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$\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ of co-occurring molluscs within a community dominated by *Crassostrea gigas* and *Crepidula fornicata* (Oosterschelde, The Netherlands)

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ABSTRACT: The aim of this study was to investigate, by use of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, the diet of co-occurring intertidal mollusc species within a community dominated by the oyster *Crassostrea gigas* and its epibiont, the common Atlantic slipper limpet *Crepidula fornicata*. The results showed that the $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ values of *C. gigas* differed from those of the deposit feeders considered but also from the other suspension-feeding molluscs (i.e. *Mytilus edulis*, *Cerastoderma edule* and *C. fornicata*), being more depleted in ^{13}C and in ^{15}N . The results suggest more similarities in the assimilated food sources of *C. fornicata*, *C. edule* and *M. edulis*. In particular, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differences between *C. gigas* and *C. fornicata* suggest that these associated suspension feeders in many shellfish culture areas may not necessarily be competitors for food sources when food is not limited.

KEY WORDS: Benthic food web · $\delta^{13}\text{C}$ · $\delta^{15}\text{N}$ · Molluscs · *Crassostrea gigas* · *Crepidula fornicata* · Oosterschelde

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Coastal ecosystems are heavily used for the cultivation of bivalves such as oysters, mussels and cockles. The diet of sedentary suspension feeders which inhabit intertidal areas is directly dependent on the nature and quantity of the organic particles that are transported by the flood tide and maintained in suspension during immersion. Previous studies have pointed out that suspension-feeding bivalves can use specific food sources within the suspended particulate organic matter (POM) pool (Kiørboe & Mohlenberg 1981, Newell & Jordan 1983, Riera & Richard 1996). In shellfish culture areas, co-occurring suspension-feeding invertebrates may feed on either the same or different components of the suspended POM.

The common Atlantic slipper limpet *Crepidula fornicata* is a marine gastropod which is native from the east coast of America from Canada to the Gulf of Mexico

(Walne 1956). It was introduced to Europe via the importation of the Japanese oyster *Crassostrea virginica*. *C. fornicata* is able to feed on suspended particles due to a large mantle cavity and a long gill (Walne 1956, Graham 1988). Its proliferation has been facilitated by human activities related to aquaculture (Hamon 1996). Trophic competition between *Crassostrea gigas* and *C. fornicata* has been hypothesised (Walne 1956, Deslous-Paoli 1985), with previous studies attempting to quantify the impact of *C. fornicata* feeding activity on the trophic resources in Marennes-Oléron Bay, France, where extensive *C. gigas* production occurs (Héral & Deslous-Paoli 1983). These studies revealed the quantitative importance of the suspended POM pool in the diet of *C. fornicata*, as well as for *C. gigas*, suggesting trophic competition between these species. However, the food sources really used by these suspension feeders within the suspended POM pool were not identified. It is necessary to clarify the actual similarity of their diet. Stable carbon and nitrogen isotopes have increasingly been used in studies whose aim is to identify the source of organic matter in the diet of consumers (Schwinghamer et al. 1983). In addition, animals which show similar carbon and nitrogen stable isotopes ratios are assumed to have similar assimilated food sources insofar as these sources have been proved to be isotopically distinct (McConaughey & McRoy 1979, Fry et al. 1987). Thus, the use of $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ may give clues about potential competition for food sources which can take place among co-occurring sedentary species.

The aim of this study was to perform diet comparisons among different mollusc species within an intertidal community by use of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. In particular, the study focussed on the diet similarity of 2 dominant species of the benthic community, namely *Crassostrea gigas* and its epibiont *Crepidula fornicata*.

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Data collection and preparation. The Oosterschelde estuary, The Netherlands, was modified during the period 1979–1986, when a storm-surge barrier was built in the seaward entrance of this estuary. Ever since, it has been disconnected from river inputs by the construction of 2 large auxiliary compartment dams at the rear end of the system. Hence, the freshwater inputs from the Scheldt, Rhine and Meuse rivers discharge mainly into the Westerchelde (Nienhuis & Smaal 1994). As a result, the Oosterschelde changed from a turbid estuary into a tidal bay. Following the reduction of tidal current velocities in the Oosterschelde, the abundance of *Crepidula fornicata* increased (Kluijver & Leewis 1994).

