



Spatial and temporal patterns of zooplankton trophic interactions and carbon sources in the eutrophic Elbe estuary (Germany)

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Abstract

Zooplankton in estuaries encounter complex physical and biogeochemical processes that affect the quantity, quality, and origin of their food sources. The knowledge about how zooplankton deal with highly variable organic matter sources is sparse. Here, we investigated the spatial and temporal patterns of zooplankton trophic dynamics and carbon sources in the intensively dredged, eutrophic Elbe estuary. For this purpose, we applied elemental and stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) on particulate organic matter (POM) and dominant meso- and macrozooplankton species, including ichthyoplankton, from five stations along the entire salinity gradient of the estuary in 2022. The $\delta^{13}\text{C}$ values of POM (-29.2 to -23.0 ‰) indicated a mixture of riverine, terrestrial, and coastal carbon sources used by most taxa for their diet. *Eurytemora affinis* (-34.0 to -23.3 ‰) and *Mesopodopsis slabberi* (-22.2 to -20.0 ‰) exhibited a broader range in $\delta^{13}\text{C}$ than POM, suggesting selective feeding on single POM components depending on the season. In winter and autumn, under high suspended matter loads and limited availability of high-quality autochthonous phytoplankton, zooplankton showed increased tendency for carnivory (higher $\delta^{15}\text{N}$ values). Our study revealed a high trophic plasticity of estuarine Elbe zooplankton to buffer hydrological-related alterations in their food source by dietary niche partitioning and a flexible switch in their feeding behaviour.

Keywords: Elbe estuary; estuarine zooplankton; trophodynamics; stable isotopes; allochthonous and autochthonous carbon sources; selective feeding

Introduction

Planktonic organisms play an important role in the production and transfer of organic matter and energy in aquatic ecosystems (Barnett et al. 2007, Koppelman et al. 2009). Especially in estuaries, planktonic communities are affected by strong variability in environmental conditions, leading to complex food web structures. Estuaries are highly productive transition zones at the interface between freshwater and marine ecosystems and are characterized by physical (e.g. river discharge, tidal advection) and biogeochemical gradients (e.g. cycling of organic matter, nutrients, and suspended solids) on various spatial and temporal scales (Hyndes et al. 2014, Geerts et al. 2017, Boynton et al. 2018, Kamjunke et al. 2023). These highly valuable habitats fulfil essential ecological functions such as transfer and sequestration of organic matter (Hyndes et al. 2014), recycling and filtering of nutrients (Boynton et al. 2018), refuge and nursery grounds for crustaceans and fish (Wilson 2002), and coastal protection (Koch et al. 2009). At the same time, estuaries are often severely impacted by anthropogenic stressors such as diking, dredging, and eutrophication (Kerner 2007, Cloern et al. 2016).

Anthropogenic pressures and estuarine gradients impact the fate of organic matter transfer throughout different trophic levels (TLs), resulting in alterations of the food web

structures and functions (Benfield 2012). Estuaries are defined by strong tidal mixing and high concentrations of nutrients and suspended particulate matter (SPM), which affect the production of autochthonous organic matter (Turner et al. 2022). Primary production is therefore often restricted to upstream freshwater areas, where light conditions are more favourable and salinity stress and water turnover are reduced (Muylaert et al. 2005). Fresh phytoplankton biomass, the most nourishing food source for zooplankton (Müller-Solger et al. 2002), is therefore less accessible to primary consumers in turbid zones (Benfield 2012). In addition, excessive loads of organic matter in estuaries facilitate microbial colonization (Zimmermann-Timm et al. 1998), resulting in intense remineralization processes (Middelburg and Herman 2007, Kamjunke et al. 2023), which increase microbial pathways in the pelagic food web (Stoecker and Capuzzo 1990, Lerner et al. 2022). This leads to strong fluctuations in the quality of food sources, which can shift from fresh phytoplankton to detrital, recalcitrant, and less nutritious carbon sources (Müller-Solger et al. 2002). Despite this high importance, the role and dynamics of detrital sources and autochthonous organic matter in the trophodynamics of estuarine zooplankton are still not well understood. Fundamental knowledge of trophic interactions within estuarine planktonic communities is needed to understand the

impact of increasing human pressures on estuarine food webs and to provide a tool for ecosystem-based management and conservation.

Assessing the trophodynamics of estuarine zooplankton is difficult due to the potential diversity of different available organic sources, which include detrital, allochthonous material derived from terrestrial origin (e.g. C3 and C4 plants, soil organic matter), as well as primary producers from riverine and marine environments (e.g. phytoplankton, benthic algae), along with heterotrophic sources, such as flagellates and ciliates. Stable isotope analysis (SIA) is a powerful tool to disentangle the structure of planktonic food webs. Carbon isotope composition in consumers changes little with the progression through a food web and thus reflects the time-integrated isotope composition of their diet (DeNiro and Epstein 1978). In addition, TLs for different organisms can be calculated based on their nitrogen isotope composition, which shifts in a predictable manner from one TL to the next (DeNiro and Epstein 1981). In general, primary carbon sources differ markedly in their stable isotopic (SI) signal, making them distinguishable as dietary sources for planktonic consumers and have already been investigated in numerous estuarine studies (Thornton and McManus 1994, Cloern et al. 2002, Martineau et al. 2004, Middelburg and Herman 2007, Christianen et al. 2017). Marine phytoplankton typically exhibit carbon and nitrogen isotopic values ranging between -22 and -17 ‰ and from 3 to 12 ‰, respectively, while freshwater algal material usually has $\delta^{13}\text{C}$ values between -32 and -23 ‰ and around 5 ‰ for $\delta^{15}\text{N}$ (Boutton 1991, Maksymowska et al. 2000, Finlay and Kendall 2007). Benthic algae that contribute to the pelagic organic sources through resuspension exhibit ^{13}C -enriched values between -22 and -11 ‰ and $\delta^{15}\text{N}$ values from 3 to 9 ‰ (Maksymowska et al. 2000, Christianen et al. 2017). Terrestrial sources, including C3 and C4 plants, as well as soil organic matter, also have distinct isotopic characteristics; C3 plants and soil organic matter range between -27.0 and -26.0 ‰ for $\delta^{13}\text{C}$ and from 3 to 18 ‰ for $\delta^{15}\text{N}$, whereas C4 plants are characterized by $\delta^{13}\text{C}$ values between -17 and -9 ‰ and $\delta^{15}\text{N}$ values from 3 to 7 ‰ (Maksymowska et al. 2000, Cloern et al. 2002, Finlay and Kendall 2007). In addition, these terrestrial sources differ considerably in their carbon to nitrogen ratios as a result of degradation processes, with ratios ranging from 15 to 50 for terrestrial plants and from 8 to 25 for soil organic matter, in contrast to that of fresh algal sources (below 8) (Thornton and McManus 1994, Finlay and Kendall 2007). Moreover, stable isotopes also yield information about the width and overlap of the dietary niches of different organisms and thus dietary niche differentiation (Newsome et al. 2007). SIA provides time-integrated dietary information over longer time periods, contrary to conventional methods, such as gut content analysis and feeding experiments, which offer short-term insights into dietary preferences (Dalerum and Angerbjörn 2005). The SI composition of organisms can therefore give a time- and space-integrated view of trophic interactions (Newsome et al. 2007) and is thus ideal for highly dynamic habitats such as estuaries.

The Elbe estuary, a highly turbid environment characterized by strong estuarine gradients and anthropogenic stressors, has so far received limited attention in determining planktonic food web structures. It is one of Europe's largest tidal estuaries, located in north-west Germany, and serves multiple ecological functions, including refuge for many zooplankton and fish species (Bernát et al. 1994, Eick and Thiel 2014). It

is also of significant socio-economic importance, particularly due to its connection to the seaport of the city of Hamburg. Over the last decades, the Elbe estuary has experienced re-occurring morphological modifications due to channel diking and dredging events to facilitate access to Hamburg Harbour (Kerner 2007, Papenmeier et al. 2014). As a result, the navigation channel exhibits a rapid change in bathymetry, with water depths ranging from ~ 5 m at the eastern edge of the city of Hamburg up to 20 m downstream of the port area (Federal Waterways and Shipping Agency (WSV) 2023). This sudden increase in water depth results in longer water residence times in and downstream of the port area, leading to enhanced accumulation of suspended particles and consequently to elevated turbidity (Kerner 2007, Geerts et al. 2017). Previous studies have indicated that this bathymetric jump in the port area contributes to a strong decline in phytoplankton biomass due to light limitation and sedimentation of algal cells to deeper layers (Wolfstein and Kies 1995, Dähnke et al. 2022, Kamjunke et al. 2023, Steidle and Vennell 2024), which, in turn, increase remineralization processes (Sanders et al. 2018, Kamjunke et al. 2023). Most of the particulate organic matter (POM) in the Elbe estuary therefore consists of allochthonous, decaying algae that originates from the shallow, non-dredged freshwater area upstream of the port (Geerts et al. 2017). Downstream of the port area, the organic matter source contains allochthonous material from adjacent coastal regions, primarily marine-like substances (Tobias-Hünefeldt et al. 2024), which are resuspended from deeper bottom water due to strong mixing forces (Spieckermann et al. 2021). In addition, the Elbe estuary is characterized by a semidiurnal, flood-dominated tidal wave that leads to steady resuspension of organic substances from benthic sources into the water column (Spieckermann et al. 2021).

