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Environmental context and trophic trait plasticity in a key species, the tellinid clam *Macoma balthica* L.☆

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ABSTRACT

Species show varying levels of plasticity regarding morphology, physiology and behaviour in relation to their immediate environment, and several trait characteristics are habitat-dependent. Determining when and how the environmental context changes trait expression is of key importance for understanding the role of individual species for ecosystem functioning. The tellinid clam *Macoma balthica* can vary its feeding behaviour, shifting between deposit- and suspension-feeding. In order to study the context-dependency of this trophic plasticity in adult clams, we conducted an experiment assessing food uptake by using stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$). We transplanted individuals between and within two shallow bays differing in exposure (exposed–sheltered) and sediment characteristics. Our results show that isotope signatures of clams differed between the two habitats and that clams in the exposed site showed stable isotope values linked to a diet of suspended particulate organic material, while values of individuals in the sheltered site corresponded to an uptake of sediment-bound organic material. Clams transplanted between these two environmental settings were gradually showing differing isotopic signatures from clams at their original habitat, over time mirroring the changes in clams in the site to which they were transferred. The shift in carbon and nitrogen stable isotopes of the clams provides insights into the context-dependent intraspecific feeding plasticity of this zoobenthic key species. The causes for this shift were coupled to contrasts in the hydrodynamic and biotic setting, implying that feeding plasticity may explain adaptation of organisms to changes in their surroundings.

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1. Introduction

The surrounding environmental context may determine the manifestation or strength of specific functional traits of an organism and thereby its role in the ecosystem (Chapin et al., 1997; Hooper et al., 2005). Today, analysing biological traits is an important tool in ecology (Albert et al., 2011, 2012; Violle et al., 2012). The focus has primarily been on trait differences *between* co-occurring species, assuming that trait variation *within* species (i.e. intraspecific or phenotypic trait variability) is of less importance. The general assumption is that, for a given species, traits are expressed in the same way regardless of the ecological context that the species occurs in (McGill et al., 2006; Petchey and Gaston, 2006; Violle et al., 2007). Thus, trait information is still often based on an average (e.g. mean values for continuous variables such as size, or qualitative categories for binary traits such as feeding habit), irrespective of the environmental setting (mean field theory, McGill et al., 2006; Weiher et al., 2011). Nevertheless, a wealth of empirical evidence shows that species can regulate behavioural, developmental and physiological characteristics depending on their biotic and abiotic contexts (Agrawal, 2001; Mooney and Agrawal, 2007; Funk and Cornwell, 2013). Thus, determining which circumstances and how environmental context change trait expression is pivotal for understanding responses in biological diversity and the consequences for ecosystem functioning in systems undergoing environmental change (Hawlena et al., 2011; Albert et al., 2012; Violle et al., 2012).

Intraspecific variability, within the functional trait-framework, has to date primarily been studied in terrestrial or freshwater systems with few examples from the marine realm (Cesar and Frid, 2012) although a high degree of plasticity in life histories (Hadfield and Strathmann, 1996) and in particular feeding habits of marine benthic animals is known to occur (Fauchald and Jumars, 1979; Riisgård and Kamermans, 2001). Plasticity in trophic traits of a species can have a direct impact on its role in the flow of energy through the food web (Frid et al., 2008). To illustrate the importance of trait plasticity in contrasting marine habitats, we studied the tellinid bivalve *Macoma balthica* that occurs over a wide geographic range in coastal waters in temperate and arctic areas (Riisgård and Kamermans, 2001; Väinölä, 2003; MarLIN, 2015). *M. balthica* is considered a key species in most areas of

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its circumboreal distribution range (Segerstråle, 1962; Beukema et al., 1977; Petersen, 1978), in which it also displays a large genetic plasticity (Väinölä, 2003). The species constitutes an important trophic node through its consumption of planktonic primary producers and deposited organic matter (Riisgård and Kamermans, 2001), as well as its role as a major prey species for invertebrate and vertebrate consumers in coastal habitats (Piersma and Beukema, 1993; Aarnio et al., 1996; Nordström et al., 2010).

M. balthica is a facultative suspension- and deposit-feeder that uses its siphon to collect suspended particles or to feed on organic material directly from the sediment surface (Bradfield and Newell, 1961; Ólafsson, 1986; Riisgård and Kamermans, 2001). Juvenile *M. balthica* lack siphons and, until such are developed, feed on deposited material using the foot (Bonsdorff, 1984). This ontogenetic shift can be tracked using the ratio of carbon stable isotopes (^{13}C:^{12}C), and is seen as a depletion in ^{13}C with an increase in the size of the clams (Rossi et al., 2004). Identifying and measuring the adult suspension-feeding behaviour, compared with the deposit-feeding action has been more difficult because of the variable movement and thus potential usage of the siphon by *M. balthica* (Kamermans, 1994; Riisgård and Kamermans, 2001). The various behaviours identified as suspension-feeding are when the siphon is kept still and/or swirled around well above the sediment surface or kept protruding just above the sediment surface, while deposit-feeding has been noted as movements of the siphon with the opening on the sediment surface (Riisgård and Kamermans, 2001). Observational studies have been able to provide indications of a switch from deposit- to suspension-feeding in the species but there has not been any direct proof of the opposite (Kamermans and Huitema, 1994; Riisgård and Kamermans, 2001). It has been argued that the deposit-feeding mode may be the inherent and dominant one based on the physiology of the species and the gardening effect on its food resource (common among deposit-feeding organisms) (Ólafsson, 1986). The occurrences of suspension feeding and causes for it are interesting to evaluate as they may elucidate the functional roles that the species plays in transportation of organic matter in the food web. Defining the factors that control switching from one mode of feeding to another has proved challenging (Riisgård and Kamermans, 2001). Four main factors have been suggested to control the adult feeding mode of *M. balthica*: 1) high current velocities preventing grazing on the sediment surface, but allowing for suspension-feeding, 2) higher food availability in the water column favouring suspension-feeding, 3) sub-lethal siphon nipping by predators restricting deposit-feeding, or 4) high lethal predation pressure and subsequent deeper burrowing only allowing for suspension-feeding (Riisgård and Kamermans, 2001). In our study, we focused on the first two of these suggested mechanisms for shifts in feeding mode, related to the physical environment of the species. Apart from observational investigations, stable isotopes have been used for quantifying variation in traits related to food consumption in benthic species, as organisms assimilate carbon and nitrogen stable isotopes in their food sources (Rossi et al., 2004, 2015; Cesar and Frid, 2012). Variability in $\delta^{13}C$ is considered to reflect differences in trophic pathways, while $\delta^{15}N$ is a proxy for the trophic level of organisms (Post, 2002). In a study on spatial variation of stable isotope ratios of benthic food-web components, adult *M. balthica* showed $\delta^{13}C$ values ranging up to 5‰ between shallow soft-sediment sites, a variation attributed to spatial differences in its feeding strategies and/or spatially differing isotope ratios of basal food sources (Nordström et al., 2010). No study so far has utilised stable isotopes to track and quantify adult plasticity in feeding habit of this key species in relation to abrupt changes in their environments (but see Rossi and Middelburg, 2011 for changing diet relationships in colonising juvenile *M. balthica* following hypoxia in muddy environments).