The sampling station was located at Yerseke on the border of the Oosterschelde ($51^{\circ} 29' 80''$ N, $4^{\circ} 3' 50''$ E). It consisted of an intertidal flat containing muddy sand as well as artificial rocky shores that border this tidal area. The benthic community included *Crepidula fornicata*, which was mostly attached to *Crassostrea gigas*. In a previous study that compared the $\delta^{15}\text{N}$ between the Oosterschelde and the Westerschelde, it was demonstrated that the benthic food web of the Yerseke sampling station was not affected by anthropogenic nitrogen inputs as was the case in the Westerschelde, which forms the catchment of a densely urbanised and polluted area (Riera et al. 2000). The Oosterschelde is therefore more favorable for shellfish culture. Sampling was carried out during January–February 1998, May 1998 and July 1998. POM, SOM (suspended particulate and sedimented organic matter, respectively) and the main benthic primary producers and mollusc species were collected. POM was sampled by collecting 2 l bottles of water on the flats at high tide (± 1 h after high tide) from a depth of about 0.5 m below the water surface. For stable isotope analyses POM was obtained by filtration on pre-combusted Whatman GF/F glass fiber filters within 2 h after collection. Subsequently, the membranes were acidified (1 M HCl) in order to remove carbonates, briefly rinsed with Milli-Q water, freeze-dried and kept at -20°C until analysis. Sediment samples were taken at low tide by scraping the upper 10 mm of mud, from a total surface of approximately 1 m^2 . For the measurements of stable isotopic ratios of the SOM, the sediment collected was acidified in a glass receptacle with 10% HCl, rinsed several times with distilled water and dried (60°C). The sediment was freeze-dried and ground using a mortar. Benthic diatoms were extracted from the sediment surface, using the method of Couch (1989), slightly modified by Riera & Richard (1996). The diatoms were then collected on previously combusted glass fiber filters, washed with 1 M HCl, briefly rinsed with Milli-Q water and freeze-dried. The filters were stored frozen (-20°C) until they were analyzed.

Macroalgae, which were present on rocky substrates at the base of the dikes, were dominated by *Fucus vesiculosus* and *Enteromorpha* sp. These were collected manually, cleaned of their epibionts, washed with 1 M HCl to remove carbonates, and rinsed with Milli-Q water. They were then freeze-dried and subsequently ground to a powder using a mortar and pestle.

Individuals of *Crepidula fornicata* and *Crassostrea gigas*, the dominant suspension feeders at this site, were collected by hand on the rocky substrates at low tide. Specimens of *Mytilus edulis* were also taken by hand on rocky substrates while *Cerastoderma edule* was collected on surficial intertidal sediments close to rocky substrates at the base of the dikes. *Littorina littorea* and *L. saxatilis*, which were abundant at this station, were collected on surficial sediment and rocky substrates at low tide. All individuals were cleaned of epibionts and kept alive overnight in the laboratory in filtered water from the sampling site to allow evacuation of gut contents. The organisms were killed by freezing. After dissection from the shell, the flesh was treated with 1 M HCl to remove any carbonate debris and rinsed with distilled water. The individuals were subsequently freeze-dried and ground to a powder using a mortar and pestle.

Carbon and nitrogen isotope ratios were determined using a Fisons CN analyser coupled on line, via a Finnigan con-flo 2 interface, with a Finnigan Delta S mass-spectrometer.

Data are expressed in the standard δ unit notation:

$$\delta X = [(R_{\text{sample}}/R_{\text{reference}}) - 1] \times 10^3$$

where $X = \text{C}$ (carbon) or N (nitrogen) and $R = {}^{13}\text{C}/{}^{12}\text{C}$ for carbon and ${}^{15}\text{N}/{}^{14}\text{N}$ for nitrogen, and are reported relative to the Vienna Pee Dee Belemnite standard (PDB) for carbon and to air N_2 for nitrogen. Average reproducibilities based on replicate measurements for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were 0.1 and 0.13‰, respectively.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ comparisons among co-occurring molluscs. $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ (range of values) of the different sources of organic matter and the intertidal benthic invertebrates at the 3 sampling periods are presented in Table 1. From these results, the main organic matter sources in the intertidal area were clearly separated by their $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ values, allowing the comparison of diets of the co-occurring molluscs of the intertidal community. The identification of food sources for the primary consumers (Fig. 1) involves a mean trophic enrichment in $\delta^{13}\text{C}$ of 1‰ (DeNiro & Epstein 1978, Rau et al. 1983) and a mean trophic enrichment in $\delta^{15}\text{N}$ of 3.5‰ (Minagawa & Wada 1984, Owens 1987) above primary producers.