Although the Elbe estuary is well-studied in terms of organic and particle matter dynamics, the role and fate of autochthonous and allochthonous organic matter in its planktonic food web, along with the spatio-temporal dynamics of utilizing different organic matter sources by zooplankton, has never been fully investigated. So far, Kerner et al. (2004) have studied the carbon utilization of micro- and mesozooplankton species only in the freshwater area of the Elbe estuary using carbon isotopes. The authors found marked shifts in the use of the consumers' carbon sources on a seasonal scale.

Here, we address this knowledge gap by investigating the trophodynamics of the planktonic food web along the entire salinity gradient of the Elbe estuary from seasonal samplings in 2022. We applied a carbon and nitrogen SIA to five dominant zooplankton taxa in the Elbe estuary (see Fiedler 1991, Bernát et al. 1994, Eick and Thiel 2014), including the calanoid copepod *Eurytemora affinis*, two mysids (*Mesopodopsis slabberi* and *Neomysis integer*), the gammarid *Gammarus zaddachi*, as well as fish larvae of *Osmerus eperlanus*. As in many other temperate estuaries of the northern hemisphere (e.g. Martineau et al. 2004, Hoffman et al. 2008, David et al. 2016), *E. affinis* is the most abundant calanoid copepod in the Elbe estuary, accounting for over 90% of the mesozooplankton abundance throughout the seasons (Bernát et al. 1994) and thereby representing an important component of the planktonic food web (Kerner 2004). In addition to the ubiquitous suprabenthic gammarid *G. zaddachi*, the two sympatric mysids, *M. slabberi* and *N. integer*, contribute significantly to the total zooplankton biomass, dominating the brackish and freshwater sections of the Elbe estuary,

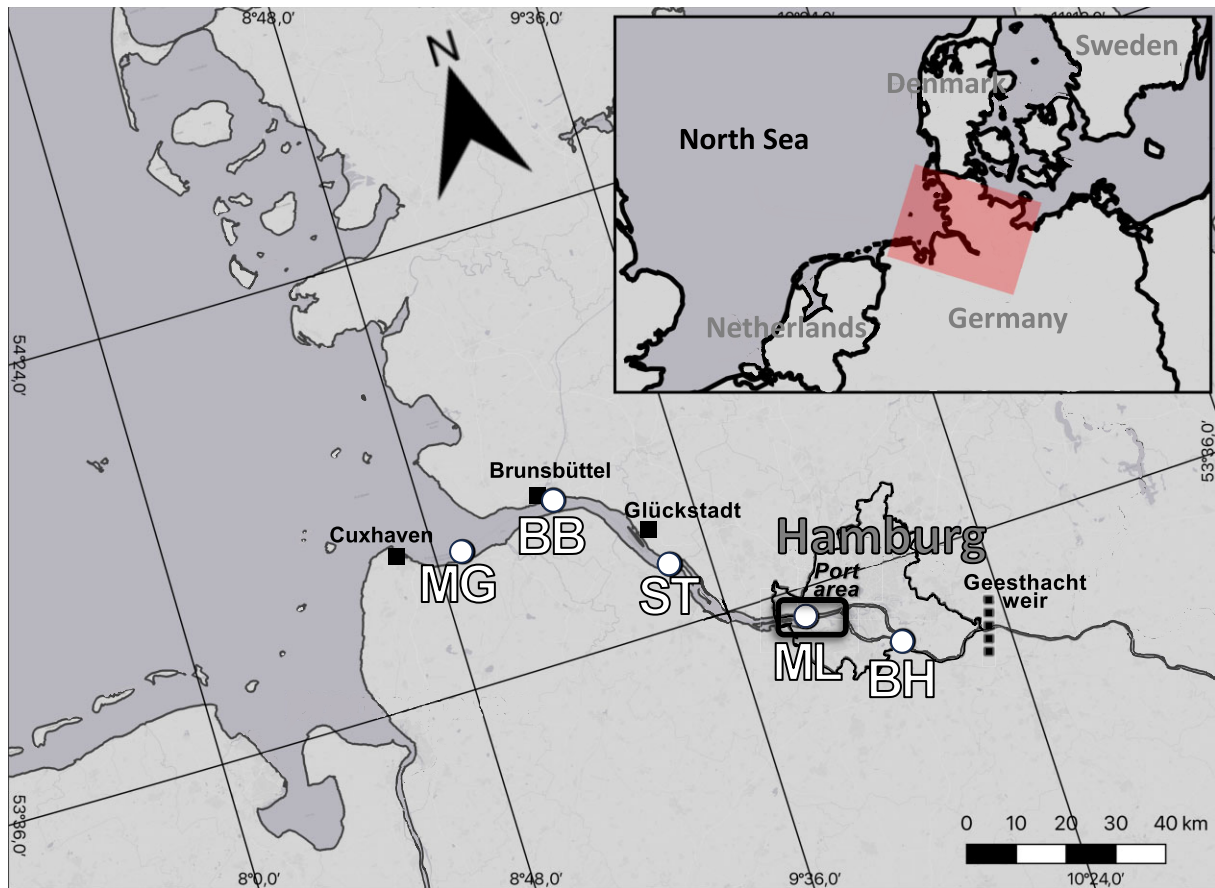


Figure 1. Map of the Elbe estuary showing the five sampling locations. Station names are abbreviated (see Table 1 for explanation). The weir at Geesthacht separates the estuary from the Elbe River. The background map has been provided by Esri, HERE, Garmin, © OpenStreetMap contributors, and the GIS User.

respectively (Fiedler 1991, Bernát et al. 1994). The fish assemblage consists of more than 95% of the species *O. eperlanus*, which uses the estuarine part of the Elbe River as an important nursery and feeding ground (Eick and Thiel 2014). We also collected bulk POM at each station and analysed its SI composition to compare it with potential organic matter sources and to determine its availability to the selected zooplankton taxa across both spatial and temporal scales. The objectives of this study were to (i) determine the isotopic signatures of the local POM and selected zooplankton species across spatio-temporal dimensions and to (ii) compare their $\delta^{13}\text{C}$ signatures with carbon baselines reported in the literature to assess the origin of their primary carbon source. In addition, the stable isotope approach enabled us to (iii) gain insights in the consumers' trophic positions and dietary niches.

Methods

Study area

The Elbe River is one of the major rivers in Europe, discharging through the Czech Republic and Germany into the German Bight in the North Sea. Its turbid estuary has a length of 142 km reaching from the weir at Geesthacht (Elbe-km 585, Fig. 1) to the river mouth at Cuxhaven (Elbe-km 727). The main channel has been heavily dredged multiple times since the beginning of the last century from a depth of 4 m (Kerner 2007) to ~20 m by 2021 [Hamburg Port Authority

(HPA) 2022] to enable access to the Port of Hamburg, the third largest port in Europe for overseas traffic, located 39 km downstream of the weir. The tidal range varies from 2 m at the weir to 3.5 m in the port area (HPA 2022). The water column is partially well-mixed (Pein et al. 2021) and characterized by a long residence time of 2–4 weeks depending on river discharge (Amann et al. 2012). It includes a prominent maximum turbidity zone (MTZ) that extends 30 km and is located around Glückstadt (Elbe-km 674) (Papenmeier et al. 2014).

Sample collection and processing

Sampling was performed during 1-day cruises with the research vessel *Ludwig Prandtl* in the main channel at five stations along the entire salinity gradient in winter (February), spring (May), summer (June), and autumn (November) 2022 (Table 1). Sampling was scheduled to the same appointed time in the tidal cycle each time, ensuring consistent conditions between the campaigns. Stations were situated in the freshwater area upstream in the non-dredged channel [Bunthäuser Spitze (BH) at Elbe-km 609], within the port area [Mühlenberger Loch (ML) at Elbe-km 633], within the MTZ [Schwarztonnensand (ST) at Elbe-km 665], in the oligohaline zone [Brunsbüttel (BB) at Elbe-km 692], and mesohaline zone in the river mouth [Medemgrund (MG) at Elbe-km 727] (Fig. 1). At each station, net samples were taken by single horizontal tows at 1 m water depth using plankton nets of 100 μm

Table 1. Overview of the sampling sites and tidal phases during sampling.

