



Short communication

Trophic plasticity of the gastropod *Hydrobia ulvae* within an intertidal bay (Roscoff, France): A stable isotope evidence

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ABSTRACT

The study investigated the trophic ecology of the gastropod *Hydrobia ulvae* in different habitat types within an intertidal bay. The results point out two major trophic pathways involving *H. ulvae* in this bay. On the one hand, in sandy/muddy sediments *Hydrobia* derives most of its energy from allochthonous detritus derived from *Enteromorpha* sp and the total SOM pool. In addition, in these sediments, the phototrophic purple bacteria mats played a substantial trophic role in the diet of *Hydrobia*. On the other hand, in a *Spartina maritima* marsh, the gastropod appears firstly dependent of autochthonous detritus derived from this plant. The minor contribution of microphytobenthos to the diet of *Hydrobia* is consistent with a relatively low presence of epipellic diatoms at the sampling sites. These results provide evidence that the trophic ecology of *H. ulvae* inhabiting intertidal sediments is quite plastic and does not necessarily rely primarily on microphytobenthos. Consequently, in a single bay, the small spatial scale variability in the origin and availability of detritus have direct implications on the food incorporation by *H. ulvae*.

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1. Introduction

In intertidal habitats, the high diversity of organic matter sources makes it difficult to determine the most important trophic pathways, and generates an important detrital organic matter pool (Mann, 1988) which can be used differently by animals. Hence, there is no paradigm stating, which main source of organic matter fuels the food web of coastal areas, and how dietary contributions can shift spatially and/or temporally for the most relevant species of these areas (Kwak and Zedler, 1997). *Hydrobia ulvae* (Pennant) is characteristically an inhabitant of intertidal mudflats and muddy/sandy sediments, which can also be found abundantly in a wide variety of intertidal substrata, including saltmarshes or macroalgae assemblages when present at sediment or rocky surface (Newell, 1965). Where abundant, the population densities of this gastropod can reach 30,000 ind m² as reported by Barnes and Greenwood (1978) who provide to *H. ulvae* a key trophic role as primary consumer and as prey for birds and fishes. Previous results concerning the dietary patterns of *H. ulvae* provided evidence of (1) its preferential trophic link with benthic diatoms in various intertidal mudflats in Western Europe (Lopez and Kofoed, 1980; Morrissey, 1988; Haubois et al., 2005) and (2) its influence on benthic diatom assemblages (Hagerthey et al., 2002). In the Aber bay of Roscoff, *H. ulvae* was reported to reach maximum densities of about

10 000 ind/m² (Rullier, 1959). Interestingly, in this bay, dense purple sulfur bacteria mats are commonly observed at the sediment surface, and reach their maximum development during summer (Riera, pers. obs.). These sulphide-oxidizing bacteria were hypothesized to contribute significantly to trophic transfers in salt marshes (Howarth and Teal, 1980). However, the possible contribution of purple bacteria to the diet of Hydrobiids remains unknown, especially as other coexisting food sources are potentially available to the gastropods. The ecological situation of the Aber bay during summer was, then, favourable to examine the significance of purple bacteria mats as food source of *H. ulvae* as compared to the other co-existing sources. In addition, in this bay, *H. ulvae* occurred abundantly in a localised *Spartina maritima* marsh allowing to investigate the trophic role of the organic matter derived from the *Spartina* for *H. ulvae*.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ distributions have further shown promise as a tool that provide a time-integrated measure of food web relationships. $\delta^{13}\text{C}$ show little enrichment ($\leq 1\text{‰}$), then being useful for the identification of the organic matter sources at the base of food chains. Because $\delta^{15}\text{N}$ of a consumer ultimately builds on the stable nitrogen isotope composition of food sources sustaining the food web, $\delta^{15}\text{N}$ can efficiently complement $\delta^{13}\text{C}$ in distinguishing among various possible diet sources.

The aim of this study was to survey the abundantly represented *H. ulvae* in different habitat types within a single intertidal bay in order (1) to determine the degree of dependence of this gastropod on locally occurring organic matter sources including purple bacteria mats and (2) to answer the question the possible trophic plasticity at small spatial scale.

