Limnol. Oceanogr., 49(2), 2004, 408–414

Interspecific and intraspecific variation of $\delta^{13}C$ and $\delta^{15}N$ in deposit- and suspension-feeding bivalves (*Macoma balthica* and *Cerastoderma edule*): Evidence of ontogenetic changes in feeding mode of *Macoma balthica*

F. Rossi,[1] *P. M. J. Herman, and J. J. Middelburg*
Netherlands Institute of Ecology (NIOO-KNAW), Korringaweg 7, 4401 NT Yerseke, the Netherlands

Abstract

Deposit and suspension feeders can switch feeding behavior and show variations in feeding mode as individuals pass through life-cycle stages. Stable carbon and nitrogen isotopes were used to trace changes in diet of the tellinid bivalves *M. balthica* (facultative deposit feeder) and *C. edule* (obligatory suspension feeder), according to their size class. Analyses of variance showed differences in the $\delta^{13}C$ between the species. *C. edule* showed a diet composed of microphytoplankton, whereas *M. balthica* could feed on a mixed diet of microalgae from benthos and plankton. Values of $\delta^{13}C$ depended significantly on body size in *M. balthica,* providing evidence of ontogenetic variation in diet with small juveniles feeding entirely on microphytobenthos, while there was a gradual tendency for larger sizes to feed more on microphytoplankton. Therefore, although these species rely on different sources of food, large animals of *M. balthica* can overlap the trophic niche of *C. edule.* Population dynamics of the animals should be considered in food-web studies.

Trophic relationships determine the abundance and size of populations, as well as the structure and functioning of ecosystems and food webs (Abrams and Roth 1994; Vander Zanden and Rasmussen 1999). Identification of the dietary components can be extremely difficult for animals living on and in sediments such as deposit and suspension feeders. Although suspension and deposit feeders can live under completely different regimes of food supply (Levinton 1972), there can be a gradual transition from the food present in the top layer of the sediment, on which surface deposit feeders rely, to the suspended matter in the water just above the sediment surface, on which benthic suspension feeders forage (Taghon and Greene 1992; Riisgard and Kamermans 2001). Animals such as polychaetes and bivalves have the ability to switch feeding mode, according to the availability of food (Levinton 1991; Taghon and Greene 1992; Kamermans 1994; Bock and Miller 1997). In addition, ontogenetic shifts in diet occur in worms that deposit feed as adults, whereas small individuals feed in a different mode in order to overcome physiological constraints (Shimeta 1996; Hentschel 1998). For instance, when juveniles have physiological limitation in the maximum rate of food uptake, compared to cospecific adults, they might rely on higher quality sources of food in order to minimize the amount of food and maximize energy uptake (Hentschel 1998).

In many shallow coastal environments, bivalve mollusks represent an important link in the food chain from primary producers, such as planktonic and benthic microalgae, to epibenthic predators (Heip et al. 1995). For example, the tellinid clams *Macoma balthica* (L.) and the edible cockles *Cerastoderma edule* (L.) are abundant and very common on sandy and muddy coasts of the Northern hemisphere. They feed mostly on algae from the sediment (facultative deposit feeder) and the water column (suspension feeder), respectively. Sometimes, they may rely on the same sources of food, characterized by a mix of benthic and planktonic algae (Kamermans 1994; Kang et al. 1999). Ontogenetic differences in diet might occur in these species, but there are very few studies that investigate such relationships (Kang et al. 1999; Herman et al. 2000). Knowledge of their diet composition and especially of their niche is, however, crucial for describing and understanding the benthic food web because individuals of different size classes can play a different functional role in the ecosystem, based on diet or habitat use (Olson 1996).

The goal of this paper is to determine whether *C. edule* and *M. balthica* rely on separate or mixed sources of food and whether variation in diet is related to the ontogenetic stages of animals. We employ stable-isotope methods, since they could be applied to the issue of ontogenetic differences. Fortunately stable isotopes have become a powerful tool to determine the diets of many organisms, especially omnivores and deposit feeders (Peterson and Fry 1987; Hentschel 1998; Vander Zanden and Rasmussen 1999; Herman et al. 2000; Middelburg et al. 2000; Riera et al. 1999, 2002; Post 2002).

Material and methods

Field collections—Animals were collected at the Molenplaat, Westerschelde estuary, the Netherlands (*see* Middelburg and Nieuwenhuize 1998 and Herman et al. 2001). Sampling took place at Sta. 4 as described in Herman et al. (2000) from June 1999 to November 2000. During this period, seven sampling dates were chosen randomly when low tide occurred during the day, at approximately an interval of 2–3 months. At each date, sediment was collected using

[1] Corresponding author (F.Rossi@nioo.knaw.nl).