Station (Abbreviation)	Coordinates		Elbe-km	Mean salinity \pm SD	Tidal phase
	Latitude ($^{\circ}$ N)	Longitude ($^{\circ}$ E)			
Bunthäuser Spitze (BH)	53.45	10.07	609	0.4 \pm 0.1	Low tide
Mühlenberger Loch (ML)	53.55	9.82	633	0.4 \pm 0.1	High tide
Schwarztonnensand (ST)	53.71	9.47	665	0.7 \pm 0.2	High tide
Brunsbüttel (BB)	53.89	9.19	692	6.1 \pm 4.2	Low tide
Medemgrund (MG)	53.84	8.89	713	11.4 \pm 7.1	Low tide

Elbe-km: Stream kilometre.

(90 cm aperture, 3 m length) and 1000 μ m (0.94 m aperture, 2.8 m net length) mesh size. Mesozooplankton and macrozooplankton were defined as organisms with sizes between 100–1000 μ m and 1–20 cm, respectively. Water samples were collected at 1 m water depth with multiple bucket hauls and filtered through pre-combusted and pre-weighted glass fibre filters (0.7 μ m pore size, GF/F, Whatman, 450 $^{\circ}$ C). The filtered water volume was adjusted at each station based on the concentration of suspended organic material to adequately coat the filters with biomass. At each station, three filters were taken to measure either chlorophyll *a* (Chl *a*) concentrations, SPM, and the stable isotopic (SI) compositions of POM samples (one replicate each). For the POM filters, water samples were sieved through 100 μ m mesh to remove large planktonic organisms. Filters and planktonic organisms from each haul were transferred to plastic trays and immediately stored at -80° C on board until further sorting and processing in the lab.

Temperature and salinity data were measured at each sampling site using an on-board *in situ* FerryBox system (see Petersen et al. 2011 for further details). River discharge data were obtained from the closest gauge station located upstream of the tidal limit in Neu Darchau (Elbe-km 536). Daily discharge rates for the corresponding sampling date were used, which can be accessed through the Federal Waterways and Shipping Agency (Federal Waterways and Shipping Agency (WSV) 2023). We compared temperature and discharge rates to historical monthly averages over short (2018–2022; past 5 years) and long-term periods (30 years) from the data portal of the WSV to check for the representativeness of the data (see Table S1 for more details).

Zooplankton samples were defrosted on ice, sorted for dominant taxa by hand using ultra-fine tweezers under a stereomicroscope, and rinsed twice in ultrapure water for removal of adherent particles. Dominant mesozooplankton (*E. affinis*), macrozooplankton (*M. slabberi*, *N. integer*, *G. zaddachi*), and ichthyoplankton (*O. eperlanus*) taxa were analysed for SI composition. The individuals were sorted into separate plastic vials, freeze-dried at -80° C for 24 h, and ground to fine powder before being transferred to tin capsules. Individuals of *E. affinis* were placed as whole animals directly into tin capsules after lyophilization. For the analysis of elemental and SI composition, triplicates of at least three individuals each of macrozooplankton and fish larvae were used if sufficient specimens were collected. Since the biomass of *E. affinis* was insufficient for triplicate measurements, single samples were analysed instead by pooling of \sim 100 adult individuals of *E. affinis*, which were equally mixed by sex.

Chl *a* was extracted by adding 10 ml of 90% acetone to the filters, which were then stored in darkness at 5 $^{\circ}$ C for 24 h before centrifugation (3000 rpm, 4 $^{\circ}$ C, 15 min). The absorbance

of the extracts was measured at a wavelength between 630 and 750 nm using a PerkinElmer photometer (LAMBDA XLS, Waltham, USA; model number: L7110189), following the method described by Jeffrey and Humphrey (1975). Filters that were not used for Chl *a* measurements were freeze-dried at -80° C for 24 h. SPM content was determined by weighing the dry filters. For the measurement of elemental and stable isotope ratios of POM, aliquots were cut out of the filter. Parts of the subsamples were placed into tin capsules for analysis of δ^{15} N and C/N without prior treatment. The other aliquots were transferred to silver capsules and treated with HCL vapour for 2 h under vacuum to remove carbonates for a separate C_{org} and δ^{13} C analysis, as carbonates potentially cause a bias in the organic carbon measurements (Jacob et al. 2005).

Analysis of elemental and stable isotope ratios

Data on elemental and SI composition of planktonic organisms were compiled from three elemental analyser and isotope ratio mass spectrometer (IRMS) system (see Table S2 for more details). SIA were performed using an elemental analyser (Euro EA CHNSO, HEKAtech, Wegberg, Germany; Thermo/Carlo Erba NC 2500, Milan, Italy; PDZ Europa ANCA-GSL, Sercon Ltd, Cheshire, UK) interfaced to an IRMS system (IsoPrime 100, Elementar, Langenselbold, Germany; DeltaPlus Advantage, Thermo Fisher Scientific, Bremen, Germany; PDZ Europa 20-20, Sercon Ltd, Cheshire, UK). Isotope ratios of carbon (δ^{13} C) and nitrogen (δ^{15} N) were expressed as parts per thousand (‰) differences from a standard reference material:

$$\delta X = \left[\left(R_{\text{Sample}} / R_{\text{Standard}} \right) - 1 \right] \times 1000, \quad (1)$$

where $X = ^{13}\text{C}$ or ^{15}N and R is the corresponding ratio of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$. Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen were used as standard reference material. Helium was used as a carrier gas. CO_2 and N_2 were used as working standards and were calibrated against international reference materials of the International Atomic Energy Agency (see Table S2 for details).

Statistical analysis

Seasonal and spatial variability in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and C:N of POM, meso- and macrozooplankton, including ichthyoplankton, were identified using a non-parametric test, Kruskal–Wallis test, since isotope ratios were not normally distributed. Post-hoc multiple pairwise comparisons (Bonferroni corrected, Dunn's test; Dunn 1961) were applied when differences were significant. C:N ratios were calculated based on their molar ratios. The ratio of chlorophyll *a* to SPM concentration (Chl *a*/SPM ratio) was used as an index for the

Table 2. Environmental conditions during the sampling campaigns in the Elbe estuary.

Season	Station	Temperature (°C)	Salinity	Chl <i>a</i> (µg l ⁻¹)	SPM (mg l ⁻¹)	Discharge (m ³ s ⁻¹)
Winter	BH	5.1	0.3	7.6	23.4	1166
	ML	5.5	0.3	6.2	80.1	
	ST	5.8	0.4	10.7	70.8	
	BB	5.6	0.8	10.3	124.3	
	MG	5.6	2.7	12.0	164.3	
Spring	BH	19.6	0.4	132.2	62.6	345
	ML	18.8	0.4	18.8	134.0	
	ST	17.0	0.9	7.3	52.6	
	BB	16.5	4.7	4.4	28.2	
	MG	16.2	10.9	7.6	36.1	
Summer	BH	21.4	0.5	152.7	37.5	231
	ML	20.5	0.5	22.6	57.9	
	ST	19.3	0.7	17.8	253.6	
	BB	18.6	9.8	7.0	40.3	
	MG	18.0	20.0	10.9	30.6	
Autumn	BH	10.9	0.5	6.4	7.6	283
	ML	12.8	0.5	6.0	40.1	
	ST	12.7	0.8	12.3	130.7	
	BB	12.5	9.2	3.9	33.8	
	MG	12.4	12.0	5.0	48.2	

Data were obtained along the entire salinity gradient (freshwater: BH, ML, ST; oligohaline: BB, mesohaline: MG) in each season in 2022. Abbreviations: SPM—suspended particulate matter; Discharge—river discharge; Chl *a*—Chlorophyll *a* concentration.

phytoplankton availability that could potentially be consumed by the zooplankton (Irigoien and Castel 1995). Since it is difficult to separate phytoplankton from heterotrophic and detrital particulate matter, including ciliates, flagellates, and rotifers of similar size, POM was used as an indicator for a primary food source. $\delta^{15}\text{N}$ ratios of the planktonic organisms were used to calculate TLs, assuming POM as an isotopic baseline for $\text{TL} = 1$. Prior trophodynamic studies on estuarine zooplankton indicate that our target species are not true herbivores, but rather omnivores with a pronounced tendency towards carnivorous feeding behaviour (e.g. Martineau et al. 2004, David et al. 2016). Given that trophic fractionation of nitrogen isotopes is typically higher for carnivores and other consumers with high-protein, animal-based diets, ranging from 3.3 to 3.4 ‰, compared to true herbivores, which exhibit a trophic enrichment factor (TEF) of 2–2.5 ‰ (Vander Zanden and Rasmussen 2001, McCutchan et al. 2003), we applied a TEF of 3.4 ‰ for our TL calculations. TLs were calculated based on the $\delta^{15}\text{N}$ values of POM and the taxa from each station and season, according to the equation of Post (2002):

$$\text{TL} = 1 + (\delta^{15}\text{N}_{\text{zooplankton}} - \delta^{15}\text{N}_{\text{POM}}) / \text{TEF}. \quad (2)$$

