



## 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 ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ). 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 (Vainölä, 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 ( $^{13}\text{C}:^{12}\text{C}$ ), and is seen as a depletion in  $^{13}\text{C}$  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  $\delta^{13}\text{C}$  is considered to reflect differences in trophic pathways, while  $\delta^{15}\text{N}$  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  $\delta^{13}\text{C}$  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 (Hinderbengtssviken 60°10'N, 19°32'E; Skeppsvik 60°11'N, 19°31'E) (Supplementary Fig. S1.). Hinderbengtssviken (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  $10.5 \pm 0.1$  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

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