Acknowledgments

We thank Bernhard Krebs, Pieter van Rijswijk, Piet de Koeyer, and Joop Nieuwenhuize for logistic, field, laboratory, and analytical support. We also thank three anonymous referees and J. D. Ackerman for their suggestions, which helped to improve the manuscript. This research has been partially supported by the EU programme ECOFLAT (ENV4-CT96-0216). This is NIOO publication 3273 and ELOISE publication 451/23

cores (11-cm diameter) to 30-cm depth. In the laboratory, animals were sorted alive, divided into size classes after measuring their body length with a caliper at a precision of 1 mm, and freeze dried. Soft parts of the bivalves were removed from the shells, after dipping animals into boiling filtered seawater. Animals of the same size were pooled together for the analyses of isotopes, when a single animal did not reach a size suitable for chemical analyses. During May 2000, at low tide, planktonic larvae of *M. balthica* were also collected, in the water column adjacent to Molenplaat. Once the water was filtered, larvae were picked by hand and pooled together to reach a size suitable for the analysis of $\delta^{13}C$.

Animals were not separated from their guts and results refer to the isotope content of the animals plus the guts. Herman et al. (2000) demonstrated that even for deliberate tracer additions with high $\delta^{13}C$ of the food, the influence of gut contents on the labeling of animals is in the order of only 1–5% after 4 d. The influence becomes negligible and is minimized by the differences in physiological response time of the individuals (small animals having a faster tissue turnover time than large ones) when considering natural variations in the isotope ratios of food (which are in the range of a few ‰ only) and time scales for this variation of several weeks.

Analytical technique—The carbon and nitrogen isotopic composition of the samples was determined using a Fisons elemental analyzer coupled on line via a Finningan conflo 2 interface to a Finningan delta S mass spectrometer. The carbon and nitrogen isotope ratios are expressed in the delta notation $\delta^{13}C$ and $\delta^{15}N$, where

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

Results are referred to Vienna PDB for C and to atmospheric nitrogen for N and expressed in units of ‰. Reproducibility of the measurements is better than 0.2‰ (Herman et al. 2000).

Analyses of data—Specifically, we examined whether the tissue compositions of $\delta^{13}C$ and $\delta^{15}N$ were (1) different between *M. balthica* and *C. edule* and (2) different among size classes.

Differences in the isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) between *C. edule* and *M. balthica* were analyzed with two-factor mixed model of analyses of variance (ANOVA). Species (fixed) and dates (random and orthogonal to species) were the factors. In order to have a balanced design, six replicates were randomly chosen from each date of sampling for the values of $\delta^{13}C$ and $\delta^{15}N$ of each species. However, only four individuals of *C. edule* were collected in June 1999, and this date was, therefore, not included. Before analysis, the homogeneity of variances was evaluated by using Cochran's test (Winer et al. 1991), and normality of the data was tested by plotting the mean against the variance estimates. Data were transformed as needed. When significant differences among treatments and their interactions were found, Student–Newman–Keuls (SNK) tests were undertaken as a posteriori comparisons (Underwood 1997).

Variability among individuals in the isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) was measured by estimating the residual variance at each sampling date. Data were log transformed before estimating variances to correct for the nonnormal distribution of variances (Searle at al. 1992). Differences between *C. edule* and *M. balthica* were analyzed using one-factor (species) analyses of variance, with variance estimates at each date as replicates.

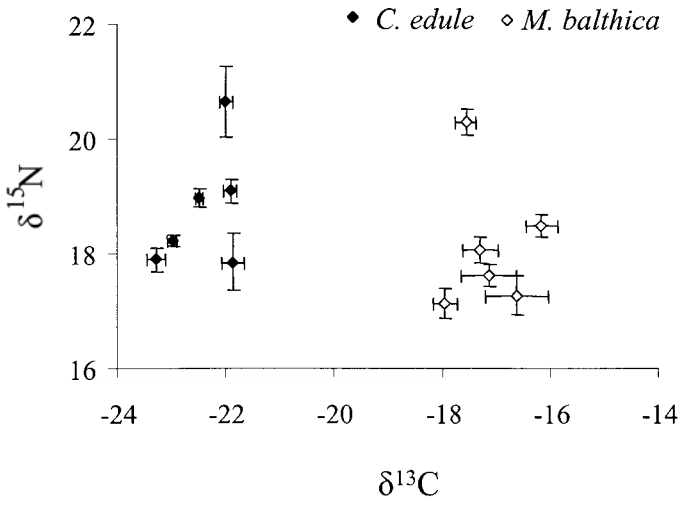

Fig. 1. Differences in the dual isotopic composition between *C. edule* and *M. balthica,* averaged from six replicates at each of the sampling dates. Error bars represent ±1 SE.

LOWESS smoothing was used to search for functional relationships (Trexler and Travis 1993). However, it did not reveal any clear functional change with the size (*see Figs. 2–4*).

The relationships between the body size of the animals and stable-isotope composition in their tissues was analyzed with one-way analysis of covariance with dates as factor, the proportion of ^{13}C and ^{15}N as variables, and body size as covariate. First, a linear regression model was tested separately for each date. If there were significant regressions ($P < 0.05$) among stable-isotope tissue and size classes, in all the dates of sampling, the homogeneity of b (as the slopes of linear regression) was tested. Although significant regressions were sometimes found in all the dates, b values were not homogeneous and the analysis of covariance was not done any further. Homogeneity of variance from regression was tested using Cochran's C test (Huitema 1980; Underwood 1997). The June 1999 dataset for *C. edule* was again eliminated from the analyses.