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2. Material and methods

2.1. Sampling site

The study was conducted in the Roscoff Aber Bay, which is about 2 km long and 1 km wide, and includes different types of intertidal sediments. The bay is shallow (average depth 4 m), totally located above the mid-tide level, has strong currents, and a tidal range of about 4 m that leads to generally good mixing and high turbidity (Chauris, 1988). The southern end of the bay is limited by a dike, which contains a sluice-gate that allows river input (Fig. 1). In this bay, three intertidal stations corresponding to three habitat-types for *H. ulvae* have been considered. The “River station” located at the river entrance into the bay consists of estuarine muddy-sandy sediments extensively covered by stranded *Enteromorpha* sp and purple bacteria mats. The “Sandy station” consists of sandy sediments largely covered by stranded *Enteromorpha* sp and purple bacteria mats during summer. The third station, located in the southern part of the bay, is colonised by a small *S. maritima* marsh from about 40–50 m in length and width. In this bay, organic matter content in muddy/sandy and *Spartina* sediments was measured between 2.5 and 4.5% while sandy sediments show values between 0.6 and 1.2% (Riera, data not published). From a recent study (Hubas et al., 2006), the median grain size of the River station corresponded to very fine-sand sediments ($132 \pm 54 \mu\text{m}$), while close to the sandy station fine-sand sediments ($215 \pm 43 \mu\text{m}$) were reported. Unfortunately, no values are available

for the *Spartina* marsh, but from its location within the bay the sediment grain size appears close to the Sandy station (Riera, pers. obs.).

2.2. Collection and sample preparation

Samples of organic matter sources and individuals of *H. ulvae* were collected during August 2004. The densities of *H. ulvae* were monitored at the three sampling sites. Five replicate samples were taken at each site with a rectangular 2 cm deep scoop of area 0.01 m². Samples were sieved on site through a 1.0 mm mesh sieve, and the retained material was transported to the laboratory and the numbers of living *Hydrobia* counted over a light box. At low tide, sediment samples were taken by scraping the upper 1 cm of the sediment. For the measurements of stable isotope ratios of the sedimented organic matter (SOM), the sand was sieved to a grain size of <63 μm to separate sand grains from most of the SOM. Then, the SOM fraction <63 μm was acidified (10% HCl) rinsed several times with distilled water, dried (60 °C) and ground to powder. The stranded *Enteromorpha* sp was abundantly present at the sediment surface and easily identified to genus level (Cabioch et al., 1992). The detrital *Enteromorpha* sp was rinsed with filtered seawater (precombusted GF/F) to clean off epibionts, treated with 10% HCl to remove any residual carbonates, and rinsed with distilled water.

At the marine entrance of the bay, POM (suspended particulate organic matter) was sampled by collecting 2-l bottles of water at high tide (± 1 h) from a depth of about 50 cm below the water surface. POM was obtained by filtration on precombusted Whatman GF/F glass fiber membranes within 2 h after collection. Subsequently, the membranes were acidified (10% HCl) in order to remove carbonates, briefly rinsed with Milli-Q water, freeze-dried and kept at -32 °C until analysis. At low tide, live and dead leaves of *S. maritima* were collected by hand and prepared as for *Enteromorpha* sp. Subsequently, the samples were dried (60 °C) and ground to powder using a mortar and pestle. Sample of free-living purple bacteria were collected in the field where dense purple mats developed at the sediment surface. These photosynthetic purple bacteria were collected by suction pipetting samples from the surface of creek sediment. At the laboratory, the samples were observed under magnifying glass to remove carefully any remaining detritus and dried at 50 °C. In the Aber bay of Roscoff, purple bacteria mats were reported to be mostly associated with the decomposition of *Enteromorpha* sp and were dominated by the purple sulphur bacteria *Thiorhodobacter* spp (Rullier, 1959).

H. ulvae was collected from the surficial sediment at low tide close to the quadrats used for density estimation. Specimens were taken by hand and kept alive overnight at the laboratory in filtered water from the sampling site to allow evacuation of gut contents. Then, they were killed by freezing, dissected and the flesh quickly treated with 10% HCl to remove any carbonate debris from the shell and rinsed with distilled water. They were then freeze-dried, ground to a powder using mortar and pestle and kept frozen until analysis.