The objective of this study was to document a potential shift in food uptake depending on the environment, and to explore causes behind any disparity in *M. balthica* carbon and nitrogen isotope ratios. We conducted a transplantation experiment, in which adult individuals of *M. balthica* were transferred between and within two sites, representing two neighbouring shallow bays of different exposure and sediment characteristics. We examined the effect of the manipulation on individual stable isotope ratios over the production season in order to detect a possible adaptation to the new local environment of the clams.

More specifically, we (1) evaluated the effect of the manipulation of clams (i.e. the process of digging animals up and putting them in experimental enclosures), by comparing the development of stable isotope ratios of replanted *M. balthica* individuals against ambient clams within each site. We hypothesised that the values and trends of replanted and ambient clams would not differ significantly over the course of the experiment. Then we (2) investigated the response in stable isotopes of the clams transplanted between the two sites, by determining differences in ratios between clams (replanted) within a site and clams transplanted from their native site. We expected that, over time, isotope ratios of transplanted clams would approach, or at least change in parallel with those of replanted clams in the new site to which they were transplanted, if they made use of the same resources. Finally, (3) we compared stable isotope ratios of transplanted clams with replanted clams at their native site. As an indication of a shift in feeding habit, we hypothesised that there has to be a distinction between the isotope ratios of clams over time.

We considered the possible causes behind contrasts in stable isotopes of clams between sites to be either i) differences in stable isotope ratios of the two food sources, or ii) shifts in feeding strategy depending on the availability and quality of the food sources (Nordström et al., 2009). These mechanisms were based on the knowledge that stable isotopes of food sources may differ between environments contrasting in local subsidies and/or wind and waves (i.e. exposure), which may change the importance of pelagic and benthic production (Nordström et al., 2010). Exposure also affects the availability (amount) of the pelagic or benthic food source (Ólafsson, 1986). Additionally, iii) the biotic context (ambient macrofaunal community) may differ between environments and for example create different competitive situations which might affect food uptake for clams and thus we included this aspect. Finally, we considered that the iv) abiotic context simply constrains the clams to either of the two feeding modes (Riisgård and Kamermans, 2001).

2. Materials & methods

2.1. Experimental sites

The two studied shallow bays are located about 1 km apart in the Åland Archipelago, the non-tidal northern Baltic Sea (Hinderbengtsviken 60°10 N, 19°32 E; Skeppsvik 60°11 N, 19°31 E) (Supplementary Fig. S1.). Hinderbengtsviken (hereafter "the exposed site") is open towards the sea to the south and southwest, and classified as exposed, based on the GIS-based wave exposure model by Isæus (2004) that makes use of shoreline coastal shape, main wind direction and a maximum fetch distance of 500 km. The grain size distribution is dominated by coarse sand and occasionally some loose-lying filamentous algae (e.g. *Pylaiella littoralis*) can occur. Skeppsvik is less open towards the sea, and classified as sheltered (hereafter referred to as "the sheltered site"). The sediment is mostly medium and fine sand and the site consists of mainly bare sandy bottoms but patches of vegetation, such as *Chara aspera*, *Potamogeton pectinatus* and loose-lying *P. littoralis* occur.

2.2. Transplant experiment and collection of samples

The experiment was conducted in 2010 and run during the productive season with initiation of the experiment on June 15th and ending eight weeks later. Adult individuals of *M. balthica* (size range 7.8–16.0 mm, average 10.5 ± 0.1 mm) were collected in early June at both experimental sites in net bags by SCUBA diving and by shovelling sediment onto a 0.5 mm sieve. The collected clams were brought to the

laboratory, where each individual was marked and measured for initial size (precision 0.1 mm). At each site, 48 PVC cylinders (diametre 110 mm, height 150 mm) were pushed down into the sediment 2 m apart, in 6 rows at 1–1.5 m depth. After deployment, the cylinders were left for 5–6 days to allow for stabilisation of the sediment prior to the transplantation experiment. When the experiment started (hereafter "t_0"), five adult *M. balthica* individuals were added to each enclosure so that 24 enclosures at each site contained clams from that same site (replanted) and 24 contained clams from the other site (transplanted), randomised within rows. To reduce the possibility of intraspecific competition in the enclosures, the number of added clams was chosen so as to not greatly exceed the ambient densities of *M. balthica*. Cylinder openings were covered with a net to keep the recently added *M. balthica* from escaping or being taken by predators while still at the sediment surface. Nets were removed when all individuals had buried into the sediment. Clams were re-collected after 7, 14, 28 and 56 days (hereafter "t_7", "t_{14}" "t_{28}" and "t_{56}") by plugging the cylinder opening and lifting each cylinder ($n = 6$/sampling occasion) and its contents into a net bag. The contents were run through a sieve with a 0.5 mm mesh. Marked specimens of *M. balthica* were taken aside, left in filtered seawater (20 μm) for 12 h to allow gut and intestine evacuation, and then frozen (−20 °C) until processing for stable isotope analysis. For analysis of benthic community structure, the faunal assemblage in each cylinder was preserved in 70% ethanol, later sorted under a dissecting microscope, and identified to lowest possible taxonomic level. Animals were counted and weighed (precision 0.1 mg dry weight). Ambient *M. balthica* individuals were also collected (as controls) for stable isotope analysis at the start and during each re-sampling event. The size of all individuals (manipulated and ambient) was determined to the nearest 0.1 mm as a rough estimate of growth.