Results

$\delta^{13}C$ and $\delta^{15}N$ of M. balthica *and* C. edule—There were marked differences in the $\delta^{13}C$ composition of tissues between *M. balthica* and *C. edule*, and the $\delta^{13}C$ values of *M. balthica* were always heavier than those of *C. edule* all over the period of sampling (Fig. 1). There were, however, temporal changes in the extent of these differences, which varied, on average, from 4‰ to 8‰ among the sampling dates (Fig. 1, ANOVA, interaction species × dates, $F_{5,108} = 4.56$, $P < 0.05$; SNK, $P < 0.05$). The $\delta^{13}C$ of *C. edule* (−22.41

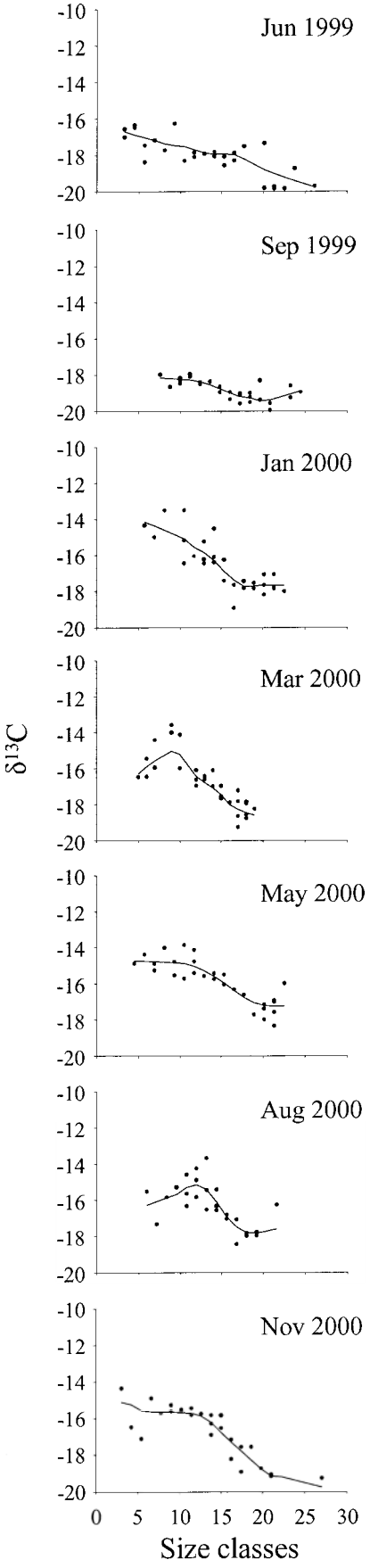

Fig. 2. Regressions of the size of *M. balthica* versus the $\delta^{13}C$ content of the tissues. LOWESS smoothing ($f = 0.5$) is shown.

$\pm$ 0.10 [mean $\pm$ SE]; $n = 60$ all over the year; and -21.41 $\pm$ 0.13; $n = 6$ in May 2000) was very similar to the one found in the larvae of *M. balthica,* as collected in May 2000 (-21.21 $\pm$ 0.44; $n = 3$). Furthermore, there was greater variability (variance estimate) in $\delta^{13}C$ for *M. balthica* (1.50 $\pm$ 0.67) than for *C. edule* (0.21 $\pm$ 0.01) (ANOVA, $F_{1,6} = 6.10$, $P < 0.05$).

Conversely, no differences between species were found for $\delta^{15}N$, which was quite variable in time, with the highest values in March 2000 in both the species (dates $F_{5,108} = 24.59$, $P < 0.01$; SNK, $P < 0.05$).

Intraspecific variation in $\delta^{13}C$ and $\delta^{15}N$—The $\delta^{13}C$ values in the tissues of *M. balthica* decreased with the size of the animals, and this pattern was consistent in all the sampling dates (Fig. 2; Table 1). The strength of this relationship, however, varied among the sampling dates, and there were significant differences in the slopes of the linear regression calculated for each sampling period ($F_{6,195} = 3.52$, $P < 0.05$). Conversely, there was no consistent trend in $\delta^{15}N$ (Fig. 3). Correlations were evident in June 1999 and March 2000 (Fig. 3). In June 1999 $\delta^{15}N$ was higher in larger animals ($r^2 = 0.79$, $b = 0.17$), whereas in March 2000 it was lower in larger animals ($r^2 = 0.78$, $b = -0.40$). Only in these two dates were there significant linear regressions ($F_{1,27} = 103.30$ and $F_{1,27} = 94.50$, $P < 0.01$, respectively).