2.3. Stable isotope measurements

Carbon and nitrogen isotope ratios were determined using a Fisons CN analyser coupled with a Finnigan Delta S mass spectrometer, via a Finnigan Con-Flo III interface. Data are expressed in the standard δ unit notation.

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

With $R = {}^{13}\text{C}/{}^{12}\text{C}$ for carbon and ${}^{15}\text{N}/{}^{14}\text{N}$ for nitrogen. The standard deviation of repeated measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of a laboratory standard was 0.10‰ versus V-PDB and 0.13‰ versus at-air,

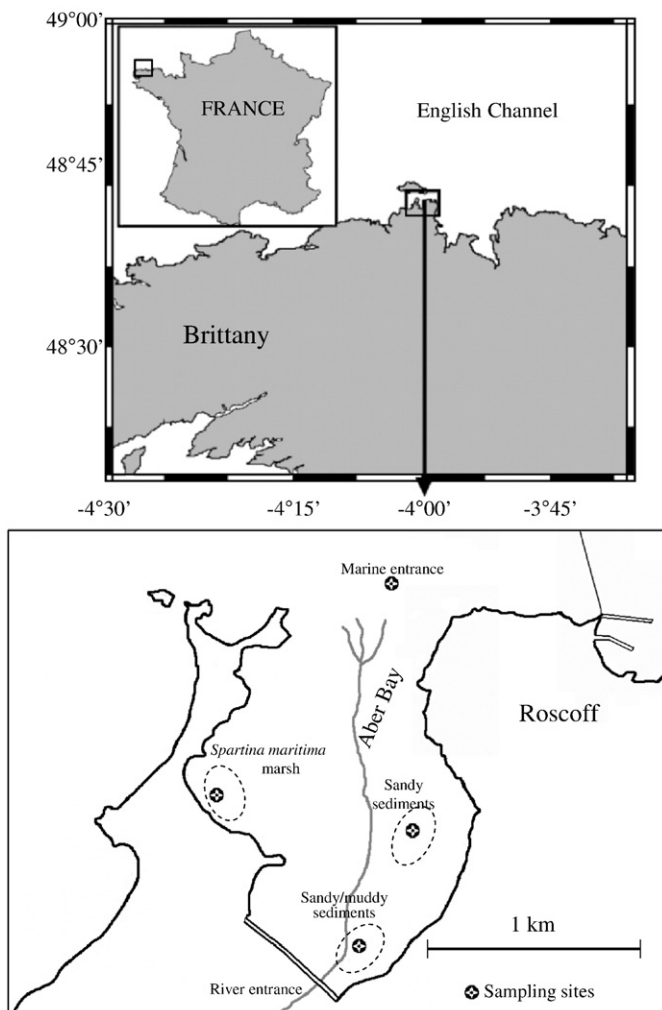


Fig. 1. Location of the sampling station in the Roscoff Aber Bay (France).

respectively. These abundances are calculated in relation to the certified reference materials Vienna Pee Dee Belemnite-limestone (V-PDB) and atmospheric dinitrogen (at-air). The VPDB and at-air scale is achieved using in-house peptone standards that have been calibrated against NBS-21 and IAEA N3 reference materials.