At the start and at each sampling occasion, temperature (°C), pH, salinity, dissolved oxygen (mg l^{-1}, %), turbidity (NTU), tot-P and tot-N (μg l^{-1}) were measured. Salinity was determined from conductivity on a conductometre, pH on a laboratory pH metre, dissolved O_2 by Winkler titration, turbidity on a turbidimetre and levels of total P and total N were determined spectrophotometrically after persulphate oxidation. To compare the hydrodynamic forcing or energy at the two experimental sites, we used a gypsum dissolution technique according to Valanko et al. (2010). The method provides an integrative measure of wind and wave energy and was conducted using five replicate gypsum blocks (diametre 45 mm, height 20 mm) at each site, placed at 0.5 m height off the seafloor for 48 h. The measure is expressed as per cent change in dry weight (60 °C, 48 h) minus mean change in weight at no-flow conditions (laboratory control).

We evaluated the availability and quality of food sources in the water and in the sediment at each site. The availability of Suspended Particulate Organic Matter (SPOM) and SEDiment particulate Organic Matter (SEDOM) was estimated as the amount of chl-*a* (μg l^{-1}) in the water and in the sediment, respectively. SPOM was collected from every sampling occasion with a 10 μm-net, concentrated on Whatman GF/C filters and stored in the freezer for stable isotope analysis. Sediment was collected for estimation of organic matter content (%) (loss-on-ignition, 3 h at 500 °C) and chl-*a* (μg l^{-1}) as well as for stable isotope analysis of SEDOM. Sediment organic matter was suspended and decanted into Whatman GF/C filters and stored in the freezer. Chl-*a* analysis followed those of Lorenzen (1967) and Sartory (1982), with extraction from sediments in 90% acetone for 24 h and then spectrophotometric measurements. The C/N ratio of SPOM and SEDOM was used as a measure of the quality of the food source, and calculated from stable isotope values ($\delta^{13}C$ and $\delta^{15}N$).

2.3. Stable isotope analysis

The frozen clams were thawed, rinsed in deionised water and cleaned of debris under a stereomicroscope. The temporal stability of organism isotopic composition depends on tissue turnover rates (McCutchan et al., 2003). In this study, we chose to analyse stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of sample tissue composed of the digestive gland, stomach and intestine as an indication of shifts in feeding behaviour. These are metabolically active tissues and therefore tend to respond more quickly to dietary changes (Tieszen et al., 1983; Hobson and Clark, 1992), than for example muscle tissue that may in primary and secondary consumers require weeks to a year to reach equilibrium under a constant diet (Hesslein et al., 1993; MacAvoy et al., 2001; McIntyre and Flecker, 2006). Previous studies of food sorting and absorption of carbon by *M. balthica* have revealed a two-phase process (Decho and Luoma, 1991). Completing digestion and assimilation of ingested elements occurs within three to four days for *M. balthica* (Decho and Luoma, 1991), which is well within the first sampling event (seven days) in our study. Each sample was treated with 1 M HCl in order to remove carbonates, oven-dried (60 °C, 48 h), homogenised and packed in a tin capsule. Each clam sample for stable isotope analysis contained pooled individuals from the same enclosure. For stable isotope analysis of ambient *M. balthica*, six replicates (enclosures) were used per site and sampling event (including the start, t_0, of the experiment). The filters with suspended particulate and sediment particulate organic matter (SPOM and SEDOM) were treated with 1 M HCl before being oven-dried and packed into tin capsules. Samples were analysed at the Stable Isotope Facility at University of California, Davis, USA. Sample stable isotope ratios of carbon and nitrogen are expressed in relation to those of international standards (V-PDB for carbon and air for nitrogen) as δ-values per mille (‰) according to the standard equation:

$$\delta^{13}C \text{ or } \delta^{15}N = \left[\left(R_{sample}/R_{standard} - 1\right)\right] \times 10^3$$

where R is ^{13}C: ^{12}C or ^{15}N: ^{14}N (Fry, 2006). Replicate laboratory standards revealed an analytical error of <0.05‰ for both C and N.

2.4. Statistical analysis

To track changes in stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$) of clams, we used linear regression analysis (Quinn and Keough, 2002), as we wanted to investigate the overall response of clams, i.e. the relationship ($\delta^{13}C$ or $\delta^{15}N$ clams = b0 + b1 × time) between stable isotope ratios and time since manipulation, rather than compare specific sampling events. We compared the responses of replanted clams against ambient ones and replanted (at new or native site) against transplanted clams by evaluating whether slopes (b0) and intercepts (b1) differed. Prior to all analyses, data was tested for meeting assumptions of normality and homogeneity of variances and transformed when necessary. We also checked for non-linearity, but found first order polynomial (linear) fit to be the best option for all treatments.

Discrepancy in initial size between replanted and transplanted *M. balthica* individuals was analysed separately for each experimental site using a Mann–Whitney test. The same analysis or a t-test, when requirements for the parametric test were met, was used to compare the size-difference (the start compared with the end of the experiment) between replanted and transplanted clams. These analyses indicated whether clams had been able to utilise the available food sources and potentially grow during the experiment.

The environmental variables wave energy (% gypsum lost), chl-*a* in the sediment, organic content (%) of the sediment, and C/N ratios of suspended particulate and deposited organic materials were compared across experimental sites. The difference in energy between sites was analysed with a Mann–Whitney test (site: exposed or sheltered, $n = 5$) while temporal analysis of chl-*a*, organic content and C/N ratio of SPOM and SEDOM was done using repeated-measure ANOVAs (site: exposed or sheltered, between-subject effect; time: t_0 to t_{56}, within-subject effect). However, for organic content analysis t_{14} was excluded due to sampling errors. Stable isotopes (^{13}C:^{12}C, ^{15}N:^{14}N) of SPOM and

SEDOM within sites and over time were analysed with repeated-measure ANOVAs (source: SPOM or SEDOM, between-subject effect; time: t_0 to t_{56}, within-subject effect). To achieve a balanced analysis, t_0, for ^{13}C and ^{15}N at the exposed site and t_{56} for ^{15}N were excluded.

The macrofaunal community in experimental cylinders was analysed using both univariate and multivariate analyses. We used repeated-measures ANOVA to determine the effect of site (exposed or sheltered, between-subject effect) and time (t_0 to t_{56}, within-subject effect) on abundance, biomass, species richness (number of taxa) and diversity (Shannon's diversity index H' [$\log_e$] and evenness J'). Differences in community composition between the two sites were analysed using repeated-measures permutational multivariate ANOVA on fourth-root transformed data with site (exposed or sheltered) and time (days from start of the experiment) as factors (Euclidean distance, 9999 permutations). Multivariate variance was homogenous between groups (multivariate dispersion, $p > 0.05$). A SIMPER analysis was applied to identify the species contributing most to similarities within and dissimilarities between the two sites.

