



Preferential food source utilization among stranded macroalgae by *Talitrus saltator* (Amphipod, Talitridae): a stable isotopes study in the northern coast of Brittany (France)

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Abstract

The importance of stranded macrophyte detritus as food sources for an amphipod inhabiting sandy beaches, *Talitrus saltator*, has been investigated by the use of stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) during summer and autumn 2000. The results showed that the different co-occurring stranded macrophytes, mostly macroalgae, had distinct $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ values. In addition, the study underlined the importance of *Talitrus saltator* as a key consumer of stranded macroalgal detritus. However, $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ strongly suggests a preferential utilization of *Fucus serratus* as a food source by *Talitrus saltator* within the available pool of detrital macroalgae, and the ability of this amphipod to use this detrital macroalgae without trophic mediation.

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1. Introduction

In several coastal ecosystems, the deposition of detrital vegetation on the shore may represent a primary food source for benthic consumers. On exposed sandy beaches, a distinctive feature is the almost complete lack of in situ primary production (Griffiths, Stenton-Dozey, & Koop, 1983). Therefore, macrofaunal organisms inhabiting exposed beaches must obtain most of their food from imported materials which include detrital marine angiosperms and macroalgae. Previous studies have pointed out that macroalgae can enter the coastal food web through different pathways. About 10% of the net macroalgal production is considered to be consumed directly by grazers whereas 90% enters various detritus food chains as particulate organic matter (POM) or dissolved organic matter (DOM) with a proportion of about 60 and 30% for POM and DOM, respectively (Mann, 1982; Pomeroy, 1980). The low grazing pressure

on living macroalgae is probably due to the presence of low digestible components including lignocellulosic compounds and polyphenols like phlorotannins in brown algae (Buchsbaum, Valiela, Swain, Dzierzeski, & Allen, 1991; D'Avanzo, Alber, & Valiela, 1991; Duggins & Eckman, 1997). An important part of the macroalgal biomass is deposited ashore after being torn off by currents, waves and during storms, then it becomes senescent (Branch & Griffiths, 1988). On a sandy beach of the west coast of the Cape Peninsula, South Africa, Griffiths et al. (1983) reported that 53% of the annual seaweed deposition was consumed by talitrid amphipods only and 18% by the other herbivores/detritivores concentrated around the drift line. The remaining 29% of seaweed deposition was thought to be degraded directly by bacteria and entered the sand column. As the assimilation efficiency of primary consumers is generally low, most of the material consumed by the amphipods was considered to return to the beach in the form of faeces or excretory products, then being colonized by associated bacteria (Griffiths et al., 1983). A part of this macroalgal-derived organic matter may rejoin the nearshore area as POM or DOM

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during periods of high tide reaching the deposition level and/or during storms (Duggins, Simenstad, & Estes, 1989; Koop & Lucas, 1983). More specifically, a feeding study based on the rate of consumption and the analysis of faeces composition of *Orchestia gammarellus* have pointed out the preferential ingestion of macroalgae vegetation material rather than angiosperms (More & Francis, 1985). In addition, these authors observed differences among the rates of consumption of different algae by *Orchestia gammarellus*. Although the importance of detritus derived from macrophytes for the coastal food web has long been recognized, field studies have focused more on the utilization of detritus produced by marine phanerogames like *Spartina* sp. (see Currin, Newell, & Paerl, 1995 for a review) than on macroalgal detritus pathways (Raffaelli & Hawkins, 1996; Wildish, 1988). Carbon and nitrogen stable isotopes have been used successfully to provide clues about the origin of animal food sources (Fry & Sherr, 1984; Deegan, Peterson, & Portier, 1990) and trophic flows in marine and coastal environments (Rau, Ainley, Bengtson, Torres, & Hopkins, 1992). This approach may

then be used to clarify the trophic role of detrital macrophytes deposited ashore, providing an accurate separation of the different species occurring within strandlines through their isotopic composition.

The aim of the present study was to investigate the transfer of organic matter from macroalgae deposited on a sandy beach into the benthic food web by the use of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. In particular, this study addresses the question of the importance of different co-occurring stranded macroalgae as food sources for a representative species inhabiting sandy beaches, namely, *Talitrus saltator*.