2.4. Estimation of food sources contributions

The contribution of the food sources to specimens of *H. ulvae* from the three sites was assessed employing the source-partitioning model (IsoSource) outlined in Phillips and Gregg (2003) to statistically constrain the relative proportions of various sources to consumers. Before the IsoSource analysis, adjustments were made for trophic fractionation which accounts for metabolic-based increases in heavier isotopes during the conversion of assimilated dietary sources to consumer tissues (DeNiro and Epstein, 1978). The mean trophic fractionation coefficients of 1‰ for $\delta^{13}\text{C}$ were subtracted from the consumers' $\delta^{13}\text{C}$ (DeNiro and Epstein, 1978). More variability is associated to $\delta^{15}\text{N}$ trophic fractionation. In particular, the mean $\delta^{15}\text{N}$ enrichment between food sources and primary consumers has been reported more variable than the usual 3.4‰ trophic enrichment because it varies between 2.5‰ (Vander Zanden and Rasmussen, 2001; Vanderkilt and Ponsard, 2003), and 3.4‰ (Post, 2002). However, previous studies along the French Atlantic coast, in similar intertidal sandy/muddy environments, allowed to precise the ^{15}N trophic enrichment associated to *H. ulvae*. In fact, in the Marenne-Oléron bay *H. ulvae* was clearly identified to feed almost exclusively on microphytobenthos (Blanchard et al., 2000). In the intertidal mudflat, a stable isotope study performed by Riera (1998) confirmed this privileged trophic link and pointed out a mean ^{15}N -enrichment of 2‰ between the microphytobenthos ($5.7 \pm 0.8\text{‰}$) and *H. ulvae* ($7.7 \pm 0.3\text{‰}$). In addition, this mean fractionation coefficient is consistent with the mean value of $2.5 \pm 2.5\text{‰}$ reported by Vander Zanden and Rasmussen (2001) for invertebrate primary consumers.

In the Aber bay of Roscoff, benthic diatoms did not occur as algal mats during the sampling period, and, then, could not be extracted for stable isotope analyses (Riera, pers.obs.). However, it was possible to collect and measure the C and N stable isotope ratios of the epipelagic diatoms in the sandy/muddy sediment of the Aber bay during August and close to the sampling stations of the present study, as reported in Riera and Hubas (2003). Even if not being an apparent substantial source in the Aber bay during the sampling period 1) it has been recognized that benthic diatoms can act as the major component in *H. ulvae* diet in other intertidal areas, 2) in fine sandy sediments, the production of microphytobenthos may be high without the formation of stable biofilms (Middelburg et al., 2000). Consequently, benthic diatoms have been considered as a potential source in the present study, through the use of mixing equations.

3. Results

The maximum density of *H. ulvae* was estimated at $52620 \pm 4939 \text{ ind/m}^2$ ($n=5$) in the sandy sediment whereas much lower values were measured in muddy/sandy sediments ($620 \pm 465 \text{ ind/m}^2$ ($n=5$) near the river entrance in the bay. In the *Spartina* marsh, *H. ulvae* reached important densities $35940 \pm 37398 \text{ ind/m}^2$ ($n=5$) similar to the sandy sediments.

3.1. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of organic matter sources and *H. ulvae*

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (range of values) of POM, SOM, food sources and *H. ulvae* are presented in Table 1. Organic matter sources differed significantly for $\delta^{13}\text{C}$ (Kruskal Wallis test, $p<0.001$) and $\delta^{15}\text{N}$ (Kruskal Wallis test, $p<0.001$). The mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for marine POM entering the bay was higher than the corresponding values of river POM, these two end-member sources being greatly ^{13}C -depleted as

Table 1

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (range of values) of the organic matter sources and *Hydrobia ulvae* of the intertidal Aber Bay in the *Spartina* marsh, the sandy and the sandy/muddy sediments.

Sample type	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n
Sources			
SOM (mud flat)	−15.9 to −15.2	5.9 to 6.7	3
SOM (<i>Spartina</i> marsh)	−15.1	6.7	1
Marine POM	−25.0 to −23.1	7.0 to 7.7	3
River POM	−28.8 to −26.7	5.4 to 7.3	3
Detrital <i>Enteromorpha</i> sp	−13.5 to −11.5	7.8 to 7.9	3
Living <i>Spartina maritima</i>	−14.3 to −13.2	5.1 to 5.6	4
Detrital <i>Spartina maritima</i>	−13.6 to −12.1	3.2 to 4.4	3
<i>Vaucheria</i> sp (<i>Spartina</i> marsh)	−17.6 to −17.3	5.4 to 6.8	3
Purple bacteria (sandy mats)	−15.0 to −14.8	6.3 to 6.6	3
Purple bacteria (muddy mats)	−15.9 to −14.6	7.5 to 7.6	3
Benthic diatoms	−17.3 to −16.9	8.3 to 9.1	3
Consumers			
<i>Hydrobia ulvae</i> (sand)	−14.4 to −13.0	7.1 to 10.8	8
<i>Hydrobia ulvae</i> (mud/sand)	−13.9 to −13.2	5.5 to 9.5	8
<i>Hydrobia ulvae</i> (<i>Spartina</i> marsh)	−14.1 to −12.1	5.1 to 6.7	8