The relationships between elemental and isotope ratios of the consumers and environmental variables were assessed using Spearman rank correlation analysis (see results in the supplementary materials, Table S3). The multivariate ellipse-based model SIBER [software version 2.1.9, Jackson et al. (2011)] was applied to check for the species-specific isotopic niches. The trophic niches were calculated globally, as a minimum of at least five individual data points of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ per taxon for each station and season are required to calculate either spatial or temporal niche space dynamics, which are not available in this study. Isotopic niche width (‰²) was calculated by the standard ellipse function SEA (including 40% of the data) for each taxon, which was corrected for small sample size using a correction mode (SEA_c). In addition, the overlap of isotopic niches was calculated by applying a Bayesian estimate of standard ellipses. The estimated Bayesian ellipses

were tested for differences between taxa by comparing the proportion of their posterior distributions in terms of magnitude, which provides a direct measurement of the probabilities. All statistical tests and visualizations were performed using R software, software version 4.3.2 (R Core Team 2023). An AI tool (ChatGPT, version GPT-4) was used to improve the writing style and readability of the final manuscript by identifying and correcting grammar and typographical errors.

Results

Environmental conditions

Temperatures at the examined stations ranged from 5.1°C in winter to 21.4°C in summer 2022 (Table 2), which falls within the range of averages recorded over the past 5 and 30 years (see supplementary material, Table S1). Salinity exhibited a gradual increase downstream, with the strongest gradient observed in summer and the weakest in winter. In spring and summer, strong phytoplankton blooms occurred exclusively at the uppermost freshwater station BH (132.2 and 152.7 µg l⁻¹, respectively), followed by a sharp decline in Chl *a* concentrations downstream from the harbour area. Chl *a* concentrations were positively correlated with temperatures (Spearman, $n = 20$, $r_s = 0.53$, $P = .02$, Table S3) and remained low at all stations during autumn and winter (maximal up to 12.3 µg l⁻¹). At station BH, generally low SPM concentrations were observed, which increased in the downstream direction, reaching high values at station ST (up to 253.6 mg l⁻¹ in summer). In winter, SPM concentrations peaked at the river mouth (station MG), when river discharge was highest. The discharge rates followed the typical seasonal patterns reported for the Elbe estuary (see Table S1), reaching their lowest values in summer.

Spatial and temporal variation in quantity, quality, and origin of POM sources

The Chl *a*/SPM ratios were highest at the uppermost freshwater station (station BH) throughout the year with the largest

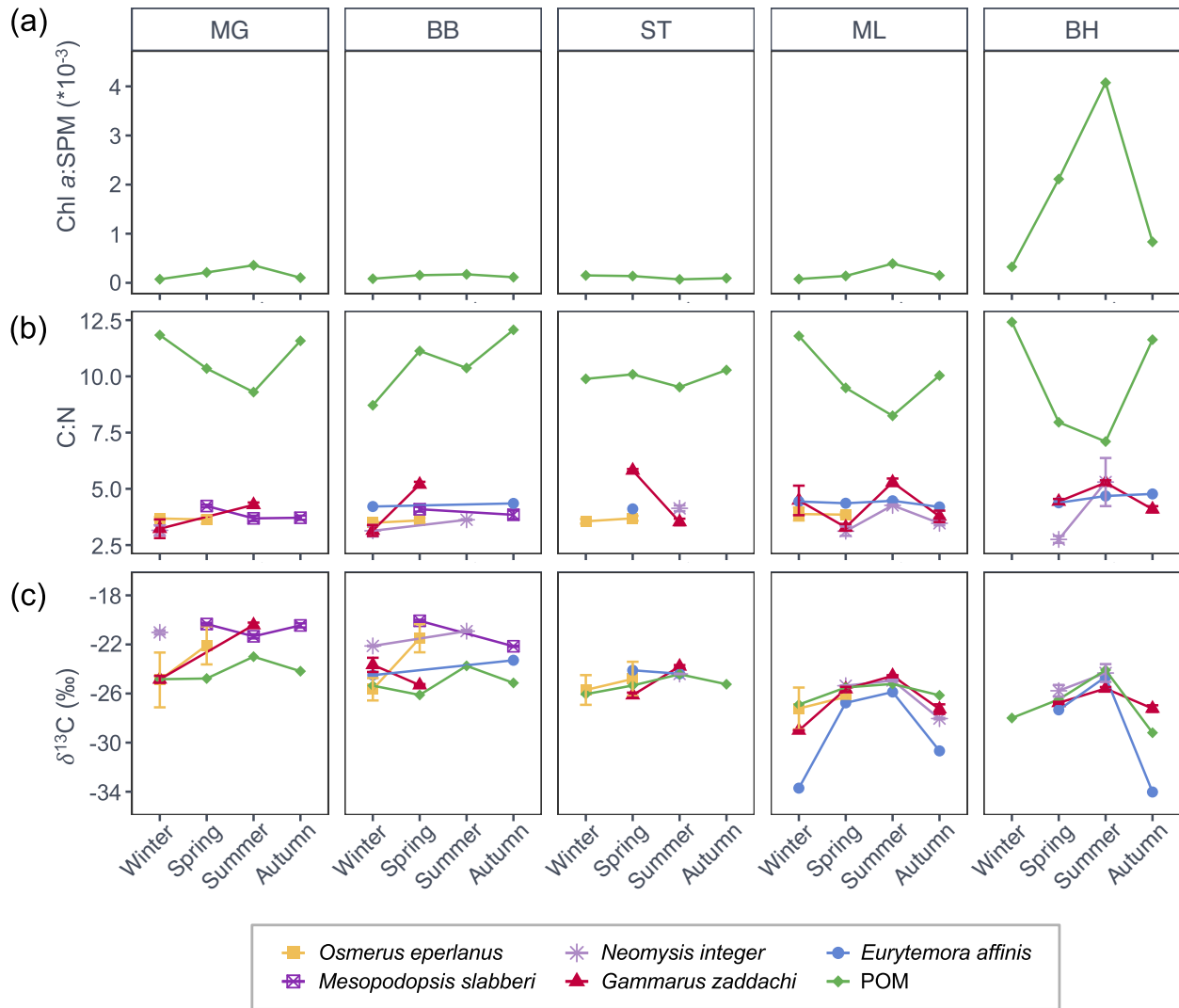


Figure 2. Seasonal and spatial changes in primary production processes and the origin of the carbon source at five stations along the entire salinity gradient (freshwater: BH, ML, ST; oligohaline: BB; mesohaline: MG) of the Elbe estuary in 2022. Mean values (\pm SD) are given when triplicate samples were measured. (a) Variations in the ratio of chlorophyll a to suspended particulate matter concentration. (b) C:N ratio and (c) $\delta^{13}\text{C}$ values of POM and the zooplankton taxa.

ratio in summer (up to 4.1×10^{-3}) (Fig. 2a) caused by low SPM concentrations (Spearman, $n = 20$, $r_s = -0.65$, $P < .01$, Table S3). Low Chl *a*/SPM ratios were consistently observed at stations ST and BB during all seasons, where SPM levels were high. C:N ratios of POM decreased significantly with increasing Chl *a* concentrations (Spearman, $n = 20$, Chl *a*: $r_s = -0.72$, $P < .001$, Table S3). Generally, C:N ratios of POM were significantly lower in summer compared to winter and autumn (KW test, Table S4) and correlated negatively with rising temperatures (Spearman, temperature: $n = 20$, $r_s = -0.72$, $P < .001$, Table S3), with a slight increasing trend seawards (e.g. from 7.1 at the uppermost station BH to 10.4 at the oligohaline station BB in summer) (Fig. 2b). At station ST, C:N ratios remained stable and high throughout the year. Similarly, $\delta^{13}\text{C}$ values of POM exhibited an increasing trend downstream (Fig. 2c), with seasonal means ranging between -26.9 ± 2.2 ‰ at the uppermost freshwater station (station BH) and -24.2 ± 0.9 ‰ at the river mouth (station

MG) (supplementary material, Table S5). Salinity and river discharge were both positively and negatively correlated with $\delta^{13}\text{C}$ values of POM, respectively (Spearman, $n = 20$; salinity: $r_s = 0.75$, $P < .001$; river discharge: $r_s = -0.60$, $P < .01$, Table S3). Moreover, in summer POM was significantly enriched in $\delta^{13}\text{C}$ compared to POM collected in winter (from -26.2 ± 1.3 to -24.1 ± 0.8 ‰, Table S5; KW test, $P < .05$, Table S4). There was no significant difference in the $\delta^{15}\text{N}$ values of POM on the spatial and temporal scale (KW test, station: $P = .9$, season: $P = .23$, Table S4, Fig. 3a).