There was no evidence of changes in the isotope composition of the tissues in *C. edule* related to the size. Sometimes, there was variation in $\delta^{13}C$ and $\delta^{15}N$, but it was unlikely that these relations were due to changes in foraging with the size of the animals. $\delta^{13}C$ values were significantly correlated to the size of the animals in September 1999 ($F_{1,8} = 19.56$, $P < 0.01$; $r^2 = 0.71$ and $b = -0.09$), January ($F_{1,8} = 8.73$, $P < 0.05$; $r^2 = 0.61$; $b = 0.06$) and August 2000 ($F_{1,8} = 2.36$, $P < 0.05$; $r^2 = 0.22$; $b = 0.04$), but the correlations were in different directions and variation between large and small animals was in the order of 1‰ only (Fig. 4). For $\delta^{15}N$, there were significant negative slopes in May ($F_{1,8} = 3.96$, $P < 0.01$, $r^2 = 0.59$, $b = -0.09$) and August 2000 ($F_{1,8} = 5.65$, $P < 0.05$, $r^2 = 0.41$, $b = -0.15$), but changes were small (from 1 to 1.5‰).

Discussion

Interpretation of $\delta^{13}C$ changes as differences in diet—The use of isotope data to trace possible differences in diet among organisms is not free from errors. Animals assimilate diet components with varying efficiency, and, as a consequence, rapidly growing juveniles might incorporate new carbon and nitrogen (relative to their tissue) more rapidly than adults (Hentschel 1998). Furthermore they might fractionate isotopes and allocate them differently in the tissues (Gannes et al. 1997). For instance, at each trophic level, fractionation estimates are usually 1‰ for ^{13}C and 3–4‰ for

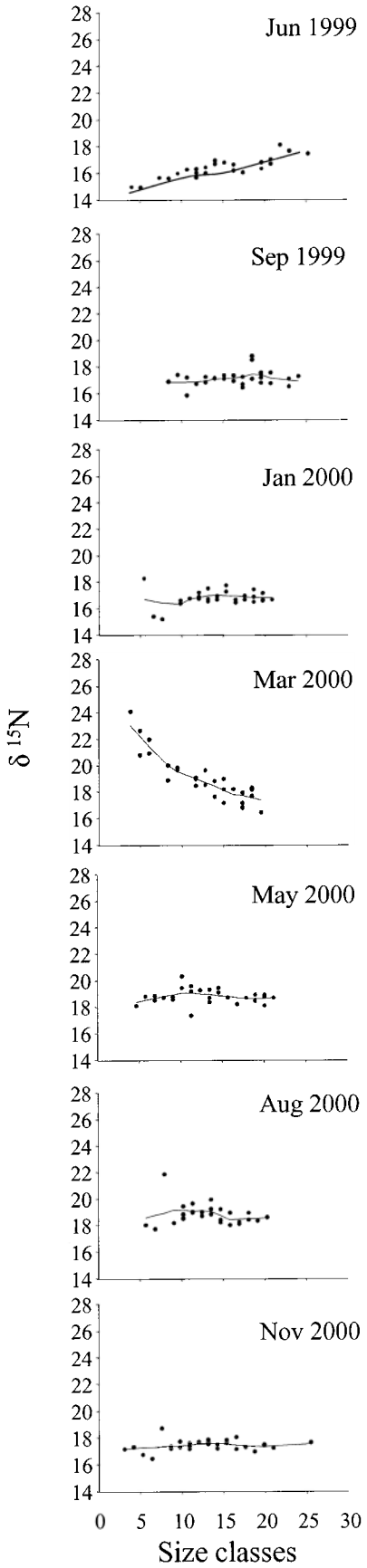

Fig. 3. Regressions of the size of *M. balthica* versus the $\delta^{15}N$ content of the tissues. LOWESS smoothing ($f = 0.5$) is shown.

Table 1. Summary of the results of the analyses of variance on the linear regression between the $\delta^{13}C$ of *M. balthica* and its size at each sampling site. The estimates of the slope (b) and the coefficient of determination (r^2) are shown. Data were not transformed, and all linear regressions were significant.

	$F_{1,27}$	b	r^2
Jun 99	43.15	−0.15	0.62
Sep 99	14.05	−0.10	0.34
Jan 00	53.45	−0.30	0.66
Mar 00	41.78	−0.27	0.61
May 00	63.40	−0.23	0.70
Aug 00	15.22	−0.25	0.36
Nov 00	39.30	−0.26	0.60

^{15}N, and fatty tissues are depleted in ^{13}C by 2‰ to 4‰ relative to muscles (e.g., Hentschel 1998; Kang et al. 1999; Vander Zanden and Rasmussen 2001; Dawson et al. 2002). Furthermore, availability and isotopic composition of resources may be quite variable over seasonal or short-term time scales, especially in estuaries (Heip et al. 1995; Riera et al. 2000). As a consequence, isotope variations among individuals and between species might indicate an artifact due to size-dependent rates of nutrient turnover, rather than ontogenetic changes in diet. To conclude that differences in isotope signatures are caused by ontogenetic changes, several individuals should be sampled for a period exceeding the time required to reflect significant changes in the isotope signature of their food (Hentschel 1998). Besides, analyzing different species with similar roles in food webs can support such interpretation of the results. In this study, in order to overcome these problems, individuals of two species were repeatedly sampled (seven times) over 18 months, which exceeds the time required to reflect changes in food resources and in food availability.