Values for benthic diatoms of Aber Bay bay are given from Riera and Hubas (2003).

compared to locally occurring sources (Fig. 2). In contrast to $\delta^{13}\text{C}$, a large $\delta^{15}\text{N}$ difference was observed between live and dead *S. maritima* which is more ^{15}N -depleted. Low $\delta^{15}\text{N}$ was reported for detritic leaves of *Spartina alterniflora* (2.6‰) by Riera et al. (2000) similar to the mean $\delta^{15}\text{N}$ of this study for *S. maritima* (1.9‰). From previous studies, $\delta^{15}\text{N}$ variation observed for detritus from marine plants (i.e., *S. alterniflora*) resulted largely from uptake of external nitrogen by bacteria associated with plant detritus as well as from adsorbed external nitrogenous compounds (Rice, 1982). This is also consistent with the recent experimental study of Fellerhoff et al. (2003), which provided evidence that heterotrophic processes do not significantly fractionate $\delta^{13}\text{C}$ during decomposition of aquatic plants whereas the detritus $\delta^{15}\text{N}$ could greatly differ from that of the source plant. Mats of purple sulphur bacteria had mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of −15.2‰ and 7.1‰, respectively.

There was no consistent differences of $\delta^{13}\text{C}$ among *H. ulvae* communities from the three sampling stations (Kruskal–Wallis test, $p=0.27$). $\delta^{15}\text{N}$ of gastropods did not differ between the muddy/sandy and the sandy stations whereas *H. ulvae* specimens inhabiting the *S. maritima* marsh showed much lower $\delta^{15}\text{N}$ when compared with $\delta^{15}\text{N}$ pooled values from both other sites (Mann–Whitney *U*-test, $p<0.001$).

3.2. Dietary analysis

Modelling isotopic signatures of *H. ulvae* inhabiting sandy sediments suggested that *Enteromorpha* sp detritus contributed the most (means 44.9 %) followed by the SOM pool and the purple bacteria mats (means 29.8 and 19.1%, respectively) whereas the marine and river POM ranked much lower (Table 2). Similar trend was observed for *Hydrobia* specimens associated to muddy/sandy sediments near the river entrance, the highest mean contributions being attained by *Enteromorpha* sp detritus (31.7%), the SOM pool and purple bacteria mats (30.8 and 26.3%, respectively), followed by minor contributions of the marine and river POM. For *H. ulvae* inhabiting the *Spartina* marsh, the mixing model showed a major contribution of *Spartina* detritus (mean value of 65.3%). Other coexisting sources were less important in the diet of the gastropod exhibiting mean contributions from 5.0% (benthic diatoms) to 9.2% (*Vaucheria* sp). In fact, in this small marsh, river POM and *Enteromorpha* sp have not been considered because this station is clearly not submitted to the river influence (Fig. 1) and *Enteromorpha* sp detritus was only scarcely represented during this summer season (Riera, pers. obs.). In these habitats, benthic diatoms appear to contribute a minor