Trophic transfer of carbon sources and SI composition of consumers

$\delta^{13}\text{C}$ values of the zooplankton displayed more variations than the POM (Fig. 2c). The planktonic consumers were generally enriched in $\delta^{13}\text{C}$ in spring and summer compared to winter and autumn (KW test, Table S4), with this pattern

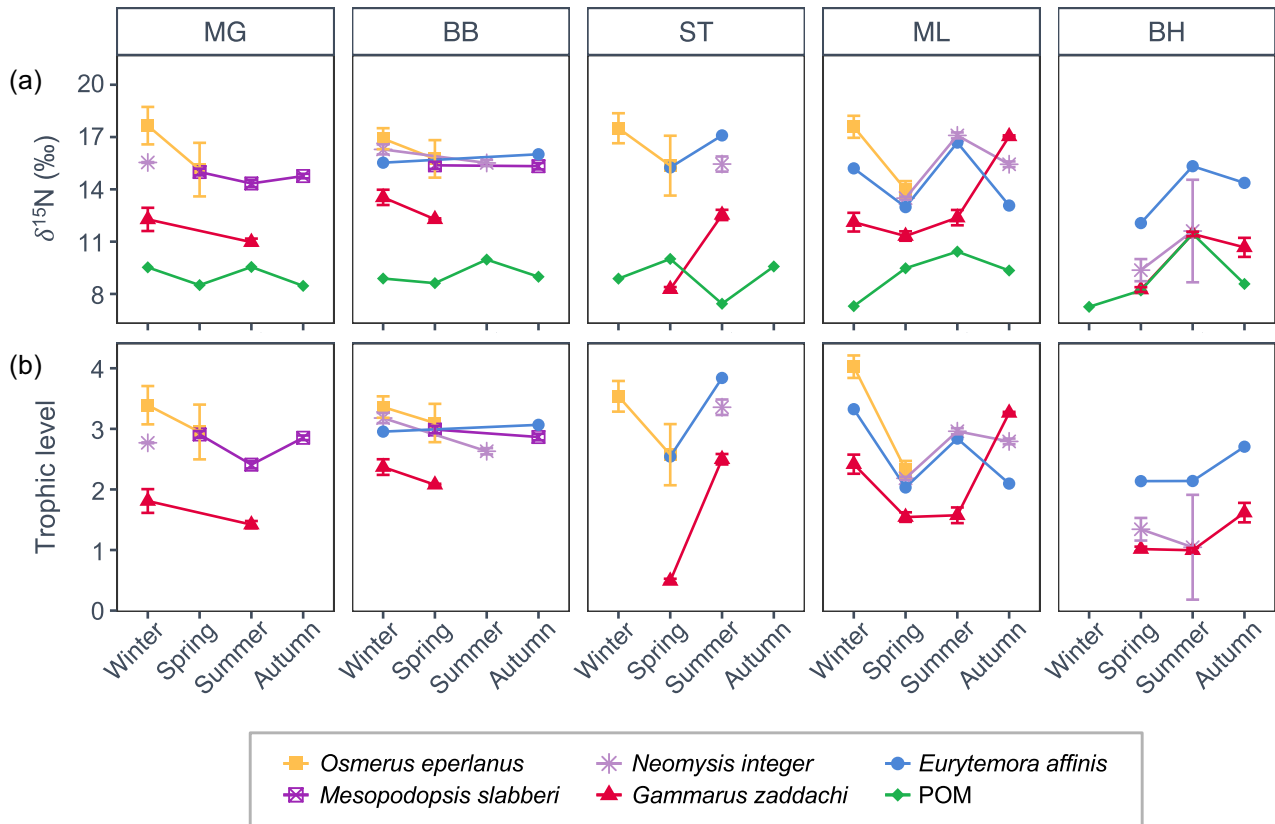


Figure 3. Seasonal and spatial variability in (a) $\delta^{15}\text{N}$ values and (b) TLs of the zooplankton taxa and POM collected at five stations along the entire salinity gradient (freshwater: BH, ML, ST; oligohaline: BB, mesohaline: MG) of the Elbe estuary in 2022. POM is not depicted in the lower plot (b) since it was set as a baseline (TL = 1) for all seasons and stations. Mean values (\pm SD) are given when triplicate samples were measured.

being more pronounced in the freshwater section of the estuary. Most of the taxa collected at the freshwater station ML or BH had significantly more depleted and uniform $\delta^{13}\text{C}$ values compared to individuals from the river mouth (station MG and BB) (KW test, Table S4), where ^{13}C -signatures were more disparate. *Mesopodopsis slabberi*, which was only found at stations BB and MG, was most enriched and showed the least variation in $\delta^{13}\text{C}$. *Eurytemora affinis*, however, showed neither significant spatial nor seasonal variability in its elemental and SI composition (KW test, Table S4), but had the lowest $\delta^{13}\text{C}$ values (up to -34.0 ‰ at station BH), especially in winter and autumn (Fig. 2c). The other taxa, *M. slabberi*, *N. integer*, *G. zaddachi*, and *O. eperlanus*, had TLs and $\delta^{15}\text{N}$ values that were lower in spring or summer compared to winter and autumn (KW test, Table S4). Their $\delta^{15}\text{N}$ values and TLs showed an increasing trend seawards from station BH to BB (Fig. 3, Table S5). In general, *G. zaddachi* exhibited significantly lower TLs and $\delta^{15}\text{N}$ values compared to the other zooplankton species, which did not show major differences in their $\delta^{15}\text{N}$ values or trophic positions (KW test, Table S4). However, in contrast to the other taxa, *O. eperlanus* at station ML displayed a trend of slightly higher TLs and $\delta^{15}\text{N}$ values in winter, which became less distinct downstream (Fig. 3). In addition, the consumers' TLs correlated globally negatively with Chl *a*/SPM ratio (Spearman, $n = 211$, $r_s = -0.22$, $P < .01$). The mean C:N ratios of the planktonic consumers, except for *E. affinis*, were significantly higher in summer and/or spring

compared to winter and autumn (KW, Table S4). The taxa did not exhibit a clear spatial pattern in their C:N ratios (Tables S4 and S5).

SI niches of the zooplankton

Species-specific SI niches, based on averaged seasonal and spatial data using the standard ellipse for small sample size (SEA_c), showed a high degree of overlap ranging from 17.7% to 31.7% between *E. affinis*, *N. integer*, and *O. eperlanus* (Fig. 4a, Table 3). *Mesopodopsis slabberi* exhibited a smaller and less variable isotopic niche, which did not overlap with those of the other taxa. *Gammarus zaddachi* shared only one small overlap with the isotopic niche of *N. integer* (overlap 5.0 ‰², 17.7%, Table 3) and clustered at the bottom along the $\delta^{15}\text{N}$ axis. Species-specific estimated niche widths (SEA_b) ranged from the smallest niche of 1.2 ‰² for *M. slabberi* to the widest niche of 19.8 ‰² for *E. affinis* (Fig. 4b). The width of SEA_b of *G. zaddachi*, *E. affinis*, and *N. integer* were similar in their mean values.

Discussion

Knowledge of zooplankton trophic interactions and carbon sources is incomplete for the intensively dredged, eutrophic Elbe estuary, which hampers understanding of food web structure and function. This study provides a better spatially and seasonally resolved view of the trophodynamics of the most