Analyses were run using the Car and Vegan packages in R (R Development Core Team, 2014), as well as GraphPad Prism and PRIMER v 6. (Clarke, 1993; Clarke and Gorley, 2006).

3. Results

First, we present the results of the transplant experiment, including whether experimental relocation of clams might have had an impact on the results, the response of clams transplanted from their native site to a new environment as well as initial size and growth of manipulated clams. Then we describe contrasts in the abiotic environment, food sources and biotic context (community structure and composition) between the two sites.

3.1. Effect of relocation of clams

Ambient and replanted *M. balthica* individuals at the sheltered site were enriched in ^{13}C by about 2.8‰ (ambient: -18.9 ± 0.6‰, replant: -19.2 ± 0.4‰) compared with the exposed site (ambient: -22.0 ± 0.2‰, replant: -21.7 ± 0.2‰). The opposite pattern was seen in $\delta^{15}N$, where clams at the sheltered site had on average 1.3‰ lower values than at the exposed site (Fig. 1).

At the exposed site, neither replanted nor ambient clams showed any temporal change in the stable isotopes (Table 1a, Fig. 1A,B). Apart from the fact that ambient clams had on average a 0.3‰ lower $\delta^{13}C$ value than the replanted ones (difference in intercept: $F_{1,57} = 7.464$, $p = 0.008$), there was no difference between the two groups of clams in terms of the trend over time for $\delta^{13}C$ and $\delta^{15}N$ (difference in slope: $F_{1,56} = 0.048$, $p = 0.827$ and $F_{1,56} = 0.734$, $p = 0.395$, respectively).

A temporal shift in both $\delta^{13}C$ and $\delta^{15}N$ was observed at the sheltered site (Fig. 1C, D). Both ambient and replanted clams became increasingly enriched in heavy carbon over the course of the experiment (Table 1b, Fig. 1C). However, ambient clams showed a greater change in carbon over time compared with the replanted ones (difference in slope: $F_{1,56} = 7.228$, $p = 0.009$). The opposite pattern was found for ^{15}N, i.e. a depletion of heavy nitrogen during the experiment (Table 1b, Fig. 1D). Both ambient and replanted clams showed similar trends in $\delta^{15}N$ over time (difference in slope: $F_{1,56} = 3.546$, $p = 0.065$).

3.2. Responses of transplanted clams to a new environment

Clams that were transplanted from one site to the other (exposed–sheltered) followed the temporal trend in stable isotope ratios of the clams in the site to which they were moved. However, the isotope ratios of the transplanted clams remained at a different level (higher or lower ratios) than the replanted ones throughout the experiment. The level depended on whether they were originally moved from the comparably ^{13}C enriched and ^{15}N-depleted sheltered site, or from the exposed site (Fig. 1).

At the exposed site, carbon ratios of replanted *M. balthica* and transplanted individuals from the sheltered site differed over the course of the experiment (difference in slope: $F_{1,56} = 10.544$, $p = 0.002$) (Fig. 1A). The $\delta^{13}C$ value of transplanted clams was on average 1.3‰ higher than that of replanted clams at the start of the experiment, and increased towards the end (Table 1a). Although the transplanted clams from the sheltered site did not approach carbon values of the

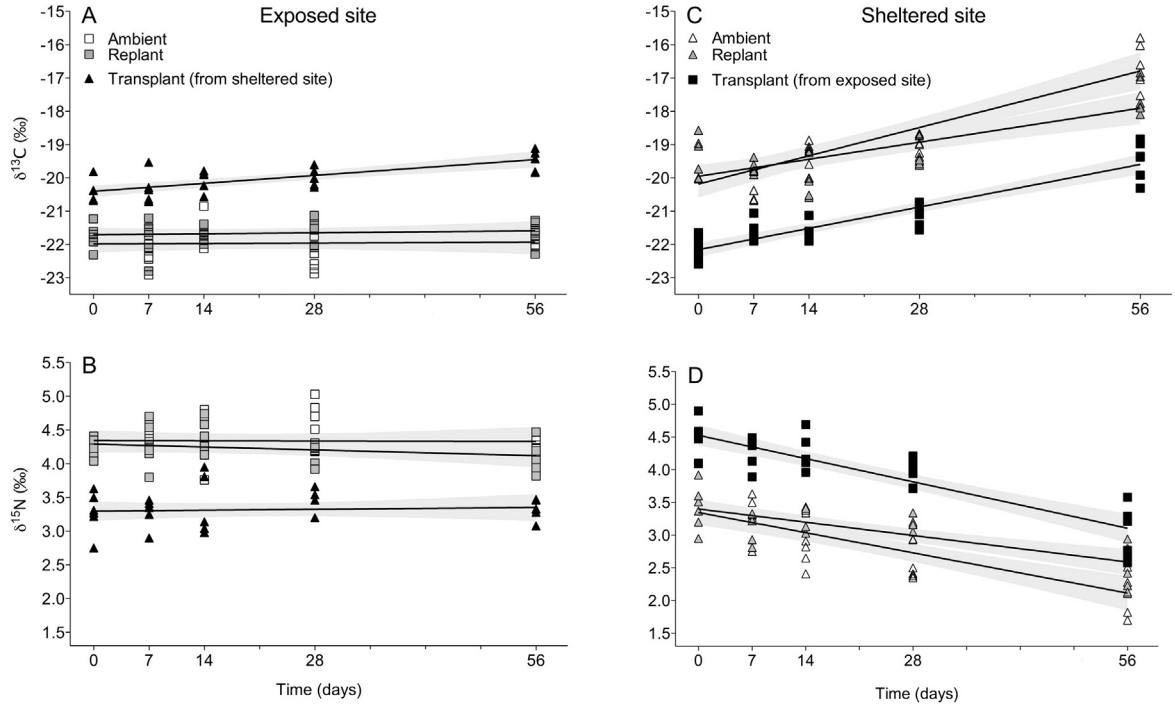

Fig. 1. Stable isotope values ($\delta^{13}C$, $\delta^{15}N$, ‰) and linear regression with 95% confidence intervals of ambient, replanted and transplanted *Macoma balthica* at the A–B) exposed and C–D) sheltered sites.