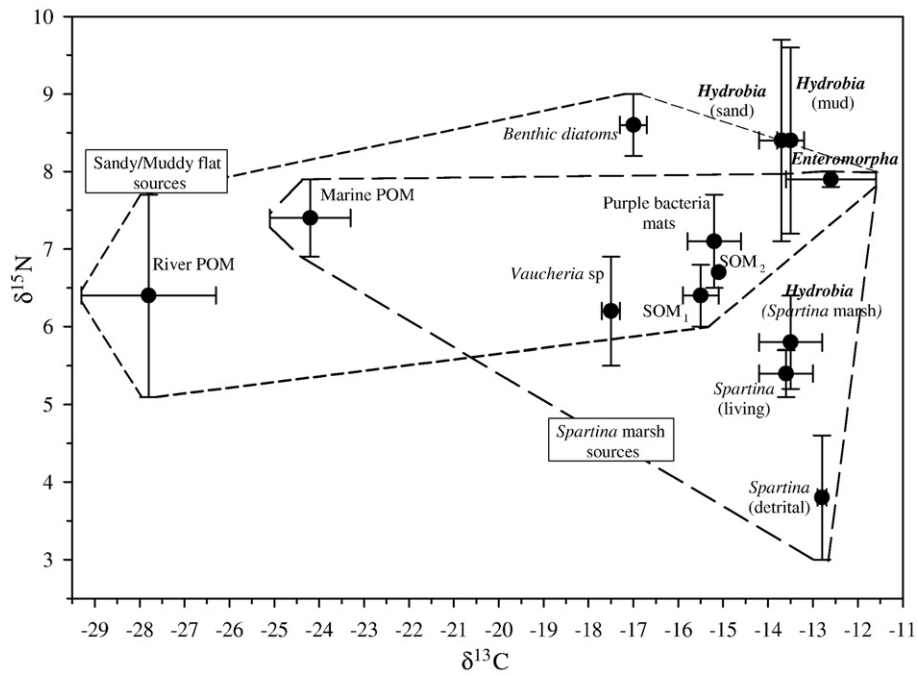


Fig. 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm standard deviation) of the main organic matter sources and *Hydrobia ulvae* from the different natural habitats in the Roscoff Aber Bay (sandy and muddy/sandy sediments and *Spartina* marsh).

part (mean values from 3.3 to 5.9%) of the diet of *H. ulvae* although they can reach up to 33% in muddy sediments.

4. Discussion

4.1. Trophic role of purple bacteria mats and *Enteromorpha* sp for *H. ulvae*

The stable isotope ratios indicate that phototrophic purple bacteria mats and *Enteromorpha* sp detritus can contribute a substantial fraction of the C and N assimilated by *H. ulvae* in sandy and muddy sediments. These important trophic links are consistent with the fact that, during the sampling period, individuals of *H. ulvae* often occurred in small depression at the sediment surface that was filled with purple bacteria mats and decaying *Enteromorpha* sp (Riera, pers. obs.). Previous $\delta^{13}\text{C}$ results suggested a carbon transfer between the phototrophic sulfur bacteria and zooplankton in lakes (Fry, 1986). More recently, *in situ* measurements showed significant carbon transfer (i.e., 75–85%) from purple sulphur bacteria and the copepod *Diaptomus connexus* in meromictic salt lake (Overmann et al., 1999). In contrast, C and S stable isotope data from the Great Sippewisset Marsh suggested that most of the marsh macrofauna, except the green head fly larvae (*Tabanus* sp.), did not incorporate a large fraction of

organic matter from the sulfur oxidizing bacteria (Peterson et al., 1986).

In the Aber bay of Roscoff, the major importance of stranded macroalgae as food was previously reported for the nematode community (Riera and Hubas, 2003). The functional role of stranded *Enteromorpha* sp in this bay is supported by regular field observations that stranded macroalgae from closely located rocks are regularly deposited by currents and waves (Riera, pers. obs.). These macroalgae represent a food source regularly available in the bay. The contribution of *Enteromorpha* sp patches to the diet of *H. ulvae* was also previously observed (Newell, 1965). This author hypothesized that *H. ulvae* used detrital algae as food but through a digestion occurring mostly on the bacterial community from the surface of the algae. $\delta^{15}\text{N}$ can be used to point out a trophic mediation within coastal ecosystems due to the mean $\delta^{15}\text{N}$ enrichment of 2.5‰ which occurs as nitrogen is transferred (Vander Zanden and Rasmussen, 2001). The present results provide evidence that detritus derived from stranded macroalgae can be directly assimilated by *H. ulvae* confirming that, as opposed to marine plants, microbial conversion is not necessary for macroalgae-derived organic matter to be consumed by marine invertebrates (Findlay and Tenore, 1982).