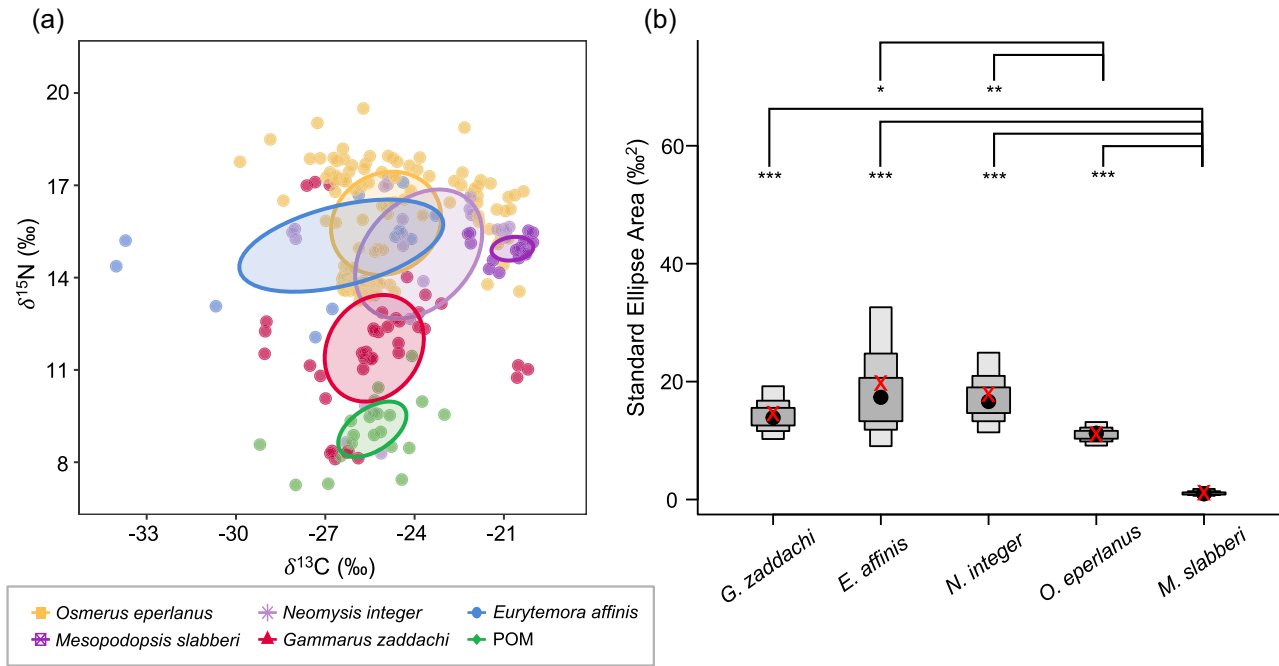


Figure 4. Results of the overall niche space dynamics of the five dominant planktonic consumers and POM sampled in the Elbe estuary in 2022. (a) Stable isotope biplot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the taxa and POM, including species-specific, small-size-corrected standard ellipse areas (SEA_c) (including 40% of the data per species). (b) Density box plots of estimated Bayesian standard ellipse area (SEA_b) for the respective planktonic consumers, which indicate 50%, 75%, and 95% credible intervals for mean estimations. Black dots depict the mean values of SEA_b , whereas the red cross represents the maximum likelihood estimate of SEA_c . The brackets above the density box indicate the probability that the posterior distribution of the SEA_b differs in magnitude between taxa (* $P < .05$; ** $P < .01$; *** $P < .001$).

Table 3. Results of the SIBER analysis, including $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the planktonic consumers collected in the Elbe estuary in 2022.

Species	<i>n</i>	TA ($\%e^2$)	SEA ($\%e^2$)	SEA_c ($\%e^2$)	Credible intervals			SEA_c overlap	
					50%	95%	99%	($\%e^2$)	(%)
<i>Eurytemora affinis</i>	11	28.6	17.8	19.8	14.0–21.4	8.5–32.5	6.0–40.7	<i>G. zaddachi</i> : 0 <i>N. integer</i> : 6.2 <i>O. eperlanus</i> : 7.4 <i>M. slabberi</i> : 0	<i>G. zaddachi</i> : 0 <i>N. integer</i> : 19.2 <i>O. eperlanus</i> : 30.8 <i>M. slabberi</i> : 0
<i>Mesopodopsis slabberi</i>	15	2.0	1.1	1.2	0.9–1.2	0.6–1.8	0.5–2.2	<i>G. zaddachi</i> : 0 <i>E. affinis</i> : 0 <i>N. integer</i> : 0 <i>O. eperlanus</i> : 0	<i>G. zaddachi</i> : 0 <i>E. affinis</i> : 0 <i>N. integer</i> : 0 <i>O. eperlanus</i> : 0
<i>Neomysis integer</i>	27	37.7	17.2	17.9	14.7–19.2	11.1–24.9	9.6–28.8	<i>G. zaddachi</i> : 5.0 <i>E. affinis</i> : 6.2 <i>O. eperlanus</i> : 7.1 <i>M. slabberi</i> : 0	<i>G. zaddachi</i> : 17.7 <i>E. affinis</i> : 19.2 <i>O. eperlanus</i> : 31.7 <i>M. slabberi</i> : 0
<i>Gammarus zaddachi</i>	39	43.4	14.2	14.6	12.4–15.4	10.2–19.2	9.0–21.3	<i>E. affinis</i> : 0 <i>N. integer</i> : 5.0 <i>O. eperlanus</i> : 0 <i>M. slabberi</i> : 0	<i>E. affinis</i> : 0 <i>N. integer</i> : 17.7 <i>O. eperlanus</i> : 0 <i>M. slabberi</i> : 0
<i>Osmerus eperlanus</i>	119	42.6	11.0	11.1	10.3–11.6	9.1–13.1	8.6–14.0	<i>G. zaddachi</i> : 0 <i>E. affinis</i> : 7.4 <i>N. integer</i> : 7.1 <i>M. slabberi</i> : 0	<i>G. zaddachi</i> : 0 <i>E. affinis</i> : 30.8 <i>N. integer</i> : 31.7 <i>M. slabberi</i> : 0

Sample size (*n*), total area (TA), standard ellipse area without (SEA) and with correction of small sample size (SEA_c) and the relative area of SEA_c overlap (in $\%e^2$ and %) between respective zooplankton species and the credible intervals of the estimated Bayesian standard ellipse area (SEA_b).

abundant meso- and macrozooplankton taxa along the salinity gradient of the Elbe estuary based on carbon and nitrogen SIA of dominant zooplankton taxa and of some potential food sources. Our focus is particularly on the spatio-temporal

patterns of POM in terms of food availability (quantity and quality) and origin, as well as trophic segregation and shifts in carbon source utilization among the dominant zooplankton taxa.

The fate and sources of POM

Our results showed substantial seasonal and spatial variations in Chl *a* concentrations, Chl *a*/SPM ratios, C:N ratios, and $\delta^{13}\text{C}$ of POM. We found high Chl *a* concentrations exclusively at the uppermost freshwater station BH in spring and summer. When passing the Hamburg Harbour, a strong decline in phytoplankton biomass occurred with low Chl *a* concentrations at the downstream stations, which corresponds to the results of earlier studies in the Elbe estuary (e.g. Wolfstein and Kies 1995, Kamjunke et al. 2023). This rapid drop in phytoplankton biomass downstream of the port area has been attributed to light limitation, resulting from a high load of SPM that is accumulated and resuspended in the dredged section of the Elbe estuary due to the sudden change in the bathymetry and a respective decrease in flow velocity (Kerner 2007, Geerts et al. 2017). We found rising SPM concentrations along the dredged area of the estuary (from station ML to MG), with levels peaking at station ST. In February 2022, the MTZ shifted seawards as the SPM peak moved closer to the mouth of the estuary, likely due to the increase in river discharge rates in winter, as also suggested by Papenmeier et al. (2014). They reported for the area around Glückstadt, which is close to station ST in our study, a similar spatio-temporal pattern in the MTZ characteristics that align with our results, with high SPM concentrations (above 150 mg l^{-1}) observed under low discharge conditions (below $400\text{ m}^3\text{ s}^{-1}$). In contrast, the shallow tidal freshwater region upstream of the Hamburg Harbour is characterized by low turbidity and reduced water turnover throughout the annual cycle (Wolfstein and Kies 1995). This can favour intense phytoplankton blooms (Turner et al. 2022) and might explain the high Chl *a* concentrations observed exclusively at station BH during warm periods. The Chl *a*/SPM ratio, as a proxy for phytoplankton availability (Irigoien and Castel 1995), correlated negatively with the SPM concentrations and thus may account for the high ratios exclusively detected at station BH. High loads of SPM may not only have impacted the available light but also led to a loss of phytoplankton due to enhanced sedimentation of plankton aggregates as a result of their stickiness. Phytoplankton produce sticky exudates during bloom conditions that increase their adhesion to other particles (Alldredge and Silver 1988). Steidle and Vennell (2024) hypothesized that the previously reported decline in Chl *a* concentration in the Hamburg Harbour may be attributed to phytoplankton adhesion to negatively buoyant suspended particles, which subsequently sink to light-limited water layers. Consequently, high loads of SPM in the Elbe estuary can lead to distinct losses of primary producers as potential food sources for planktonic consumers, particularly in the dredged sections downstream from the port area, and can be subjected to pronounced seasonal variations depending on river discharge rates.

C:N ratios give an indication of the quality of the organic matter sources, with values below 8 indicating fresh and high-quality POM and values above 8 representing detrital material, as algal detritus has increased C:N ratios due to diagenesis (Thornton and McManus 1994, Sterner and Elser 2003, Finlay and Kendall 2007). Indeed, high Chl *a* concentrations in spring and summer coincided with a decline in C:N ratios below 8 for POM at station BH, indicating a higher contribution of high-quality POM in the upstream section of the estuary during these seasons. The negative correlation between C:N ratio and Chl *a* concentration in the present study aligns with the seasonal patterns observed in other river systems (e.g.