Table 1
Linear regression models of stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of ambient, replanted and transplanted clams as a function of time (days since start of experiment, t_0 to t_{56}) in the a) exposed and b) sheltered sites. Intercept (Const.), slope (Coeff.), p-value and R^2 of the models are presented in the table. Degrees of freedom (DFn, DFd) for all models were 1 and 28, respectively. Significant values (0.001***) denote that the slope is different from zero (i.e. increasing or decreasing). Model comparison indicated the best-fit to be linear.

	Variable	Const.	Coeff.	p-Value	R^2
a) Exposed site					
$\delta^{13}C$	Ambient	−22.0	0.00	0.844	0.001
	Replant	−21.7	0.01	0.550	0.013
	Transplant (from sheltered site)	−20.4	0.12	<0.001***	0.531
$\delta^{15}N$	Ambient	4.34	−0.00	0.943	0.001
	Replant	4.29	−0.02	0.156	0.071
	Transplant (from sheltered site)	3.30	0.01	0.700	0.010
b) Sheltered site					
$\delta^{13}C$	Ambient	−20.2	0.06	<0.001***	0.740
	Replant	−20.0	0.30	<0.001***	0.585
	Transplant (from exposed site)	−22.2	0.32	<0.001***	0.847
$\delta^{15}N$	Ambient	3.35	−0.02	<0.001***	0.630
	Replant	3.40	−0.10	<0.001***	0.565
	Transplant (from exposed site)	4.53	−0.18	<0.001***	0.762

replanted ones at the exposed site, their $\delta^{13}C$ values still indicated a response to the new and contrasting environment when compared with the replanted clams at their native site (Fig. 2). A significantly greater enrichment in ^{13}C over time was noted for the clams remaining at the sheltered site than the ones that were relocated to the exposed environment (difference in slope: $F_{1,56} = 31.650$, $p < 0.001$) (Fig. 2).

At the sheltered site, the transplanted clams showed a significant increase in $\delta^{13}C$ over time (Table 1b, Fig. 1C). The transplanted clams paralleled, although on a lower level (average 2.0‰), the values of the replanted clams throughout the experiment (difference in slope: $F_{1,56} = 1.777$, $p = 0.188$). The strong response of the transplanted clams was also evident in the distinct disparity in $\delta^{13}C$ to their replanted counterparts at their native exposed site (difference in slope: $F_{1,56} = 74.670$, $p < 0.001$) (Fig. 2).

In terms of $\delta^{15}N$ values of the manipulated clams, patterns generally mirrored those of the $\delta^{13}C$ values at each site. Contrary to the significant contrasts in the development of carbon values over time between replanted and transplanted clams at the exposed site, the trend in $\delta^{15}N$ over time did not differ between the two groups of clams (difference in slope: $F_{1,56} = 1.555$, $p = 0.218$), but the transplanted clams had on average a 0.9‰ lower $\delta^{15}N$ value (difference in intercept: $F_{1,57} = 200.532$, $p < 0.001$, Fig. 1B). At the sheltered site, the difference in $\delta^{15}N$ between transplanted and replanted clams decreased steadily over the course of the experiment (difference in slope: $F_{1,56} = 9.174$, $p = 0.004$), but the $\delta^{15}N$ of transplanted clams did not fully reach those of replanted ones (Fig. 1D).

3.3. Initial size and growth of manipulated clams

At the start of the experiment, the size of replanted and transplanted clams differed at both sites. Replanted clams (10.9 ± 0.1 mm) were on average 1.0 mm larger than transplanted ones (9.9 ± 0.1 mm) at the exposed site (Mann–Whitney $p < 0.001$). The opposite pattern was found for the sheltered site (Mann–Whitney $p < 0.001$), where the difference was 0.7 mm between replanted (10.3 ± 0.1 mm) and transplanted (11.0 ± 0.2 mm) individuals.

Manipulated *M. balthica* individuals increased in size whether replanted within the same site or transplanted from the site (mean growth: 0.3 ± 0.1 mm), indicating that clams utilised the food sources present. A significant difference in growth of clams (Mann–Whitney $p < 0.001$) was noted in the exposed site, where replanted individuals had increased more in size (0.7 ± 0.1 mm) than transplanted ones (0.1 ± 0.1 mm) at the end of the experiment (t_{56}). For the sheltered site, no statistical difference in growth between replanted and transplanted individuals was found ($t_{23} = 0.825$, $p = 0.418$).

3.4. Contrasts in the abiotic environment, food sources and quality

In accordance with previous qualitative descriptions (Nordström et al., 2010) and the Isæus index of the site, the hydrodynamic energy (estimated as % gypsum lost) was significantly higher at the exposed site, compared with the sheltered one (Mann–Whitney $p = 0.008$) (Table 2). This was also in agreement with other hydrographical measurements in this study (Table 2). The amount of chl-*a* in the water column was 2.1 ± 0.4 μg l^{-1} at the exposed site and 2.2 ± 0.7 μg l^{-1} at the sheltered site (Table 2). Chl-*a* in the sediment, on the other hand, was on average higher at the sheltered site (1.0 ± 0.1 μg l^{-1}) than at the exposed one (0.6 ± 0.1 μg l^{-1}) (Table 2). The difference was significant at the start (t_0) and at all events but the first resampling event (t_7) (site × time: $F_{4,32} = 11.720$, $p < 0.001$). This pattern was due to a drop in sediment chl-*a* at the sheltered site between the start (t_0: 1.1 ± 0.1 μg l^{-1}) and the first sampling event (t_7: 0.6 ± 0.1 μg l^{-1}). The organic content of the sediment varied more over time, being overall higher at the sheltered site (Table 2), but differed significantly between sites only at the start of the experiment (t_0) and after 28 days (t_{28}) (site × time: $F_{3,24} = 9.060$, $p < 0.001$).