2. Material and methods

2.1. Sampling site

The sampling site was a sandy beach located in Santec near Roscoff (Fig. 1), facing the English Channel. The beach is located on the northern coast of Brittany which receives a vast input of torn off

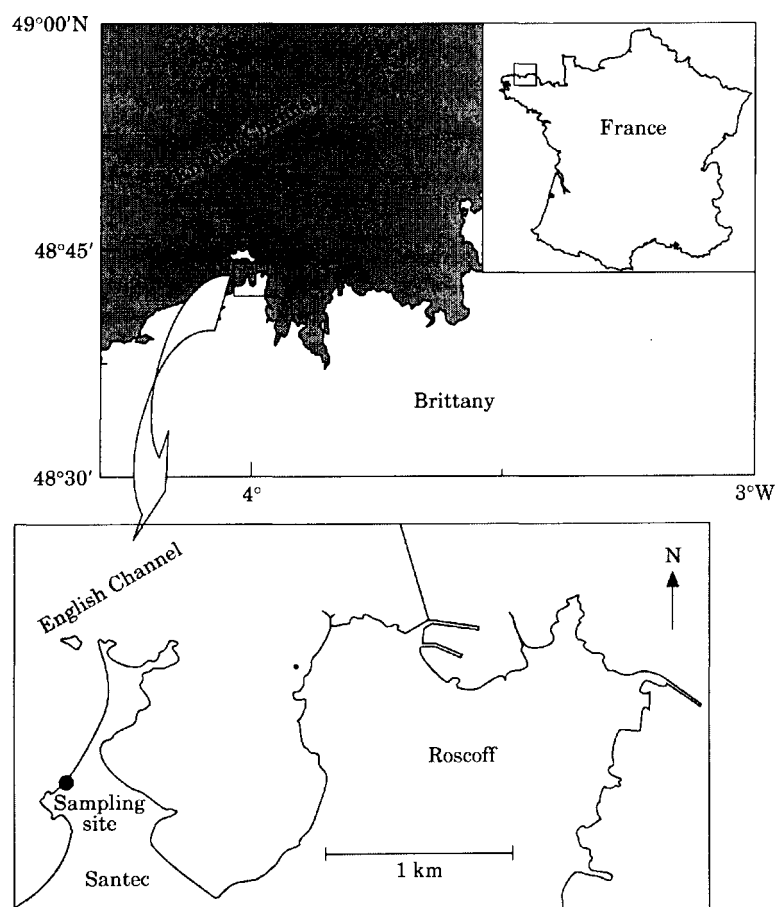


Fig. 1. Location of the sampling site in the northern coast of Brittany (France).

macroalgae from highly productive seaweed fields along the rocky coast. In these areas the seaweed deposits can be observed to cover the beaches. In the area adjacent to the sampling site, a primary production of 1000–1700 g C m⁻² yr⁻¹ for macroalgae has been recorded compared with 100–1000 g C m⁻² yr⁻¹ for phytoplankton (Bajjouk, pers. comm.). Due to this abundance and diversity of macroalgae (Cabioc'h et al., 1992), the northern coast of Brittany represents a favourable site to investigate the potential role of macroalgae in providing a food source for the littoral food web.

2.2. Sample collection and preparation

Talitrus saltator occurs in and below strandline algae on sandy beaches (Morritt, 1998). *Talitrus saltator* inhabits burrows above the high tide level during the day to avoid desiccation stress and emerges at night to feed on nearby stranded assemblage of macroalgae, preferably at low tide (Fallaci et al., 1999). At the sampling site, *Talitrus saltator* was abundant from summer to mid-autumn while its abundance strongly decreased in winter (Adin & Riera, pers. obs.). In fact, North Eastern Atlantic populations of *Talitrus saltator* hibernate during winter (Spicer, Morritt, & Taylor, 1990). Samples of stranded macrophytes and adult individuals of *Talitrus saltator* were carried out in