The mean $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ values of the deposit feeders *Littorina littorea* and *L. saxatilis* set them apart from the suspension-feeding molluscs (i.e. *Crassostrea gigas*, *Mytilus edulis*, *Cerastoderma edule*, *Crepidula*

Table 1. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (mean \pm SD) of POM (particulate organic matter), SOM (sedimented organic matter), algae and intertidal molluscs in the Oosterschelde (The Netherlands) during winter, spring and summer 1998. n: number of individuals; -: not sampled

	Winter $\delta^{13}\text{C}$	Winter $\delta^{15}\text{N}$	n	Spring $\delta^{13}\text{C}$	Spring $\delta^{15}\text{N}$	n	Summer $\delta^{13}\text{C}$	Summer $\delta^{15}\text{N}$	n
Sources									
SOM	-21.8 \pm 0.4	7.3 \pm 0.1	3	-22.0 \pm 0.1	-	3	-19.2 \pm 0.2	7.8 \pm 0.5	3
POM	-23.2 \pm 0.6	1.4 \pm 1.6	3	-22.2 \pm 0.1	4.2 \pm 0.1	2	-20.9	6.2	1
Benthic diatoms	-11.3 \pm 0.1	9.1 \pm 0.2	2	-14.5 \pm 0.2	7.2 \pm 0.3	4			
<i>Fucus vesiculosus</i>	-18.5 \pm 0.4	6.3 \pm 0.2	2	-	-		-15.3 \pm 0.5	12.6 \pm 0.2	2
<i>Enteromorpha</i> sp.	-19.3 \pm 1.1	7.3 \pm 1.3	4	-	-		-11.0 \pm 0.2	12.3 \pm 0.1	2
<i>Ulva</i> sp.									
Intertidal molluscs									
<i>Crepidula fornicata</i>	-16.2 \pm 0.3	10.7 \pm 0.3	5	-16.3 \pm 0.4	10.4 \pm 0.3	3	-	-	
<i>Crassostrea gigas</i>	-17.3 \pm 0.3	10.1 \pm 0.1	5	-17.7 \pm 0.3	10.2 \pm 0.2	3	-17.9 \pm 0.6	9.6 \pm 0.5	5
<i>Mytilus edulis</i>	-16.6 \pm 0.4	10.9 \pm 0.1	5	-17	12	1	-17.3 \pm 0.2	10.6 \pm 0.2	4
<i>Cerastoderma edule</i>	-15.9 \pm 0.2	10.4 \pm 0.5	7	-16.2 \pm 0.3	11.2 \pm 0.7	2	-17.1 \pm 0.3	10.5 \pm 0.3	4
<i>Littorina littorea</i>	-15.0 \pm 0.5	12.2 \pm 0.7	3	-12.7 \pm 0.9	15.4 \pm 1.3	2	-14.1 \pm 0.7	13.2 \pm 0.2	3
<i>Littorina saxatilis</i>	-16.0 \pm 1.4	12.0 \pm 1.2	2	-	-		-	-	