Stable isotope analyses of the two food resources, suspended particulate (SPOM) or sediment particulate (SEDOM) organic matter, indicated a significant variation of sources over time at both sites and in terms of both ^{13}C and ^{15}N (Fig. 3). The difference in $\delta^{13}C$ between SPOM and SEDOM varied over time at both the exposed (source × time: $F_{3,18} = 88.310$, $p < 0.001$) and the sheltered sites (source × time: $F_{4,16} = 8.583$, $p = 0.001$) (Fig. 3A, C). At the exposed site, carbon values of SEDOM ranged from −18.4 ± 0.1‰ at the first sampling event (t_7) to −18.3 ± 0.1‰ at the last (t_{56}) one, while SPOM varied from

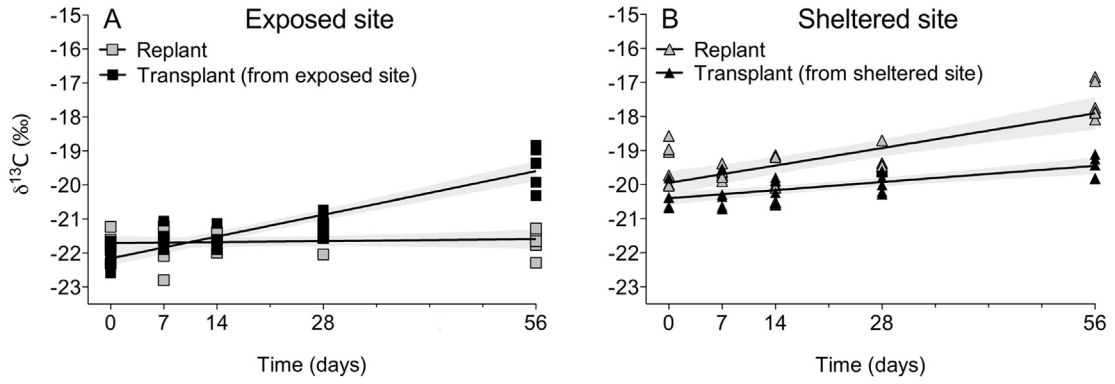

Fig. 2. $\delta^{13}C$ values (‰) and linear regression with 95% confidence intervals of *Macoma balthica* individuals from the same site, i.e. replanted within and transplanted from, A) exposed and B) sheltered sites.

Table 2
Abiotic and biotic variables of the experimental sites (mean ± SE). Variables highlighted (bold) were analysed statistically and significant differences between sites (single variable: site, or interaction: site × time) are indicated with an asterisk (*).

		Exposed site	Sheltered site
Abiotic	**Energy (% gypsum lost)***	53.1 ± 4.8	31.2 ± 1.2
	Temp. (°C)	15.9 ± 1.7	17.2 ± 2.1
	pH	8.2 ± 0.1	8.4 ± 0.1
	Salinity	5.5 ± 0.1	5.6 ± 0.1
	O_2 (mg/l)	10.1 ± 0.6	11.6 ± 0.7
	Turbidity (NTU)	1.0 ± 0.3	1.2 ± 0.6
	Tot-P (μg l^{-1})	19 ± 2.5	41 ± 14
	Tot-N (μg l^{-1})	280 ± 15	390 ± 57
	Chl-*a* (μg l^{-1}, water)	2.1 ± 0.4	2.2 ± 0.7
	Chl-*a* (μg g^{-1} dry wt., sediment)*	0.6 ± 0.1	1.0 ± 0.1
	Org. content (LOI%)*	0.22 ± 0.01	0.27 ± 0.02
	C/N ratio SPOM*	8.0 ± 0.4	6.6 ± 0.2
	C/N ratio SEDOM*	6.2 ± 0.1	6.8 ± 0.1
Biotic	**Abundance (ind. m^{-2})***	89.1 ± 11.3	385.6 ± 59.2
	Biomass (g DW m^{-2})*	1.0 ± 0.3	1.4 ± 0.2
	S (Total)*	4.0 ± 0.2 (16)	5.8 ± 0.5 (24)
	H	0.8 ± 0.1	0.9 ± 0.1
	J*	0.8 ± 0.1	0.6 ± 0.1

−22.2 ± 0.2‰ to −19.5 ± 0.1‰, respectively (Fig. 3A). At the sheltered site, SEDOM was also enriched compared with SPOM, and varied from −19.3 ± 0.0‰ at the start of the experiment (t_0) to −16.6 ± 0.5‰ at the end (t_{56}) (Fig. 3C). The corresponding values of SPOM were −20.7 ± 0.1‰ (t_0) and −18.8 ± 0.3‰ (t_{56}). In terms of heavy nitrogen, SEDOM was again enriched compared with SPOM at the exposed site, in all but the first sampling events (t_7) (source × time: $F_{3,12} = 10.060$, p = 0.001) (Fig. 3B). At the sheltered site, both sources showed a significant variation over time (source × time: $F_{3,12} = 13.660$, p < 0.001), but an opposite pattern was found, where SPOM was enriched and varied from 2.3 ± 0.1‰ (t_0) to 3.6 ± 0.1‰ (t_{28}), compared with SEDOM that varied from 1.7 ± 0.0‰ (t_0) to 1.5 ± 0.0‰ (t_{28}) (Fig. 3D).

In addition, the quality of the two food sources (C/N ratio of SPOM and SEDOM) did differ between the sites, but only at occasional sampling events (Table 2). The C/N ratio of SEDOM was higher at the sheltered bay at the first (t_7) and the second (t_{14}) sampling events (site × time: $F_{4,24} = 22.080$, p < 0.001). The ratio varied more for SPOM but without any clear pattern, as it was higher at the sheltered site in the beginning (t_7) while it was opposite in the last two sampling events (t_{28} and t_{56}) (site × time: $F_{3,12} = 32.790$, p < 0.001).

3.5. The biotic context — benthic community structure and composition

Analysis of the macroinvertebrate community structure and composition sieved from the experimental enclosures indicated contrasting biotic settings. The sheltered site had on average a higher faunal abundance, biomass and species richness than the exposed one (Table 2). The two sites showed significant contrasts in abundance at all events but the first sampling event (t_7) (site × time: $F_{3,66} = 24.920$, p < 0.001), while biomass varied more over time and was significantly higher in the sheltered site at 7 and 28 days (site × time: $F_{3,66} = 2.910$, p = 0.041). Species richness was only significantly higher at the last sampling event (t_{56}) (site × time: $F_{3,66} = 22.030$, p < 0.001). Diversity increased somewhat over time but there was no difference between the sites (site × time: $F_{3,66} = 1.850$ p = 0.147, site: $F_{1,66} = 3.520$, p = 0.074, time: $F_{3,66} = 4.270$, p = 0.008). In contrast to the other variables describing community structure, evenness was slightly higher at the exposed site at all events except the first sampling event (t_7) (site × time: $F_{3,66} = 3.550$, p = 0.019), indicating a dominance of a few species at the sheltered site. The average number of *M. balthica* individuals per enclosure, including the added clams, was 6.0 ± 0.2 at the exposed site, and 13.4 ± 0.5 at the sheltered site.