4.2. Importance of the SOM pool as a food source

The importance of the SOM in the diet of *Hydrobia* indicates that this species typically acts as a grazer of the surficial SOM pool in muddy/sandy areas. The proximity of $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ of purple bacteria mats and detritic *Enteromorpha* sp with the SOM pool suggests a major contribution of these sources to SOM, in contrast to marine and river POM which are too ^{13}C -depleted (Fig. 2). This is consistent with the abundance of these bacteria and *Enteromorpha* sp at the sediment surface of the Aber bay during summer. Benthic diatoms may also contribute a substantial part of the SOM pool. However, their high $\delta^{15}\text{N}$ and the absence of brown mats at the sediment surface seem to prevent them from a dominant contribution to the SOM pool.

In fact, although it consists of a mixture of various sources under decomposition, the SOM pool can be considered as a potential source

Table 2

Mean contributions (%) together with ranges in brackets) of the main organic matter sources in the diet of *Hydrobia ulvae* in the three natural sediments in the field calculated by a mixing model run according to Phillips and Gregg (2003) using an increment of 1‰ and a tolerance of 1‰. — : source virtually absent from the site.

	Sandy sediments	Muddy/sandy sediments	<i>Spartina maritima</i> marsh
Marine POM	1.6 (0–10)	2.9 (0–18)	5.6 (0–23)
River POM	1.3 (0–9)	2.4 (0–15)	—
<i>Enteromorpha</i> sp (detritic)	44.9 (19–67)	31.7 (0–67)	—
Purple bacteria	19.1 (0–81)	26.3 (0–100)	7.0 (0–41)
SOM	29.8 (0–72)	30.8 (0–100)	7.9 (0–45)
<i>Vaucheria</i> sp	—	—	9.2 (0–53)
<i>Spartina maritima</i> (detritic)	—	—	65.3 (47–93)
Benthic diatoms	3.3 (0–19)	5.9 (0–33)	5 (0–29)

in the present study because (1) $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ signature cannot be explained by a simple mixture of the pure sources occurring at this site, and (2) in regard to consumers, the total SOM pool can be considered as an additional food source. In fact, the sedimented POM is affected by diagenetic processes, and its $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ change due to a selective removal of particulate components which vary in isotopic ratio (Altabet, 1996). For example, the preferential utilisation of ^{14}N during remineralization can enrich organic substrates in ^{15}N (Benner et al. 1991; Thornton and McManus, 1994). In addition, the $\delta^{15}\text{N}$ of decaying tissues may be either higher or lower than the $\delta^{15}\text{N}$ of living plants, depending on species and season (Cloern et al., 2002). Consequently, due to these chemical modifications, the SOM pool can be considered as a new organic matter pool, whose isotopic signature is not a simple mixture of end-member sources and can be used directly as a food component.

4.3. *Spartina*-derived organic matter as food source for *H. ulvae*

Considering the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the sources, the ^{15}N -depletion of the *Hydrobia* specimens inhabiting the *Spartina* marsh can be explained by a preferential utilization of detritus of *S. maritima*. In addition, the $\delta^{15}\text{N}$ difference between *H. ulvae* and *Spartina* detritus and the $\delta^{15}\text{N}$ difference between living and detrital *Spartina* of about 2.5‰ indicate that the organic matter derived from *Spartina* makes an important contribution to the diet of *H. ulvae* (up to 86%) via a trophic pathway in the detritus food web. The utilization of *Spartina* detritus by *H. ulvae* may appear surprising because marine plant detritus are not as readily utilisable for primary consumers as other sources like algae, which contain higher amounts of nitrogen (Findlay and Tenore, 1982). However, microbially mediated processes occurring during decomposition of marine plants result in the production of detritus and associated living bacteria, which are more nutritious and readily utilisable (Tenore et al., 1982). The decomposition of *Spartina* detritus has been shown to largely involve bacterial and fungal carbon-conversion (Newell and Hicks, 1982). In addition, trophic mediation between gastropods and *S. alterniflora* may occur through associated bacteria or fungi as suggested for the periwinkle *Littorina irrorata* (Newell et al., 1989). In fact, the nitrogen content of the detritic complex tends to increase during degradation, especially as original substrates are refractory (Rice, 1982). In the present study, the $\delta^{15}\text{N}$ suggests an absence of trophic intermediate between *H. ulvae* and detritic complex derived from *Spartina* because their mean $\delta^{15}\text{N}$ difference of 2‰ likely correspond to only one trophic level. Hence, the major utilization of *S. maritima* detritus by hydrobiids is consistent with the general pattern of use of detritus derived of marine phanerogams by marine invertebrates, the availability of organic matter derived from macrophytes depending on microbial colonization. In addition, these results confirm the ability of the $\delta^{15}\text{N}$ value to efficiently differentiate specific dietary sources, and to provide evidence of different trophic pathways toward a single species.