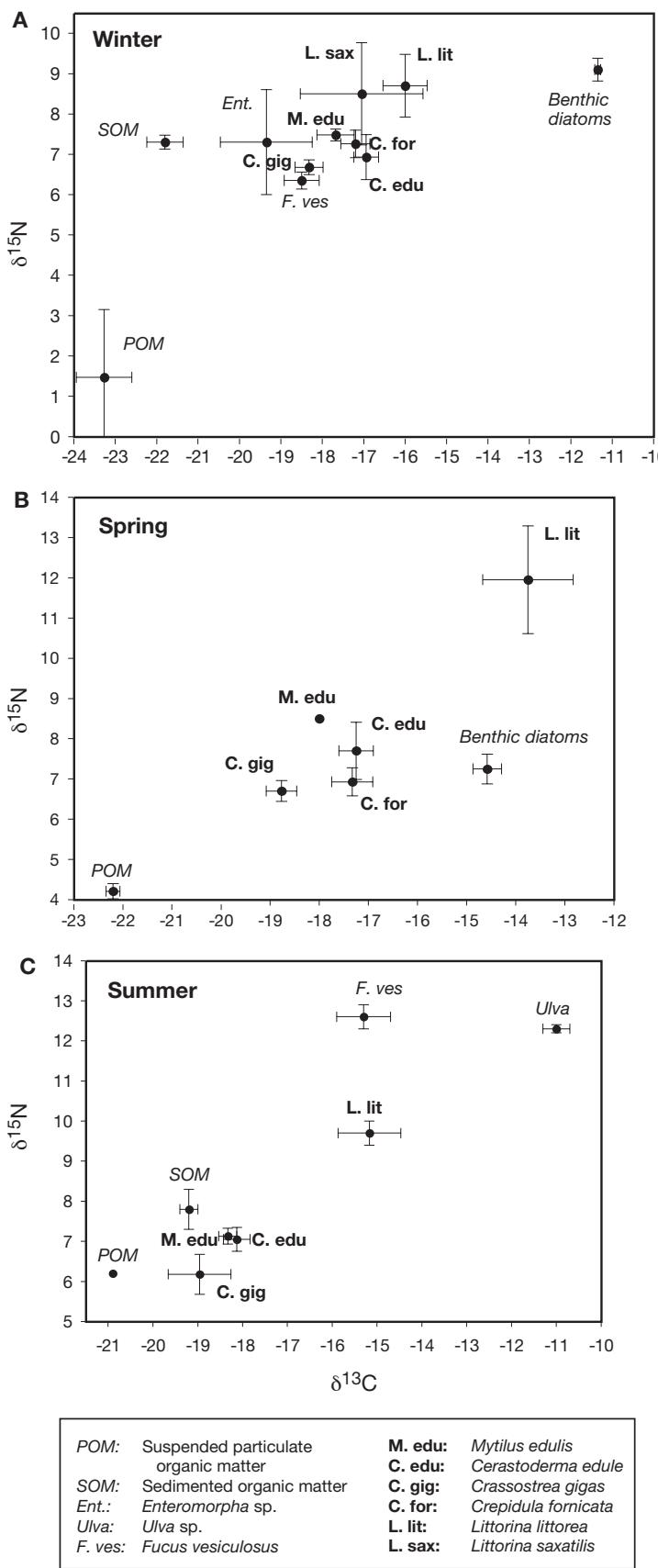
fornicata). In winter, the $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ values of littorinids may probably be explained by a mixed diet including SOM and resuspended benthic diatoms (Fig. 1A). However, in spring and summer, benthic diatoms could not entirely explain the mean $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ values of *L. littorea*. These $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ values were most likely due to a mixed diet including SOM and macroalgae, namely *Ulva* sp. and/or *Fucus vesiculosus* (Fig. 1C). In addition, although their $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ values were not determined, epiphytic and/or epilithic microalgae that cover the seaweeds and the rocky substrate could also contribute to the diet of littorinids (Jennings et al. 1997). The results of the present study demonstrate the ability of *L. littorea* to use different food sources within its habitat during the 3 sampling seasons (Kruskall-Wallis test, p = 0.09 and p = 0.06 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively).

During winter and spring, the suspension-feeding invertebrates exhibited $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ values suggestive of a mixed diet of benthic diatoms and suspended POM, with possible input of *Fucus vesiculosus* (Fig. 1A,B). However, unless it is highly fragmented, the macroalgae *F. vesiculosus* is not directly available to *Crepidula fornicata* and bivalves due to their suspension feeding mode. In any event, the $\delta^{15}\text{N}$ values indicate that detritus derived from *F. vesiculosus* did not contribute significantly to the suspended POM pool (Fig. 1A), whereas benthic diatoms could represent a primary food source for intertidal bivalves (Riera & Richard 1996, Riera et al. 1999). In summer, no benthic diatoms mats were present at the sediment surface (Riera pers. obs.); the food sources assimilated by the suspensivores were mostly from the suspended POM pool (Fig. 1C). Thus, the $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ values of the filter-feeding molluscs were likely to result from (1) a mixed diet including resuspended benthic diatoms and suspended POM and/or

(2) the utilisation of specific components of the suspended POM which included phytoplankton and detritus.