summer (8 August 2000) and in autumn (12 October 2000). At each date, the most abundant detrital macroalgae and seagrass were collected by hand within an area of about 10 m diameter depending on their presence within the stranded assemblage (Table 1). The stranded macroalgae and seagrass were easily recognizable as recently deposited and were identified to genus or species level (Cabioc'h et al., 1992). The two dominant dune plants located high on the beach including *Agropyron junceum* and *Atriplex laciniata* were also sampled because, at each sampling occasion, *Talitrus saltator* was observed to be present on the dunes. Individuals of *Talitrus saltator* were taken out of the sand by hand below the strandline macrophyte. Sandy sediment was sampled below the deposited algae where *Talitrus saltator* occurred. At the laboratory, for the measurement of the $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$, the detrital macroalgae, dune plants and the seagrass *Zostera marina* were rinsed with filtered seawater (pre-combusted GF/F) to clean off epibionts, treated with 10% HCl to remove any residual carbonates, and rinsed with distilled water. These samples were dried (60 °C) for 48 h and ground to a fine powder using a mortar and pestle. Individuals of *Talitrus saltator* were kept alive over night at the laboratory to allow evacuation of gut contents prior to analysis and then killed by freezing (–20 °C). The individuals were rapidly acidified with 10% HCl and

Table 1

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (range of values) of *Talitrus saltator*, stranded macroalgae and seagrass, vascular plants, and sedimented organic matter (SOM) in summer and autumn 2000

Samples	Summer 2000			Autumn 2000		
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	<i>n</i>	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	<i>n</i>
<i>Talitrus saltator</i>	–15.9 to –13.5	9.1 to 11	28	–16.1 to –14.0	9.8 to 10.7	15
Brown algae						
<i>Ascophyllum nodosum</i>	–16.2 to –15.4	4.7 to 7.0	3	–17.2 to –15.3	7.0 to 9.5	3
<i>Fucus serratus</i>	–15.5 to –13.1	6.7 to 7.0	3	–15.8 to –14.3	5.6 to 7.4	3
<i>Fucus vesiculosus</i>	–14.9 to –13.1	6.8 to 7.6	3	–16.7 to –15.0	5.7 to 6.3	3
<i>Himanthalia elongata</i>	–12.1 to –10.6	8.0 to 8.7	3	–16.0 to –12.6	5.2 to 8.0	3
<i>Laminaria</i> sp.	—	—	—	–18.6 to –16.0	4.4 to 6.2	3
<i>Pelvetia canaliculata</i>	–18.6 to –17.2	7.0 to 7.4	3	–19.2 to –18.3	5.8 to 7.2	3
<i>Sargassum muticum</i>	–17.9 to –16.6	5.7 to 6.8	3	–18.8 to –16.7	4.6 to 5.2	3
Red algae						
<i>Callophyllis laciniata</i>	—	—	—	–33.7 to –33.5	6.1 to 7.1	3
<i>Chondrus crispus</i>	—	—	—	–20.0 to –19.7	6.8 to 7.2	3
<i>Phycodrys rubens</i>	—	—	—	–34.6 to –34.3	6.7 to 6.9	3
Green algae						
<i>Enteromorpha</i> sp.	–16.7 to –14.1	9.1 to 9.2	3	–15.8 to –13.8	8.6 to 8.9	3
<i>Ulva</i> sp.	—	—	—	–14.2 to –11.3	6.6 to 7.0	3
Seagrass						
<i>Zostera marina</i>	—	—	—	–10.4 to –9.7	6.6 to 7.0	3
Vascular plants						
<i>Atriplex laciniata</i>	–14.3 to –12.9	7.9 to 8.4	3	—	—	—
<i>Agropyron repens</i>	–25.4 to –25.0	2.0 to 2.6	5	–29.8 to –28.4	2.0 to 3.3	3
SOM	–18.6 to –18.1	7.8 to 8.1	3	–20.6 to –19.9	7.7 to 8.2	3

n: number of samples. —: not present.

rinsed with distilled water. They were dried (60 °C) and after removal of the entire cuticle animals were ground to a fine powder using mortar and pestle. For the measurements of stable isotopic ratios of the SOM, the sand was sieved to a grain size of <63 µm to separate sand grains from most of the sedimented particulate organic matter. The SOM collected was then acidified in a glass receptacle with 10% HCl, rinsed several times with distilled water and dried (60 °C). Finally, all samples were kept frozen (–32 °C) until analysis.