Multivariate analysis highlighted a clear contrast in macrofaunal community composition over time (site × time: $F_{1,90} = 17.360$ p < 0.001). Similarity within the sampled enclosures at the exposed site (57%) was lower and composition was more varied than at the sheltered site (68%) where *Marenzelleria* spp., *M. balthica* and Chironomidae contributed most to similarity within the site, but also dominated the community composition (Supplementary Table S1). Species contributing to the similarity within the exposed site were *Bathyporeia pilosa*, Oligochaeta and *Pygospio elegans*, all belonging to the five most

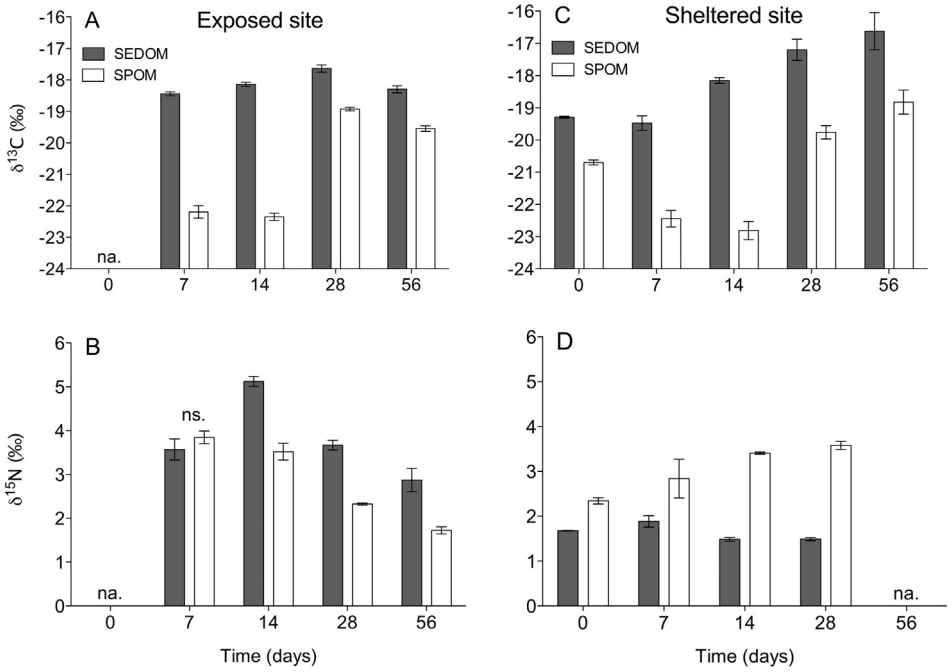

Fig. 3. Stable isotope values of basal resources ($\delta^{13}C$ and $\delta^{15}N$, ‰, mean ± SE) of deposited organic matter in sediment (SEDOM, grey colour) and suspended particulate organic matter in the water column (SPOM, white colour) at the A–B) exposed and C–D) sheltered site. Non-significant results are indicated (ns.), all other comparisons are significant, p < 0.05. na. = data not available. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

dominant taxa. In this site, *M. balthica* ranked fifth in terms of abundance (Supplementary Table S1).

4. Discussion

The aim of this study was to document whether differences in environmental context may induce a shift in feeding behaviour identifiable through carbon and nitrogen stable isotopes. We illustrated this in a transplantation-experiment using adult individuals of the key species *M. balthica*, a species known from observational studies to be able to express plasticity in feeding habit, displaying either suspension or deposit-feeding and possibly shifting between these depending on the ecological context (Ólafsson, 1986, 1989; Riisgård and Kamermans, 2001). Utilising two neighbouring bays differing in exposure (exposed–sheltered), sediment characteristics, and community composition, we were able to explore the causes behind this context-dependency in terms of food availability and quality as well as the biotic and abiotic settings.

4.1. Trophic plasticity in M. balthica

We found that adult *M. balthica* showed marked differences in stable isotope signatures (δ^{13}C and δ^{15}N) between two environmentally contrasting coastal bays, consistent with earlier studies (Nordström et al., 2010). At the exposed site, ambient and replanted clams were depleted in carbon but enriched in nitrogen compared with the ambient and replanted individuals at the sheltered site. The similar pattern in stable isotopes between ambient and replanted clams indicated, as hypothesised, no significant effect of the experimental procedure. The two examined food sources, suspended particulate (SPOM) and sediment particulate organic matter (SEDOM) showed differing carbon stable isotope signatures over the course of the experiment where SPOM was depleted compared with SEDOM. As basal food sources are reflected in the diet of organism (Post, 2002), the carbon stable isotope values of the ambient and replanted clams at the exposed site (ambient: -22.0 ± 0.2‰, replant: -21.7 ± 0.2‰) are likely to reflect a diet of suspended particulate organic material. At the sheltered site, carbon isotope signatures in clams (ambient: -18.9 ± 0.6‰, replant: -19.2 ± 0.4‰) suggested an uptake of sediment particulate organic material.

Clams transplanted from their native site to a new environment showed context-dependent change over time. Their isotope ratios remained either enriched or depleted throughout the experiment depending on their native environment. Transplanted clams from the exposed site to the sheltered site indicated an adaptation to the new environment by increasing their carbon values and following the pattern of the replanted (within the site) clams over time. The nitrogen values of the transplanted clams even approached those of the replanted ones, showing a true shift in stable isotopes. Furthermore, the significant difference in carbon values of the transplanted clams from those of the replanted ones in their native environment also supports this shift. The response thus implies a shift from suspension to deposit-feeding of the clams, a behaviour also found in observational studies (Ólafsson, 1986). At the exposed site, transplanted clams did show an increase over time in their carbon values compared with the replanted clams. Although statistically significant, this change was not comparable with the magnitude of difference between the transplanted clams and the replanted ones in their original site. The replanted clams in the sheltered site increased significantly in δ^{13}C over time, in accordance with the development of SPOM values, while transplanted clams did not follow this strong response and changed little over the experiment. The change in δ^{13}C of clams transplanted from the sheltered site followed more that of the sediment particulate organic matter. This result, in combination with the parallel development of δ^{15}N of transplanted and replanted clams at the exposed site, suggests an adaptation and possibly a shift to uptake of the suspended particulate material.