4.4. Feeding behaviour characteristics of *H. ulvae* in the Aber bay of Roscoff

The present results depart from several recent investigations which clearly pointed that *Hydrobia* species are major consumers of epipellic benthic diatoms. In fact, the importance of Hydrobiid snails in the food chain of intertidal mudflats was largely investigated in Western Europe (Lopez and Kofoed, 1980; Morrissey, 1988; Haubois et al., 2005). For example, in the intertidal mudflats of Marennes-Oléron Bay, $\delta^{13}\text{C}$ showed a preferential utilization of benthic diatoms (mean $\delta^{13}\text{C}$: -16.1‰) as food source by *H. ulvae* (mean $\delta^{13}\text{C}$: -15.1‰) in accordance with $\delta^{15}\text{N}$ data which provided evidence of a direct trophic link between these trophic compartments (Riera, 1998). In contrast, in the Aber bay of Roscoff, benthic diatoms played a minor role in *Hydrobia*'s diet, even during summer, as microphytobenthic microalgal mats can be observed at the sediment surface. Considering that,

when significantly present, benthic diatoms have been often described as the privileged food source for *H. ulvae* in intertidal flats, the minor contribution of microphytobenthos to their diet is consistent with a relatively low presence of epipellic diatoms in these sediments. The absence of microphytobenthic mats at the sediment surface of the sampling sites can be due to local hydrodynamic conditions and/or the fact that the sediment surface is largely and regularly covered by decaying algae (i.e. detritic *Enteromorpha* sp) limiting its exposure to illumination (Riera, pers.obs.).

Interestingly, *H. ulvae* specimens exhibited a high variability in $\delta^{15}\text{N}$ especially in sandy and muddy sediments. However, due to the well recognized trophic status of primary consumer of the species, the $\delta^{15}\text{N}$ variability observed in this study does not reflect different trophic levels for the individuals considered. Most likely, the intra-specific $\delta^{15}\text{N}$ variability of *H. ulvae* could be explained by a high diversity in its diet, which confirms the trophic plasticity. A similar observation was previously reported for other opportunistic primary consumers, *Ligia oceanica* and *Littorina saxatilis*, by Laurand and Riera (2006).

Otherwise, an ecological characteristic of *H. ulvae* is its ability to float within the water column being resuspended by tidal currents or suspended beneath the air/water interface during calm conditions (Little and Nix, 1976). From these authors, this "floating activity" likely leads to a rapid and extensive dispersion of individuals within an intertidal area. However, in spite of this capacity, the differences in $\delta^{15}\text{N}$ for specimens inhabiting the *Spartina* marsh and the other sites of the bay suggest relative sedentarity for *H. ulvae* specimens within specific habitat types. The duration of this sedentary period must be at least enough to incorporate the isotopic signature of the trophic habitat in which they occur.

5. Conclusion

Hence, this study points out major sources of nutrition for *H. ulvae* different from living epipellic benthic microalgae. This is consistent with the predominance of detritic organic matter of intertidal sediments in *H. ulvae* diet which was reported previously (see Newell, 1965, for review). Because *H. ulvae* constitutes a main food source for many predators such as fishes, and birds, this study illustrates the key role of the close trophic links among *Enteromorpha* sp detritus, *Spartina* detritus, phototrophic purple bacteria and *H. ulvae* in the transfer of organic matter toward higher trophic levels. Finally, the high variability observed at the base of a trophic cascade for a single key species, even within a single intertidal soft bottom bay, limits the generalisation of simple consumer-resource models among similar ecosystems.

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