2.3. Stable isotope analysis

For analysis of carbon and nitrogen isotope ratios, the samples were combusted in a CARLO EBRA Elemental Analyser and the resulting gases (CO₂ and N₂) were separated by gas chromatography and analysed in Continuous-Flow mode on a Micromass OPTIMA double inlet, triple collector mass-spectrometer.

Data are expressed in the standard δ unit notation where

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

with $R = {}^{13}\text{C}/{}^{12}\text{C}$ for carbon and ${}^{15}\text{N}/{}^{14}\text{N}$ for nitrogen, and reported relative to the Vienna Pee Dee Belemnite standard (PDB) for carbon and to air N₂ for nitrogen. Precision in the overall preparation and analysis was $\pm 0.13\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

3. Results

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (range of values) of SOM, stranded macroalgae, vascular plants, and *Talitrus saltator* are presented in Table 1. The *Fucus* species were more ${}^{13}\text{C}$ -enriched than the *Fucus* species previously examined by Riera, Richard, Gremare, and Blanchard (1996) in the Marennes-Oléron Bay, France, whereas the corresponding $\delta^{15}\text{N}$ were similar to $\delta^{15}\text{N}$ reported by Riera (1998) for *Fucus vesiculosus* and *Fucus serratus*. $\delta^{13}\text{C}$ for *Ascophyllum nodosum* were similar at the two sampling seasons while the corresponding $\delta^{15}\text{N}$ were slightly higher in autumn (Table 1). *Himantalia elongata* was more ${}^{13}\text{C}$ -depleted in autumn as compared with summer while this alga was more ${}^{15}\text{N}$ -enriched in summer than in autumn. At both sampling seasons, $\delta^{13}\text{C}$ for *Pelvetia canaliculata* were close, while $\delta^{15}\text{N}$ for this algae decreased slightly from 5.7 to 6.8‰ in summer to 4.6 to 5.2‰ in autumn. The red algae *Callophyllis laciniata* and *Phycodrys rubens* form a distinct group as species characterized by highly negative $\delta^{13}\text{C}$ compared to other algal species, as previously reported (Maberly, 1990; Maberly, Raven, & Johnston, 1992). *Chondrus crispus* had $\delta^{13}\text{C}$ higher than the other red algae but closer to $\delta^{13}\text{C}$ values of the brown algae considered in this study.

In contrast, $\delta^{15}\text{N}$ for *Chondrus crispus* were close to $\delta^{15}\text{N}$ of the other two red algae considered. In summer, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for *Enteromorpha* sp. were close to the corresponding values previously reported by Riera et al. (1996) for *Enteromorpha* sp. *Ulva* sp. showed a large range of $\delta^{13}\text{C}$, between –14.2 and –11.3‰, consistent with previous observations (Riera et al., 1996). *Zostera marina* had $\delta^{13}\text{C}$ close to $\delta^{13}\text{C}$ reported previously for this seagrass (Fry & Sherr, 1984; Wiedemeyer & Schwamborn, 1996). $\delta^{13}\text{C}$ for *Atriplex laciniata* were typical for terrestrial C4 plants (Deines, 1980), while $\delta^{13}\text{C}$ of *Agropyron junceum* ranged from –29.8 to –25‰ which is characteristic for C3 species (Smith & Epstein, 1971). *Talitrus saltator* exhibited $\delta^{13}\text{C}$ from –15.9 to –13.5‰ in summer, higher than $\delta^{13}\text{C}$ values observed in autumn which ranged from –16.1 to –14‰. Corresponding $\delta^{15}\text{N}$ showed closer values during summer (from 9.1 to 11‰) and autumn (from 9.8 to 10.7‰).

