterial resource channelling differed strongly among the 15 taxa/species studied. The differential channelling of bacterial-based resources also contributed to the fact that the bacterial channel varied across taxa with both salt marsh zone and season. Corresponding with the general pattern in the USM, high bacterial NLFA marker concentrations in *D. gustavii* and Hypogastruridae in October likely reflect high input of senescent plant biomass (see Section 4.1.) (Bouchard et al. 1998, Bouchard & Lefeuvre 2000). In contrast to the general pattern, high bacterial NLFA marker concentrations in July for *Amischa* sp., *Z. quadrivertex* and *U. repleta* may be related to low soil water content and high salinity in the USM and LSM at that time (Meier et al. 2020a,c, Pieck et al. 2021), which may have contributed to increased input of plant litter-boosting bacteria in the soil (Bouchard et al. 1998, Morris & Jensen 1998, Bouchard & Lefeuvre 2000).

Fungal NLFA marker concentration also varied across seasons, but not consistently among taxa/species. Reflecting the pattern across taxa, it peaked in October in *Amischa* sp. and Staphylinidae larvae, whereas it peaked in April and October in *A. besselsi* and in July in *D. gustavii*. Overall, this suggests that senescent plant materials colonized predominantly by fungi (Calado & Barata 2012, Calado et al. 2019, Calabon et al. 2021) are available throughout the year, but their input peaks in October.

Although generally low, algal NLFA marker concentrations in Oppiidae, *Amischa* sp. and Staphylinidae larvae peaked in April and July, and this is consistent with the peak in algal PLFAs early in the year (Rinke et al. 2022). By contrast, the algal NLFA marker peaked in October in *Z. quadrivertex*. Presumably this is due to frequent inundations enriching the LSM soil with microalgae, as shown by Bouchard et al. (1998). The presence of algal NLFA markers

across seasons in *A. besselsi*, *D. gustavii* and Hypogastruridae, however, also shows that algae contributed to the diet of salt marsh consumers throughout the year, but their contribution remained generally low.

5. CONCLUSIONS

We investigated spatial and temporal changes in the channelling of basal resources through the soil–animal food web of the Wadden Sea salt marsh. Overall, the results indicate that autochthonous plant litter resources and associated bacteria form the dominant basal resources of the Wadden Sea soil–animal food web. Fungi were generally less important and the channelling of fungal resources was restricted to certain taxa/species. In 6 of the 15 taxa/species, NLFA marker concentrations varied significantly among salt marsh zones, indicating pronounced spatial variations in the channelling of basal resources through the salt marsh food web. Generally, plant NLFA marker concentrations declined towards lower salt marsh zones, whereas fungal marker concentrations did not vary among zones and variations in bacterial marker concentrations depended on season. Algal NLFA marker concentrations were generally low and did not vary consistently among taxa between zones and the same was true for animal NLFA markers. Similar to the spatial variation, NLFA marker concentrations varied with season in 8 taxa/species, indicating that the channelling of basal resources also varies markedly among seasons. Plant NLFA marker concentrations generally peaked in October, coinciding with increased plant litter input, whereas bacterial and fungal NLFA marker concentrations did not vary consistently among taxa with seasons. Similar to the spatial variations, the low NLFA marker concentrations for algae and animals did not vary consistently with seasons. Overall, the results indicate that the channelling of basal resources through the salt marsh food web varies both in space and time, with the changes being mainly driven by seasonal dynamics in the input of autochthonous resources, i.e. litter material from vascular plants.

Data availability. The datasets generated and/or analysed during the current study are available in the DRYAD repository (doi:10.5061/dryad.mcvdnck3m). Link for peer-review: https://datadryad.org/stash/share/bW_i2JRMjPCgJXXVxNDDy3ZfzuoyS2OVhupzfk-SLAW

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