Ontogenetic changes in M. balthica—*M. balthica* did not change diet from juvenile to adult stages. Rather, larger animals tended to include dietary compounds typical of phytoplankton. Changes in diet might be more drastic when there is a metamorphoses or a change in habitat. Hentschel (1998) also described a gradual niche shift, with food sources stabilizing as animals approached adulthood. However, the black rockfish (*Sebastes inermis*) showed a dramatic difference in $\delta^{13}C$ between the young of the year (pelagic stage) and large, settled animals (benthic stage) (Takai et al. 2002). Hentschel (1998) suggested that shifts in diet with size might result from physiological constraints of juveniles in deposit-feeder worms. Small individuals have a small gut, which may not be able to process enough sediment to satisfy nutritional requirement for growth and metabolic functions. Sediment is nutrient poor, and the strategy adopted to increase diet quality might be to forage in a more macrophagous way, choosing highly nutritive particles such as benthic

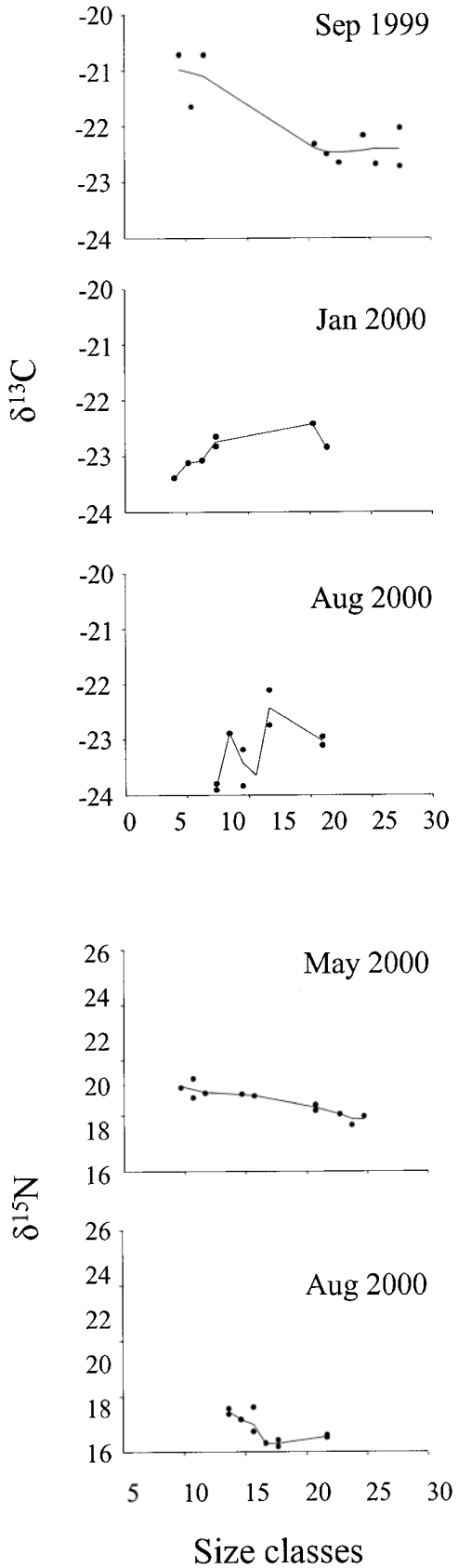

Fig. 4. Regressions of the size of *Cerastoderma edule* versus the $\delta^{13}C$ and $\delta^{15}N$ content of the tissues. Only significant regressions and LOWESS smoothing ($f = 0.5$) are shown.

diatoms. Consistently, in *M. balthica,* shift in diet and, thus, in feeding behavior might be related to some physiological constraints. For instance, suspension-feeding mode can be limited when animals are small. Like other bivalves (Zaklan and Ydenberg 1997), when *M. balthica* is buried deep, the siphon is maximally stretched to reach the surface of the sediment and animals can only rely on planktonic microalgae (de Goeij and Luttikhuizen 1998). Conversely, when *M. balthica* is buried shallow, it can still suspension feed with the siphon partially retracted but, preferentially, deposit feed and exploit the pool of benthic microalgae (de Goeij and Luttikhuizen 1998). However, small individuals do not have a siphon long enough to keep foraging (suspension feeding) and bury deep (Zwarts and Wanink 1989). Indeed, they tend to live shallower than large animals. Animals (smaller than 10 mm) decreased their depth of burial with decreasing size (Zwarts and Wanink 1989; Edjung and Bonsdorff 1992; Kamermans and Huitema 1994). Conversely, adults can burrow either deep or shallow and deposit and suspension feed, moving vertically to forage (de Goeij and Luttikhuizen 1998). Therefore, the shift in diet observed might be consistent with the size of the animals because of their vertical distribution in the sediment. Small animals might bury shallow more often and, thus, feed on the surface of the sediment, while large animals could vary their burial depth and feed on the sediment or on the water column.