4.2. Mechanisms influencing feeding behaviour

The availability or amount of food has been suggested to be a mechanism determining suspension-feeding in a dynamic environment such as an exposed coastal bay (Riisgård and Kamermans, 2001). In this study, neither the availability nor the quality (C/N ratio) of the food sources could clearly explain the disparity in stable isotopes and shifts in feeding habit. These measures varied over time but did not show any persistent differences between sites. The availability of suspended food for clams is also determined by the horizontal flux of organic matter along the seafloor (Kamermans, 1994; Peterson and Skilleter, 1994), important also for sediment–animal interactions in non-tidal areas similar to the sites in this study (Valanko et al., 2010). Our point-estimates of food sources (levels of chl-*a* and sediment organic matter) may not be sufficient to fully capture between-site variability in the availability of food.

The third mechanism proposed in the study suggests that the biotic setting could affect food uptake. The structure and composition of the other macrofauna in the enclosures were used as a proxy for e.g. differential competition among individuals or groups of consumers. Contrasts in feeding behaviour due to interspecific interactions could not be ruled out as the faunal community differed between the two sites, the sheltered site having a more rich and diverse community than the exposed one, and simultaneously being more similar in composition over time. The species composition of the two sites also reflected the abiotic contrasts in exposure as *B. pilosa* and *P. elegans* are often characteristic of exposed sandy bottoms while *Marenzelleria* spp. and species of Chironomidae are found in more sheltered muddy habitats (Kraufvelin et al., 2011). The dominating taxa in the studied sites are generally co-occurring with *M. balthica* (Herman et al., 2000; Rossi et al., 2004). Concerning intraspecific competition, our aim was to account for *M. balthica* individuals present in the cylinders, and the decision to add specifically five individuals per cylinder was based on previous knowledge of clam density in the sites. Adult clam densities measured in this study (Supplementary Table S1) were similar to those found in other studies from the region (Hiddink and Wolff, 2002; Aarnio et al., 2011). The sheltered site had a higher ambient density of clams than the exposed one and thus the potential for intraspecific competition was higher. According to Ólafsson (1986), density-dependency may occur in deposit-feeding populations of *M. balthica*, affecting the growth of the clams as food uptake might be lowered because of interactions from clam movement or siphons meeting other individuals. In our study, intraspecific competition was probably not a significant factor as both replanted and transplanted clams had grown during the experiment in the sheltered site. We acknowledge that our size measurements represent rough estimations of growth as they relied on shell size only, rather than a combination of size and weight, growth rings or lines (Bonsdorff and Wenne, 1989; Cardoso et al., 2013). Shell size is variable in this species (Beukema and Meehan, 1985), but also used as a common measure for differentiating size-related changes in stable isotope ratios in *M. balthica* (Rossi et al., 2004; Rossi and Middelburg, 2011). The large number of replicates in this study provides some reliability to the measure and indication of clam activity in the experiment.

Finally, the hydrodynamic regime was a strong differentiating factor of the sites and is likely to have affected the food uptake of the clams by constraining the clams to either of the two feeding modes, as suggested by Riisgård and Kamermans (2001). At the exposed site, with a higher hydrodynamic regime (based on measurements of energy and known sediment characteristics), stable isotopes of ambient and replanted clams suggested that suspension-feeding was conducted to some degree while the opposite was thought to be the case for clams at the sheltered site. Hence, it is likely that the hydrodynamics at the exposed site prevented grazing on the sediment surface, but allowed suspension-feeding.

To summarise, the mechanisms considered here can probably not alone determine feeding behaviour as they are in various ways

interlinked. In addition to physical constraints on feeding behaviour, faster flows (in an exposed bay) imply greater fluxes of suspended particles and thus enhanced energetic rewards, while slower flows (in a sheltered site) imply enhanced deposition of food particles, favouring deposit feeding (Peterson and Skilleter, 1994; Bayne, 2004). However, clams living in highly dynamic environments, such as exposed bays, face not only adaptation to short term (hours, days) variability in food flux and characteristics (particle size and composition) but particularly the dynamics of the seasonal input of material from phytoplankton production, which might be more pulse-like than in sheltered areas (Peterson and Skilleter, 1994). The hydrodynamic setting shaping community composition, might not only present *M. balthica* with differing levels of interactions between other consumers as discussed above, but also predation by other macrofauna (Bonsdorff et al., 1995) or higher trophic levels such as fish (Peterson and Skilleter, 1994). This additional proposed mechanism (Riisgård and Kamermans, 2001) was not studied here but affects especially the deposit feeding behaviour and thus likely clams inhabiting more hydrodynamically stable and often high productive muddy environments.

4.3. Conclusions

To conclude, our study provides information on the isotopic gradient across which adult *M. balthica* forage, and suggests that stable isotopes offer insights into intraspecific patterns in feeding plasticity. Our results highlight the context-dependency of feeding behaviour and indicate that causes for plasticity are possible to disentangle and thus predict to some degree. It would therefore be of value to assess the importance of this context-dependent plasticity in relation to an ecosystem function such as the structure or dynamics of the food web (Nordström et al., 2010; Bolnick et al., 2011). In addition, as suggested by Nordström et al. (2010), and supported by the results of the transplanted clams in this study, the same species in neighbouring contrasting environments may function differentially. The flexible feeding ability of *M. balthica* in combination with the species dominance in both sandy and muddy habitats calls for further quantitative studies of trophic transfer as an ecosystem function. Many studies examining effects of environmental heterogeneity on marine ecosystem functioning have focused on the interspecific variability in traits (e.g. Vaughn et al., 2007; Rossi et al., 2008; Griffin et al., 2009). In these studies, identity effects or complementarity among species, are linked to variability in the environment and to enhancement of ecosystem functioning (Griffin et al., 2009). However, the intraspecific plasticity of organisms may potentially blur the effect of differences between species (Violle et al., 2012). Complicating the assessment of plasticity in traits and ecosystem function further is the fact that trait plasticity might also lay latent until needed (Hawlena et al., 2011). Hence, better understanding of variability within species' traits may provide insights not only to different context-related functional effects but also to the adaptability of species to changes in their surrounding habitat or new and contrasting environments, which may be highly important e.g. in the light of predicted climate-change scenarios.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2015.06.015.

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