Several differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were observed among the co-occurring suspension-feeding species considered. In fact, *Crassostrea gigas* exhibited lighter $\delta^{13}\text{C}$ than *Cerastoderma edule* in winter (Mann-Whitney U-test, p < 0.01), summer (p < 0.05) and spring (p = 0.08), and lighter $\delta^{15}\text{N}$ in summer (p < 0.05) and spring (p = 0.08). In contrast, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values did not differ significantly between *Crepidula fornicata* and *C. edule* (p > 0.1 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in winter and spring). These results strongly suggest more similar assimilated food sources for *C. fornicata* and *C. edule* than between *C. gigas* and *C. edule*. In winter, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *Mytilus edulis* were heavier than those of *C. gigas* (Mann-Whitney U-test, p < 0.05) but were similar to those of *C. fornicata* (p > 0.1 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). In addition, differences in isotopic signatures between *C. gigas* and *C. fornicata* were observed during winter (Mann-Whitney U-test, p < 0.01 and p < 0.05 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) and spring (p < 0.05 for $\delta^{13}\text{C}$). Together, these results suggest that the assimilated food sources of *C. gigas* differed from those of the 3 other suspension-feeding molluscs (*M. edulis*, *C. edule* and *C. fornicata*).

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *Crassostrea gigas* and *Crepidula fornicata*: implication for trophic competition studies. The intertidal community considered was largely dominated by *C. gigas* used as substrate shell by *C. fornicata*. *C. fornicata* has been often considered as a competitor for food with commercially important bivalves to which they are attached and, in particular, with the Japanese oyster *C. gigas* (Walne 1956, Newell & Kofoed 1977, Deslous-Paoli 1985). In the present study, *C. gigas* and *C. fornicata*, exhibited different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures, indicating that they did not



have the same assimilated food sources. The isotopic differences may be explained by assuming the use of the same food sources, namely benthic diatoms and the suspended POM (Fig. 1A,B), but in different proportions and/or the assimilation of different specific components within the suspended POM pool. Although no isotopic measurements were performed on partitioned POM available to this suspension-feeding community, significant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differences among different size classes of marine suspended POM and plankton have been reported from the Woods Hole Harbor (Wainright & Fry 1994) and from the northern Baltic proper (Rolff 2000). From these studies and the present results we hypothesise that isotopic differences between the suspension-feeding invertebrates are due to the preferential utilisation of different POM size classes, as reported by Lesser et al. (1992) for *Mytilus edulis*, *C. fornicata* and *Ciona intestinalis*. The ability of *Crassostrea* species to select for specific organic matter components within the available suspended POM pool was observed previously (Newell & Jordan 1983, Riera & Richard 1996). This ability to utilise different parts of the available suspended POM pool as a food source may reduce competition for food between *C. gigas* and *C. fornicata*. Thus, we can hypothesise that in the presence of food limitation, competition between *C. gigas* and *C. fornicata* is unlikely because of diet differences. This ability may also partially explain the successful proliferation of *C. fornicata* together with *C. gigas* observed in several shellfish culture areas (Blanchard 1995).

The temporal variation of the isotopic composition of a species can give clues about the variability of its food sources throughout the annual cycle. In this study, the absence of differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of *Crassostrea gigas* among the 3 sampling periods (Kruskall-Wallis ANOVA, $p > 0.1$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) suggests an overall stability of their food sources from winter to summer 1998. Consistent with these results, in coastal marine environments where no river inputs occurred, *C. gigas* exhibited very little $\delta^{13}\text{C}$ monthly variation throughout the year due to its ability to preferentially utilise benthic and/or planktonic microalgae (Riera & Richard 1997). Unfortunately, no samples were taken in summer, but a similar temporal trend

Fig. 1. $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ (mean \pm SD) of intertidal molluscs corrected for trophic fractionation, compared with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of POM, SOM and the main organic matter sources in the Oosterschelde (The Netherlands) during winter, spring and summer 1998. Values of 1 and 3.5‰ of primary consumers have been subtracted from the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively, to correct for trophic fractionation

may also be suggested for *Crepidula fornicate*, which exhibited no significant variation for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between winter and spring (Mann-Whitney *U*-test, $p > 0.1$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$).

In conclusion, the most abundant suspension-feeding molluscs in this intertidal area assimilate different food sources from the available suspended POM pool. *Crepidula fornicate* is apparently not a competitor for *Crassostrea gigas*. These results underline the need for complementary studies to investigate the question of competitive interactions for food among intertidal communities that include commercially important bivalves.

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