4. Discussion

4.1. Identification of stranded *F. serratus* as the most exploited food source by *Talitrus saltator*

The main sources of organic matter had distinct $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ values (Fig. 2a,b), which allowed their use to infer food sources for *Talitrus saltator*. The mean isotopic composition of *Talitrus saltator* diet can be estimated from the consumer's by considering 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 3.4‰ (DeNiro & Epstein, 1981; Minagawa & Wada, 1984; Owens, 1987) as a result of the assimilation of food. The trophic enrichments in ${}^{13}\text{C}$ and ${}^{15}\text{N}$ have been reported in Fig. 2a,b (dashed line) starting from the mean $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ of *Talitrus saltator* for the two sampling periods. According to this procedure, the expected mean isotopic ratios for the preferentially exploited food resource would be –15.5 and 6.9‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, in summer (Fig. 2a) and –16.5 and 6.8‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, in autumn (Fig. 2b). These values are very similar to the mean $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ of *Fucus serratus* in summer and in autumn (Fig. 2a,b). The closer the theoretical values of *Talitrus saltator* food are to the ones of a pure food source, the higher is the proportion of that source in the diet of the consumer.

A mixing diet can, however, also be hypothesized to explain the isotopic composition of *Talitrus saltator*. In summer, the $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ for the theoretical food of *Talitrus saltator* could also result from a mixing diet of *Himantalia elongata* and *Ascophyllum nodosum* (Fig. 2a). Unfortunately, no quantitative measurement of the biomass of the different algae within the strandline pool was performed in the present study. Although *Himantalia*