Rhone River, Harmelin-Vivien et al. 2010). When passing the port area, the C:N ratio of POM still showed a similar trend of decreasing values during spring and summer, but was distinctly enriched with values above 8, indicating a change in the organic matter composition to more detrital material and less fresh phytoplankton carbon sources. In the zone of maximum turbidity (station ST), we even observed poor POM quality year-round, as indicated by persistently high C:N ratios. These findings are in line with the spatio-temporal pattern in organic matter processing and degradation that has been reported for resuspended (Spieckermann et al. 2021) and POM (Dähnke et al. 2022, Kamjunke et al. 2023) in the Elbe estuary. We hypothesize that the absence of high-quality food from the Hamburg Harbour seawards could be related to a shift from an autotrophic system at station BH towards a heterotrophic system along the dredged sections of the estuary. This shift is likely caused by light-limiting conditions and enhanced microbial processing, as associated with the high SPM load and reduced flow velocities (Kerner 2007, Geerts et al. 2017).

The local bulk POM in the Elbe estuary consisted of a mixture of multiple carbon sources, including riverine planktonic and terrigenous organic matter, as well as marine algal input, as indicated by intermediate $\delta^{13}\text{C}$ values ranging from $-26.9 \pm 2.2\text{ ‰}$ (station BH) to $-24.2 \pm 0.9\text{ ‰}$ (at station MG), which is consistent with the SI composition of POM reported for other European [e.g. Scheldt, Gironde, Ems (Middelburg and Herman 2007)] and North American estuaries like San Francisco (Cloern et al. 2002) and St. Lawrence (Martineau et al. 2004). The most seaward station (MG) was mesohaline and therefore does not represent a SI signal of true marine material, which is generally difficult to obtain in estuaries (Middelburg and Herman 2007). Still, we observed a trend of ^{13}C -enrichment downstream, suggesting an inflow of marine organic matter that was probably diluted upstream by tidal mixing processes. The ^{13}C -signal of POM from the freshwater section is close to the carbon baseline for terrestrial C3-plants and also falls within the $\delta^{13}\text{C}$ range for riverine phytoplankton (Boutton 1991, Maksymowska et al. 2000, Finlay and Kendall 2007). While the low C:N ratios at station BH (e.g. values below 8 in spring and summer) and $\delta^{13}\text{C}$ values ranging between -29.2 to -24.1 ‰ suggest the input of fresh algal material from the upstream freshwater section, the $\delta^{15}\text{N}$ signal of POM at all stations (7.1 – 12.4 ‰) implies a pronounced contribution of terrestrial organic matter to the local POM (Maksymowska et al. 2000, Finlay and Kendall 2007). This is further supported by the significantly higher C:N ratios in winter and autumn, which are markedly greater than the typical ratio for fresh phytoplankton and more closely align with allochthonous material, such as terrestrial material and soil organic matter, that underwent diagenesis (Thornton and McManus 1994, Finlay and Kendall 2007). In addition, in winter, POM exhibited significantly lower $\delta^{13}\text{C}$ values compared to summer. The seasonal dynamics of the Elbe River discharge are typically characterized by elevated flow rates between January and March (see Table S1), which mostly result from high areal precipitation (Bartl et al. 2009). We therefore assume that high river discharge rates during the winter sampling (i.e. in February) likely transported an increased amount of terrestrial material into the main channel of the estuary, resulting in a predominance of ^{13}C -depleted terrigenous organic matter in the POM. In addition, $\delta^{13}\text{C}$ values of POM are substantially influenced by species composition (Cloern et al. 2002,

Finlay and Kendall 2007), and seasonal changes in the phytoplankton community structure are well known for the Elbe estuary (Martens et al. 2024a,b). In particular, for the year 2022, Martens et al. (2024a) observed a transition from the predominance of diatoms in summer to mixotrophic flagellates in winter in the Elbe estuary as a result of unfavourable light conditions. Since flagellates are more ^{13}C -depleted than diatoms (Gearing et al. 1984), a shift in the phytoplankton community towards a higher contribution of flagellates in the POM could have also led to depleted $\delta^{13}\text{C}$ values observed during winter and autumn. In contrast, POM showed neither spatial nor temporal patterns in the $\delta^{15}\text{N}$, which is in line with findings from Middelburg and Herman (2007) across multiple European estuaries. As in our study, the authors explained the consistent $\delta^{15}\text{N}$ values by a rapid nitrogen turnover driven by intense microbial activity paired with continuous lateral inputs from adjacent marshlands. Nevertheless, other components like respiration, photosynthetic rates as well as the dissolved inorganic carbon and nitrogen pool also influence the isotopic composition of aquatic primary producers (Finlay and Kendall 2007), which were not assessed in this study.

Zooplankton diet and trophic segregation

The $\delta^{13}\text{C}$ values of the examined consumers in our study exhibited high variability, ranging from -34 to -20 ‰, which was consistent with stable isotope studies from estuaries of the northern hemisphere (Martineau et al. 2004, Hoffman et al. 2008, Modéran et al. 2012, David et al. 2016). Overall, the zooplankton species followed the general seasonal and spatial isotopic pattern of POM, which showed an enrichment of $\delta^{13}\text{C}$ during seasons of high primary production and downstream towards the river mouth. All consumers had a wider range of $\delta^{13}\text{C}$ values compared to POM, indicating that the selected taxa did not directly consume POM as a whole, but were likely feeding on selective components that exhibited more seasonal and spatial differences in isotopic fractionation compared to bulk POM (Bouillon et al. 2000). The discrepancy between the carbon isotopic composition of POM and the taxa appears to shift along the estuarine gradient, as organisms collected from upstream sites had more similar $\delta^{13}\text{C}$ signatures than taxa sampled in the river mouth. Tidal mixing processes could have led to a larger variety of carbon sources (e.g. riverine and marine phytoplankton, resuspended benthic algae) at stations BB and MG, allowing taxa to exploit a more diverse range of organic matter sources. However, assigning these components to certain primary carbon sources is difficult due to processes such as microbial diagenesis of organic matter or species-specific isotopic fractionation, which hamper the precise identification of the consumers' diet. Compound-specific SIA or a combined biomarker approach using fatty acids would help in determining the origin of carbon sources in the consumers' diet when multiple sources are available and their isotopic signals may overlap (Cloern et al. 2002, Finlay and Kendall 2007).

The exploitation of distinct components of POM by the selected taxa is also reflected in the position and compactness of their isotopic niches. Most of the taxa showed an opportunistic feeding strategy, as reflected by their broad isotopic niche width. For *E. affinis*, *M. slabberi*, and *N. integer*, the nitrogen isotopic signatures did not differ significantly among taxa, indicating that they largely shared food sources derived

from the same trophic position, although mysids, particularly *N. integer*, are known to preferentially prey on *E. affinis* in estuarine systems (Modéran et al. 2012, David et al. 2016). Differences in the $\delta^{15}\text{N}$ values between the consumers and POM were clearly higher, or in the case of *G. zaddachi*, lower than the typical TEF of 3.4 ‰ (Vander Zanden and Rasmussen 2001). These results highlight that the consumers are highly selective feeders, likely relying on only a minor fraction of the local bulk POM, while fulfilling most of their carbon requirements from similar heterotrophic sources. Omnivorous feeding is widely documented in estuarine systems (e.g. Hughes et al. 2000, Martineau et al. 2004, David et al. 2006, Hoffman et al. 2008, Modéran et al. 2012, Hitchcock et al. 2016). Suspended organic matter, in particular detrital matter, is often populated by bacteria, protozoans and small metazoans, which can be passively ingested by grazers feeding on these aggregates (Stoecker and Capuzzo 1990) or actively preyed upon, as noted for e.g. *E. affinis* (Tackx et al. 2003, Cabrol et al. 2015). Feeding on heterotrophic sources is accompanied by a rise in the consumers' $\delta^{15}\text{N}$ values, leading to an increase in food chain lengths (Lerner et al. 2022). In addition, organic matter sources of terrigenous origin are often characterized by a $\delta^{15}\text{N}$ signature that is enriched relative to autochthonous sources (Maksymowska et al. 2000, Cloern et al. 2002, Finlay and Kendall 2007). Grazing on detrital, terrigenous sources could therefore also explain the high $\delta^{15}\text{N}$ values of the zooplankton taxa. The inflow of allochthonous organic matter in the local POM has been documented as important carbon supply utilized by estuarine zooplankton when autochthonous sources are scarce, e.g. in winter under low-light conditions (e.g. Hoffman et al. 2008, Hitchcock et al. 2016). In fact, we observed a rise in the consumers' $\delta^{15}\text{N}$ values and TLs seawards, as well as during winter and autumn, when the carbon dynamics in the Elbe estuary shifted to a predominantly heterotrophic system due to limiting primary production. Feeding on heterotrophic sources results in lower C: N ratios for the consumers (Elser et al. 2000) as presented by the seasonal trends in the C: N ratios of consumers in this study. However, we cannot exclude the possibility that the seasonal changes in the C: N ratio may be derived from shifts in the lipid content, as lower lipid content in organisms is usually related to lower C: N ratios (Sterner and Elser 2003).