Interspecific and intraspecific differences in the bivalves—For some bivalves, diet composition, as reflected in their isotope ratio, varied over time according to the availability of food (Riera et al. 2002). Our results showed that there were time-dependent changes in the values of $\delta^{13}C$ between the two species, but the signature of $\delta^{13}C$ for *M. balthica* was always enriched relative to that for *C. edule.* The consistency of patterns through time and the large difference in $\delta^{13}C$ between the two species were very important in order to ensure that the interpretation of the results as differences in diet was not a flaw due to biochemical and physiological processes. These differences (5–6‰) were also consistent with the differences (average of 5‰) between the values of $\delta^{13}C$ in coastal fauna using benthic carbon sources and animals deriving their carbon from phytoplankton (France 1995). They were also greater than the depletion of ^{13}C occurring between different tissues in the same animal (2‰ to 4‰).

Therefore, in this area, *M. balthica* and *C. edule* were likely to rely on different sources of food over their life cycle and, thus, to play a different role in soft sediments. However, the large variability of $\delta^{13}C$ in the tissues of *M. balthica* indicated that individuals of this species might rely on a wider range of sources of food than *C. edule* and, probably, might switch their feeding mode from suspension to deposit feeding. Contrary to our findings, Kamermans (1994) found similarity in food sources between *C. edule* and *M. balthica* in the Dutch Wadden Sea. Both species have been shown to use a mixed diet of benthic diatoms and phytoplankton in other studies (Kang et al. 1999; Riera et al. 1999). For *C. edule,* however, these results were attributed to the uptake of microphytobenthos resuspended in the water column (seston) rather than to a shift in the feeding mode. A deliberate

Table 2. Stable carbon and nitrogen isotope signatures (‰) of organic carbon and nitrogen sources in the intertidal areas of Westerchelde (for the location of the sites and more details see Moens et al. 2002).

C and/or N sources	Location	Date	$\delta^{13}C$	$\delta^{15}N$	Source*
Microphytobenthos	Molenplaat	1997	−14 to −16		1, 2
Bacteria (top mm)	Molenplaat	1997	−14.5		1
Suspended POM	Lower estuary	1994	−20 to −24	8 to 11	3
	Lower estuary	1996–1998	−22 to −26	7 to 15	4
Sediment POM	Lower estuary	1994	−21 to −24	8 to 13.5	3
	Molenplaat	1997	−19 to −23	14.2	2
Terrestrial POM	Estuary	1994	−26	3.5	3
C. edule	Molenplaat	1999–2000	−21 to −24	16 to 26	5
M. balthica	Molenplaat	1999–2000	−14 to −20	16 to 22	5
Larvae of *M. balthica*	Molenplaat	1999–2000	−21.21		5

* Sources: (1) Middelburg et al. 2000: (2) Herman et al. 2000: (3) Middelburg and Nieuwenhuize 1998: (4) Middelburg unpubl. data: (5) this study.

^{13}C-enrichment experiment in this area (Herman et al. 2000) revealed that uptake of ^{13}C-enriched microphytobenthos was relatively small for *C. edule*, whereas *M. balthica* was strongly labeled, indicating that it feeds mainly on benthic microalgae, consistent with the present results.

Whereas the relative values of $\delta^{13}C$ indicated that there was a clear difference in the dietary composition between the species analyzed, any statement on the absolute values of the sources of food cannot be conclusive because we did not measure the $\delta^{13}C$ values in different food sources at the time of sampling. Nevertheless, on the Molenplaat, high plant and phytodetritus of riverine origin are negligible food for macrobenthos (Herman et al. 2000), and $\delta^{13}C$ in the tissues of herbivorous animals, such as the study animals, reflects the isotope values of sedimentary and suspended microalgae. Values of $\delta^{13}C$, in the tissues of *C. edule* and *M. balthica*, corresponded to values of suspended particulate organic matter (POM) and microphytobenthos, which were measured previously in Molenplaat (Table 2). As well, values of *C. edule* coincide with $\delta^{13}C$ values in larvae of *M. balthica* (Table 2), which rely entirely on planktonic microalgae and provide a good estimate for microphytoplankton at the time of sampling (May 2000). Eventually, the limited range in $\delta^{13}C$ for *C. edule*, an obligatory suspension feeder, indicated that temporal variability in isotope signatures of phytoplankton is limited (Table 2).