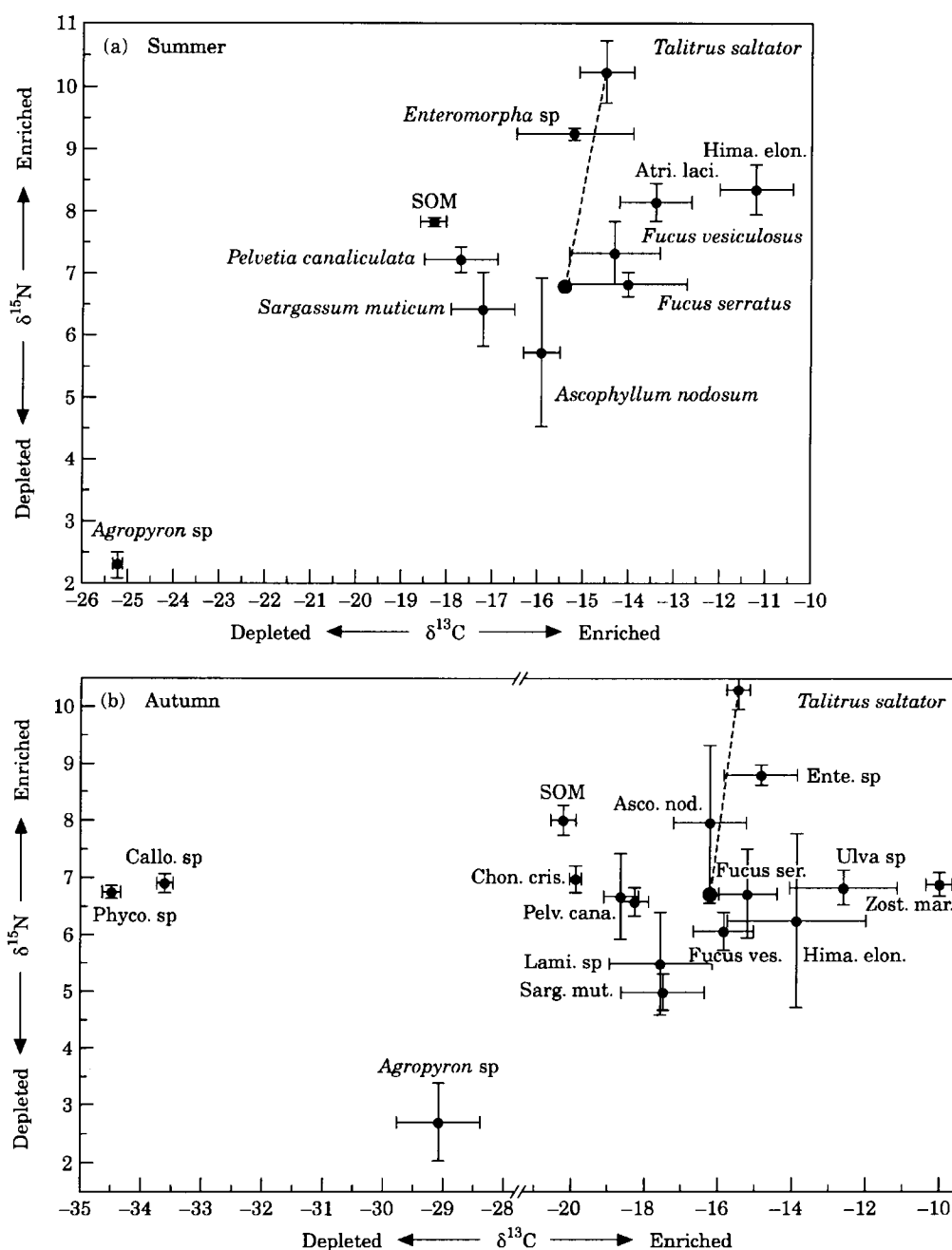


Fig. 2. $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ (mean \pm SD) for *Talitrus saltator*, stranded detrital macroalgae, vascular plants and sandy SOM in summer 2000 (a) and in autumn 2000 (b). (O) Average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values corresponding to the theoretical food source of *Talitrus saltator* taking into account the trophic enrichment of 1 and 3.4‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. (---) Trophic enrichment of carbon and nitrogen. *Asoc. nod.* = *Ascophyllum nodosum*; *Atri. lac.* = *Atriplex laciniata*; *Ente. sp.* = *Enteromorpha* sp.; *Fucus s.* = *Fucus serratus*; *Fucus v.* = *Fucus vesiculosus*; *Hima. elo.* = *Himantalia elongata*; *Pelv. can.* = *Pelvetia canaliculata*; *Sarg. sp.* = *Sargassum muticum*; *Call. lac.* = *Callophyllis laciniata*; *Chon. cri.* = *Chondrus crispus*; *Lami. sp.* = *Laminaria* sp.; *Phyc. rub.* = *Phycodrys rubens*; *Zost. mar.* = *Zostera marina*.

elongata and *Ascophyllum nodosum* contributed to the strandline, they were less abundant than *Pelvetia canaliculata*, *Fucus vesiculosus*, *Enteromorpha* sp. and *Sargassum nodosum* (Adin & Riera, pers. obs.). In addition, *Himantalia elongata* and *Ascophyllum nodosum* had mean $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ values very different from the $\delta^{13}\text{C}$ vs.

$\delta^{15}\text{N}$ values of the theoretical food of *Talitrus saltator*, and to reach this theoretical value through a mixing diet would imply a quantitative utilization of the two algae in about the same proportion by *Talitrus saltator* as suggested in Fig. 2a. Consequently, it seems unlikely that *Himantalia elongata* and *Ascophyllum nodosum*

contributed significantly to the feeding of *Talitrus saltator*, as compared with *Fucus serratus*. In summer, these results suggest that, *Fucus serratus* recently deposited ashore, was the preferentially utilized food source of *Talitrus saltator* because no other single food source could so strongly match these theoretical values. Particularly, these data indicate that the other predominantly represented algae within the strandline, namely, *S. nodosum*, *Enteromorpha* sp. and *P. canaliculata* (Fig. 2a), did not contribute to the diet of *Talitrus saltator*.

In autumn, the theoretical $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ for the food of *Talitrus saltator* was also very close to the mean $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ of *Fucus serratus* (Fig. 2b). Particularly, the red algae, which were observed to form an important part of the stranded macroalgal pool were not utilized by *Talitrus saltator*. In addition, the results point out that the dune plants (*Agropyron* sp. and *A. laciniata*) and the seagrass, *Zostera marina*, were not used as food sources by *Talitrus saltator*. Similar to summer, a diet consistent with the $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ of the theoretical *Talitrus saltator* diet may also consist of a mixture including *Ulva* sp., *Fucus vesiculosus* and *Himantalia elongata* because these algae also had mean $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ close to the theoretical value of *Talitrus saltator* food (Fig. 2b). Although *Ulva* sp. was present in the strandline in autumn, this algae was however much less abundant than *Fucus serratus*, *Fucus vesiculosus* and *Himantalia elongata* (Adin and Riera, pers. obs.). In addition, a significant contribution of *Himantalia elongata* to the diet of *Talitrus saltator* in autumn, following an absence in the utilization of this algae in summer (Fig. 2a) is rather unlikely. Finally, the hypothesis that assimilated carbon and nitrogen originated from different macroalgae is very unlikely because, as opposed to vascular plant detritus, detrital macroalgae contain relatively high amounts of nitrogen that can be readily assimilated by benthic primary consumers (Findlay & Tenore, 1982; Tenore, Cammen, Findlay, & Phillips, 1982).