Among the species, *E. affinis* exhibited the most depleted $\delta^{13}\text{C}$ values, especially in winter and autumn. During periods of limited primary production or low food quality, *E. affinis* may have selectively consumed ^{13}C -depleted constituents of the POM, either from autochthonous algae or terrestrial origin, and heterotrophic sources as indicated by the enriched $\delta^{15}\text{N}$ signature, resulting in a broad isotopic niche width. The copepod probably preferentially consumed an increasing amount of autochthonous organic matter in the POM under phytoplankton blooming conditions in spring and summer, as indicated by their slightly enriched $\delta^{13}\text{C}$ values. The ability of *E. affinis* to select its prey among suspended inorganic particles and to feed on detrital organic sources (Tackx et al. 2003, Cabrol et al. 2015) to cover its nutritional requirements is in line with the results of Kerner (2004) for the Elbe estuary and has also been reported for other estuaries (Martineau et al. 2004, David et al. 2006, 2016, Hoffman et al. 2008, Modéran et al. 2012).

In contrast to this, *M. slabberi* displayed $\delta^{13}\text{C}$ values ranging from -22.2 to -20.0 ‰, generally up to 4 ‰ more ^{13}C -enriched than those of the POM, exhibiting a narrow

and unique dietary niche, which did not overlap with other taxa. The carbon isotopic signature of marine phytoplankton closely matched those of *M. slabberi*, suggesting that the mysid relied partly on marine algae to fulfil its carbon requirements. This might be further supported by their exclusive occurrence in the mouth of the estuary. In winter, this species was absent, as it only migrates into the inner part of estuaries for reproduction and growth in spring (Hamerlynck and Mees 1991). Nevertheless, we cannot definitively exclude microphytobenthos as a potential food source, which falls within the range of $\delta^{13}\text{C}$ range for *M. slabberi*, as it can constitute a considerable proportion of the total pelagic POM through resuspension from tidal flats (De Jonge and Van Beusekom 1992). The tendency of *M. slabberi* to graze preferentially on a ^{13}C -enriched marine diet is in agreement with previous studies (e.g. Modéran et al. 2012, David et al. 2016). Food-niche partitioning allows *M. slabberi* to reduce food competition and to co-exist with the sympatric mysid *N. integer*, which fed on ^{13}C -depleted components, similar to *E. affinis*. The exploitation of distinct carbon sources among sympatric mysids has also been noted by Winkler et al. (2007) for the taxa *Mysis stenolepis* and *Neomysis americana* in the St. Lawrence estuary.

Gammarus zaddachi exhibited clearly lower $\delta^{15}\text{N}$ values than the other consumers, indicating a preference for a primarily herbivorous diet, which is in line with previous studies (Korpinen et al. 2006). Their $\delta^{13}\text{C}$ values suggest a carbon source based on autochthonous riverine or detrital, terrestrial organic matter that have been noted for sister species (e.g. *Gammarus tigrinus*) in other estuaries (Hughes et al. 2000, Hoffman et al. 2008). For *O. eperlanus*, our findings suggest an omnivorous to carnivorous feeding behaviour. In winter, the fish larvae exhibited slightly elevated $\delta^{15}\text{N}$ values, approximately one TL higher than the other taxa. This pattern was most pronounced at station ML, which is located near a freshwater tidal flat that is recognized as an important area for the reproduction and retention of planktonic organisms (Fiedler 1991, Peitsch et al. 2000) and fish, such as *O. eperlanus* (Eick and Thiel 2014). In this region, Thiel et al. (1996) analysed the stomach contents of early life stages of *O. eperlanus* and identified *E. affinis* and *N. integer* as the main prey items, which were most abundant in the digestive tract of the fish larvae. In our study, the elevated $\delta^{15}\text{N}$ values and TLs of *O. eperlanus* in late winter can likely be attributed to the high densities of copepods and mysids documented for this area near station ML (Fiedler 1991, Peitsch et al. 2000), which may have served as preferred food sources for the fish larvae. This feeding pattern might also be reflected in the large overlap in the $\delta^{13}\text{C}$ values between *O. eperlanus* and both potential prey items, i.e. *E. affinis* and *N. integer*, which should not differ strongly if fish larvae preyed on them to any extent. In spring and at the stations downstream, we found that *O. eperlanus* exhibited lower TLs and $\delta^{15}\text{N}$ values, close to those of the other zooplankton taxa (i.e. *E. affinis* and the mysids). This pattern may result from the limited availability of these potential prey items and could suggest that *O. eperlanus* preyed on similar food as *E. affinis* and *N. integer*. This dietary shift corresponds to the findings by Thiel et al. (1996), who observed that larvae of *O. eperlanus* transitioned to alternative prey items during the same period, which was linked to a decline in the *E. affinis* population resulting from high predation pressure. Additionally, the enriched $\delta^{15}\text{N}$ values of *O. eperlanus* during the winter sampling could also be related to the fact that the fish

larvae were only a few weeks old and likely fed from the yolk sac, indicating the isotopic signature of the adults, which the fish can retain for several weeks due to long tissue turnover rates (Vander Zanden et al. 2015).

In summary, selective feeding might be an important strategy for the zooplankton in the Elbe estuary to optimize the use of available carbon sources to avoid competition and to survive stressful periods (i.e. winter and autumn) when food quality and availability (i.e. at the MTZ) are low. When primary carbon sources were limited, a switch to alternative food sources, like protozoans and small metazoans, was likely performed. Mixotrophic pathways have also been reported for phytoplankton taxa in the Elbe estuary, especially for taxa in the MTZ or during winter (Martens et al. 2024a). The ability to feed opportunistically and use alternative sources of material is a crucial aspect of the trophic plasticity of planktonic consumers, helping to stabilize and maintain food web structures (e.g. David et al. 2006, Hoffman et al. 2008, Modéran et al. 2012, Hitchcock et al. 2016, Lerner et al. 2022). This adaptability likely plays a central role for zooplankton in the Elbe estuary to cope with the environmental forces and to avoid competition.

Conclusion

Our results highlighted that temporal and spatial variations in the quality and quantity of food for zooplankton in the Elbe estuary are influenced by primary production processes and the amount of SPM in the water column resuspended by strong tidal mixing processes. Autochthonous algal material was mainly produced in the non-dredged freshwater area of the Elbe estuary upstream of Hamburg Harbour, which probably was subject to intense heterotrophic decomposition downstream of the port area. The SI signatures of POM indicate a mixture of coastal and riverine-derived organic matter in the carbon source, which was predominated by the input of terrigenous matter from adjacent marshlands, especially during periods of high river discharge. High suspended matter loads and low availability of high-quality phytoplankton impacted the trophodynamics both temporally and spatially, reflected by a considerable increase in $\delta^{15}\text{N}$ and, consequently, also an increase in TLs of the consumers. The investigated planktonic organisms were generally able to cope with strong variations in food quality and quantity due to opportunistic feeding behaviour. Selective feeding, portioning of dietary niches, and switching from herbivorous to omnivorous nutrition allow species to co-exist and to optimize the use of allochthonous and autochthonous organic material. This trophic plasticity of the zooplankton may thus be an essential feature to withstand alterations in the hydrology of the Elbe estuary related to human disturbances (i.e. variations in turbidity and flow velocity) and natural estuarine gradients. This study helps to understand the impact of increasing human pressures on estuaries by providing a powerful tool for ecosystem-based management and conservation.

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Author contributions

Johanna Biederbick (Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing), Christian Möllmann (Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing), Elena Hauten (Investigation, Resources, Validation, Writing – review & editing), Vanessa Russnak (Investigation, Resources, Validation, Writing – review & editing), Niko Lahajnar (Investigation, Resources, Writing – review & editing), Thomas Hansen (Investigation, Resources, Writing – review & editing), Jan Dierking (Conceptualization, Formal analysis, Methodology, Supervision, Writing – review & editing), and Rolf Koppelman (Conceptualization, Formal analysis, Methodology, Supervision, Writing – review & editing)

Supplementary data

Supplementary data are available at *ICES Journal of Marine Science* online.

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Data availability

The data underlying this article are available in the research data repository of the Universität Hamburg at <https://doi.org/10.25592/uhhfdm.14727>.

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