The $\delta^{13}C$ values in the tissues of *M. balthica* decreased with the size of the animals. The smallest ones had heavier carbon, with values closer to the $\delta^{13}C$ typical of benthic diatoms than the largest animals, with more negative values, closer to the values measured in the tissues of their planktonic larvae and in *C. edule* (Table 2). As discussed before, we interpret these differences as evidence that small animals fed on microphytobenthos more than large animals. Conversely, the differences among size classes in *C. edule* occurred only at certain dates and had a very small interval of variation (1‰). In addition, such relationships, when occurring, were inconsistent, since sometimes they showed an increase and sometimes a decrease in $\delta^{13}C$ with the size of the animals.

In contrast to the pattern found for $\delta^{13}C$, tissues of both *C. edule* and *M. balthica* had quite similar and rather high values of $\delta^{15}N$ (Table 2). Published values of $\delta^{15}N$ are quite variable, especially during spring blooms of phytoplankton (Middelburg and Nieuwenhuize 1998; Riera et al. 1999) and during organic pollution, when $\delta^{15}N$ in all the components of food webs may rapidly respond to nitrogen inputs due to human activities (Riera et al. 2000; Gartner et al. 2002). Since the Westerschelde is largely recognized as a eutrophic area (Riera et al. 2000), the very high $\delta^{15}N$ values found in the two species might reflect extensive inputs of nutrients and prevent any discrimination between different sources of food.

Therefore, we propose that in this area, *M. balthica* and *C. edule* rely on different sources of food. *M. balthica* occupies a broader niche, feeding on either microphytobenthos or microphytoplankton, while *C. edule* feeds almost exclusively on microphytoplankton. The broader niche occupied by *M. balthica* partially depends on the size-class composition of *M. balthica*. Adults might partially overlap the food resources of both juveniles and adults of *C. edule*. This finding reveals the importance of considering the population dynamics of the animals when depicting trophic relationships.

References

Abrams, P. A., and J. D. Roth. 1994. The effects of enrichment of three-species food chains with nonlinear functional responses. Ecology **75:** 1118–1130.

Bock, M. J., and D. C. Miller. 1997. Particle-bound organic matter as a cue for suspension feeding in tentaculate polychaetes. J. Exp. Mar. Biol. Ecol. **215:** 65–80.

Dawson, T. E., S. Mambelli, A. Plamboek, P. H. Templer, and K. P. Tu. 2002. Stable isotopes in plant ecology. Annu. Rev. Ecol. Syst. **33:** 507–559.

de Goeij, P., and P. Luttikhuizen. 1998. Deep-burying reduces growth in intertidal bivalves: Field and mesocosm experiments with *Macoma balthica*. J. Exp. Mar. Biol. Ecol. **228:** 327–337.

Ejdung, G., and E. Bosdorff. 1992. Predation on the bivalve *Macoma balthica* by the isopod *Saduria entomon*: laboratory and field experiments. Mar. Ecol. Prog. Ser. **88:** 207–214.

France, R. L. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: Food web implications. Mar. Ecol. Prog. Ser. **124:** 307–312.

Gannes, L. Z., D. M. Obrien, and C. M. delRio. 1997. Stable isotopes in animal ecology: Assumptions, caveats, and a call for more laboratory experiments. Ecology **78:** 1271–1276.

Gartner, A., P. Lavery, and A. J. Smit. 2002. Use of $\delta^{15}N$ signatures of different functional forms of macroalgae and filter-

feeders to reveal temporal and spatial patterns in sewage dispersal. Mar. Ecol. Prog. Ser. **235**: 63–73.

HEIP, C. H. R., N. K. GOOSEN, P. M. J. HERMAN, J. KROKAMP, J. J. MIDDELBURG, AND K. SOETAERT. 1995. Production and consumption of biological particles in temperate tidal estuaries. Oceanogr. Mar. Biol. Annu. Rev. **33**: 1–149.

HENTSCHEL, B. T. 1998. Intraspecific variation in $\delta^{13}C$ indicates ontogenetic diet changes in deposit-feeding polychaetes. Ecology **79**: 1357–1370.

HERMAN, P. J. M., J. J. MIDDELBURG, AND C. H. R. HEIP. 2001. Benthic community structure and sediment processes on an intertidal flat: Results from the ECOFLAT project. Cont. Shelf Res. **21**: 2055–2071.

———, ———, J. WIDDOWS, C. H. LUCAS, AND C. H. R. HEIP. 2000. Stable isotopes as trophic tracers: Combining field sampling and manipulative labelling of food resources for macrobenthos. Mar. Ecol. Prog. Ser. **204**: 79–92.

HUITEMA, B. E. 1980. The analysis of covariance and alternatives. Wiley Interscience, New York.

KAMERMANS, P. 1994. Similarity in food source and timing of feeding in deposit- and suspension-feeding bivalves. Mar. Ecol. Prog. Ser. **104**: 63–75.

———, AND H. J. HUITEMA. 1994. Shrimp (*Crangon crangon* L.) browsing upon siphon tips inhibits feeding and growth in the bivalve *Macoma balthica* (L.). J. Exp. Mar. Biol. Ecol. **175**: 59–75.