In summer and autumn, although the contribution of other macroalgal species occurring in the strandline may also contribute to the diet of *Talitrus saltator*, this study suggests that this amphipod preferentially utilized *Fucus* sp. (mostly *Fucus serratus*) as food source. Consistent with this result, it has been reported that several amphipods reveal distinct food preferences, even though these species would be able to assimilate organic matter from various different food sources (van Alstyne, Ehlig, & Whitman, 1999; Karez, Engelbert, & Sommer, 2000; Pavia, Carr, & Aberg, 1999). For example, a laboratory feeding experiment performed by Karez et al. (2000) showed that the amphipod *Gammarus locusta* also preferred *Fucus vesiculosus* to *Ulva* sp. and green epiphyte algae as food source. Also, Moore and Francis (1985) suggested that the debris of *Laminaria digitata* were more easily consumable than that of fucooids by the amphipod *Orchestia gammarellus*.

4.2. Use of detrital macroalgae: importance of the nutritive value

Considering some recent studies related to the nutritive characteristics of different macroalgae, one could be surprised that a brown alga (i.e. *Fucus serratus*) is preferred to a green alga as food source. Brown algae are generally considered to be source of lower nutritive value compared with the red and green algae (Buchsbaum et al., 1991; Duggins & Eckman, 1997) because these algae are characterized by a high content of low digestible refractory components, such as phlorotannins (Boettcher & Targett, 1993; Tugwell & Branch, 1992) and a protein content, which accounts for only about 10% of their dry weight (Lüning, 1985). In contrast, red and green algae have a protein content from 20 to 30% of their dry weight (Lüning, 1985) and a lower content of polyphenolic compounds (Buchsbaum et al., 1991), which make these algae potentially more readily consumable. This apparent discrepancy may be partly explained by considering the temporal variation of the nutritive value for different macroalgae and vascular plants during decomposition (Buchsbaum et al., 1991). These authors observed that, although living red and green algae may form a more nutritive food source than the living brown algae, they lose most of their nutritional values more rapidly than the brown algae (i.e. *Fucus vesiculosus*) during the first month of decay. The preferential utilization of the *Fucus* species by *Talitrus saltator* may thus be partly explained by this change of nutritive value during the decomposition of the different macroalgae recently deposited ashore. This hypothesis would, however, need further experimental investigations.

Furthermore, the availability of organic matter derived from macrophytes for primary consumers can depend on trophic mediation which may occur through associated bacteria (Crosby, Newell, & Langdon, 1990; Langdon & Newell, 1990) or through protozoa (Posch & Arndt, 1996). $\delta^{15}\text{N}$ values can be used to point out a trophic mediation within coastal ecosystems (Riera, 1998) because an increase in $\delta^{15}\text{N}$ by about 3.4‰ per trophic level occurs as the nitrogen is transferred (Minagawa & Wada, 1984; Wada, Terazaki, Kabaya, & Nemoto, 1987). In the present study, the $\delta^{15}\text{N}$ values suggest an absence of a trophic intermediate between *Talitrus saltator* and *Fucus serratus* because their mean $\delta^{15}\text{N}$ difference correspond to only one trophic level (3.4 and 3.6‰ in summer and autumn, respectively).

In conclusion, this study points out that the different co-occurring stranded macrophytes, mostly macroalgae, deposited on a sandy beach were not used uniformly as food sources by the detritivorous amphipod *Talitrus saltator*. These results suggest the ability of *Talitrus saltator* to select a specific alga within the stranded detrital macroalgal pool (i.e. *Fucus serratus* in the

present study), which it can use as food source directly without trophic mediation.

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