KANG, C. K., P. G. SAURIAU, P. RICHARD, AND G. F. BLANCHARD. 1999. Food sources of the infaunal suspension-feeding bivalve *Cerastoderma edule* in a muddy sandflat of Marennes-Olèeron Bay, as determined by analyses of carbon and nitrogen stable isotopes. Mar. Ecol. Prog. Ser. **187**: 147–158.

LEVINTON, J. S. 1972. Stability and trophic structure in deposit-feeding and suspension feeding communities. Am. Nat. **106**: 472–486.

———. 1991. Variable feeding behaviour in three species of *Macoma balthica* (Bivalvia: Tellinacea) as a response to water flow and sediment transport. Mar. Biol. **110**: 375–383.

MIDDELBURG, J. J., C. BARRANGUET, T. S. BOSCHKER, P. M. J. HERMAN, T. MOENS, AND C. H. R. HEIP. 2000. The fate of intertidal microphytobenthos carbon: An in situ ^{13}C-labeling study. Limnol. Oceanogr. **45**: 1224–1234.

———, AND J. NIEUWENHUIZE. 1998. Carbon and nitrogen stable isotopes in suspended matter and sediments from the Schelde estuary. Mar. Chem. **60**: 217–225.

MOENS, T., C. LUYTEN, J. J. MIDDELBURG, P. M. J. HERMAN, AND M. VINCX. 2002. Tracing organic matter sources of estuarine tidal flat nematodes with stable carbon isotopes. Mar. Ecol. Prog. Ser. **234**: 127–137.

OLSON, M. 1996. Ontogenetic niche shifts in largemouth bass: Variability and consequences for first-year growth. Ecology **77**: 179–190.

PETERSON, B. J., AND B. FRY. 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. **18**: 293–320.

POST, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods and assumptions. Ecology **83**: 703–718.

RIERA, P., L. J. STAL, AND J. NIEUWENHUIZE. 2000. Heavy $\delta^{15}N$ in intertidal benthic algae and invertebrates in the Schelde estuary (The Netherlands): Effect of river nitrogen inputs. Estuar. Coast. Shelf Sci. **51**: 365–372.

———, ———, AND ———. 2002. $\delta^{13}C$ versus $\delta^{15}N$ of co-occurring molluscs within a community dominated by *Crassostea gigas* and *Crepidula furnicata* (Oosterschelde, The Netherlands). Mar. Ecol. Prog. Ser. **240**: 291–295.

———, ———, ———, P. RICHARD, G. BLANCHARD, AND F. GENTIL. 1999. Determination of food sources for benthic invertebrates in a salt marsh (Aiguillon Bay, France) by carbon and nitrogen stable isotopes: Importance of locally produced sources. Mar. Ecol. Prog. Ser. **187**: 301–307.

RIISGARD, H. U., AND P. KAMERMANS. 2001. Switching between deposit and suspension feeding in coastal zoobenthos. *In* Ecological comparisons of sedimentary shores. Ecol. Stud. **151**: 73–101.

SEARLE, S. R., G. CASELLA, AND C. E. MCCULLOCH. 1992. Variance components. Wiley.

SHIMETA, J. 1996. Particle-size selection by *Pseudopolydora paucibranchiata* (Polychaeta: Spionidae) in suspension feeding and in deposit feeding: Influences of ontogeny and flow speed. J. Exp. Mar. Biol. Ecol. **126**: 479–488.

TAGHON, G. L., AND R. R. GREENE. 1992. Utilization of deposited and suspended particulate matter by benthic "interface" feeders. Limnol. Oceanogr. **37**: 1370–1391.

TAKAI, N., Y. A. MISHIMA, A. YOROKU, AND A. HOSHIKA. 2002. Carbon sources for demersal fish in the western Seto Inland Sea, Japan, examined by $\delta^{13}C$ and $\delta^{15}N$. Limnol. Oceanogr. **47**: 703–741.

TREXLER, J. C., AND J. TRAVIS. 1993. Nontraditional regression-analyses. Ecology **74**: 1629–1637.

UNDERWOOD, A. J. 1997. Experiments in ecology. Their logical design and interpretation using analysis of variance. Cambridge Univ. Press.

VANDER ZANDEN, M. J., AND J. B. RASMUSSEN. 1999. Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. Ecology **80**: 1395–1404.

———, AND ———. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: Implications for aquatic food web studies. Limnol. Oceanogr. **46**: 2061–2066.

WINER, B. J., D. R. BROWN, AND K. M. MICHELS. 1991. Statistical principles in experimental design, 3rd ed. McGraw-Hill.

ZAKLAN, S. D., AND R. YDENBERG. 1997. The body size-burial depth relationship in the infaunal clam *Mya arenaria*. J. Exp. Mar. Biol. Ecol. **215**: 1–17.

ZWARTS, L., AND J. WANINK. 1989. Siphon size and burying depth in deposit- and suspension feeding benthic bivalves. Mar. Biol. **100**: 227–240.

Received: 20 May 2003
Accepted: 18 November 2003
Amended: 1 December 2003