

## Trophic diversity of idoteids (Crustacea, Isopoda) inhabiting the *Posidonia oceanica* litter

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### Abstract

The coexistence of three idoteid species in *Posidonia oceanica* litter raises the question of trophic diversity and their role in the litter degradation process. Hence, diet composition of *Idotea balthica*, *Idotea hectica* and *Cleantis prismatica* was studied using a combination of gut contents and stable isotopes analysis. Gut content observations indicate that *P. oceanica* dead leaves are an important part of the ingested food for the three species, although their tissues are constituted of only a small to medium fraction of *P. oceanica* carbon. Our results also underlined the potential role of these species in the degradation of *P. oceanica* litter by mechanically fragmenting the litter and by assimilating a small to medium fraction of carbon. Moreover, we showed that there were considerable inter- and intra-specific differences in diet composition. Diet differed between juveniles and adults for *I. balthica*. Crustaceans are an important food source for adults of *I. balthica*, while *I. hectica* indicated a major contribution of algal material. *C. prismatica* showed an intermediate diet. This trophic diversity is probably one of the factors allowing these species to coexist in the same biotope.

### Introduction

In the Mediterranean Sea, *Posidonia oceanica* (L.) Delile is the most common seagrass and is an important primary producer in coastal areas. Herbivory on this particular species accounts for 2-57% of the annual leaf production (Cebrián et al. 1996; Havelange et al. 1997; Prado et al. 2007). The remaining fraction of primary production passes into the detritus food web (Wittmann et al. 1981; Mateo and Romero 1997; Pergent et al. 1994). In September and October, *P. oceanica* leaves fall and contribute to the formation of a leaf litter that remains within the meadow, frequently in sand patches, or are exported to other ecosystems (e.g., upper littoral, sand ecosystems and even deep coastal waters) where it may represent a trophic input of considerable importance (Fenchel 1977). Such leaf litter, often mixed with *P. oceanica* rhizomes and drift macroalgae from adjacent habitats, forms dense packs and may persist for a few days only or for several months or even years, depending on its degree of exposure to hydrodynamic movements and biological phenomena (e.g., bacterial degradation and activity of the detritivorous macrofauna; Wittmann et al. 1981).

*Posidonia oceanica* litter provides a structural habitat as well as potential food sources for an abundant animal community (Gallmetzer et al. 2005). Crustaceans (mainly amphipods and isopods) are the dominant component of the macrofauna, playing a significant role in the litter degradation process of seagrass systems (Fenchel 1970; Wittmann et al. 1981). Seagrass leaf litter is often an important constituent of material ingested by animals, but the question of assimilation rates of this material for various macroinvertebrates is still being debated (Mateo et al. 2006). Other food sources present in the same biotope, such as epiphytic algae or drift algae are perhaps more readily utilized by consumers than higher plants. Algae are richer in nutrients such as nitrogen, while *Posidonia* leaves are characterized by a high lignocellulose content (Buia et al. 2000; Klap et al. 2000), which does not allow easy digestion. *P. oceanica* litter is also colonized by microorganisms (diatoms, bacteria and fungi) that could constitute a potential food source for the detritivore communities (Mazzella et al. 1992; Lepoint et al. 2006).

The importance of the different sources in the diet of a consumer can be approached by the examination of gut contents. Nevertheless, this current method cannot provide any information on the assimilated materials. One method that allows measurement of assimilated materials is stable isotope analysis. Indeed, the isotopic composition of an animal is the weighted mixing of the isotopic composition of its food source(s) (after accounting for isotopic fractionation) (DeNiro and Epstein 1981). The stable isotope approach has already been

used to study the trophic regimes of consumers in *P. oceanica* ecosystem (Dauby 1989, 1995; Jennings et al. 1997; Lepoint et al. 2000; Vizzini et al. 2002) and in litter accumulations (Lepoint et al. 2006).

The diet of marine detritivore species has been infrequently studied. In the Mediterranean Sea, the idoteids *Idotea balthica basteri* (Audouin, 1827) and *Idotea hectica* (Pallas, 1772) and the idoteid-like *Cleantis prismatica* (Risso, 1826) are commonly found in *P. oceanica* litter. *I. balthica* and *C. prismatica* primarily inhabit *P. oceanica* litter (Gallmetzer et al. 2005; Dimech et al. 2006), whereas *I. hectica* is classically described as characteristic of the foliar stratum of the *P. oceanica* bed (Lorenti and Fresi 1983a). In terms of abundance, *I. balthica* can account for 9-14% of the total litter macrofauna, with mean density exceeding 520 individuals per m<sup>2</sup> (Cox 2004; Dimech et al. 2006). Other two idoteids reach in general a mean of 75 individuals per m<sup>2</sup> for *I. hectica* (Dimech et al. 2006) and between 3 and 5 individuals per kilogram dry weight of *P. oceanica* litter for *C. prismatica* (Gallmetzer et al. 2005). To make coexistence possible and reduce competition, co-occurring detritivores usually differ in terms of feeding apparatus morphology, feeding strategies, nutritional requirements or digestive capabilities (Arsuffi and Suberkropp 1989; Graça et al. 1993; Zimmer et al. 2002; Zimmer and Bartholmé 2003). Hence, the coexistence of these species in the same biotope raised the question about trophic diversity in this particular environment. To our knowledge, no data are available about the feeding ecology of *I. hectica* and *C. prismatica*, while *I. balthica* food includes both vegetable (plant and algae) and animal materials (Naylor 1955; Nicotri 1980; Jormalainen et al. 2001). Laboratory observations suggested that *I. balthica* actively consume living and decaying *P. oceanica* material (Lorenti and Fresi 1983b). This latter is generally considered, together with the sparid fish *Sarpa salpa* and the echinoid *Paracentrotus lividus*, as a potential consumer of *P. oceanica* leaves. However, the literature does not provide any complete information about the ability of these isopod species to assimilate this matter.

This study combined gut content and stable isotope analyses to (1) examine inter- and intra-specific differences in diet composition of these three shallow-water idoteid isopods associated to *P. oceanica* litter; (2) evaluate the importance of *P. oceanica* litter in their diet in order to better elucidate the transfer of organic matter from primary producers to detritivores and (3) clarify the potential role of these species in the ecosystem through the consumption and assimilation of *P. oceanica* litter.

## Materials and methods

### Study area

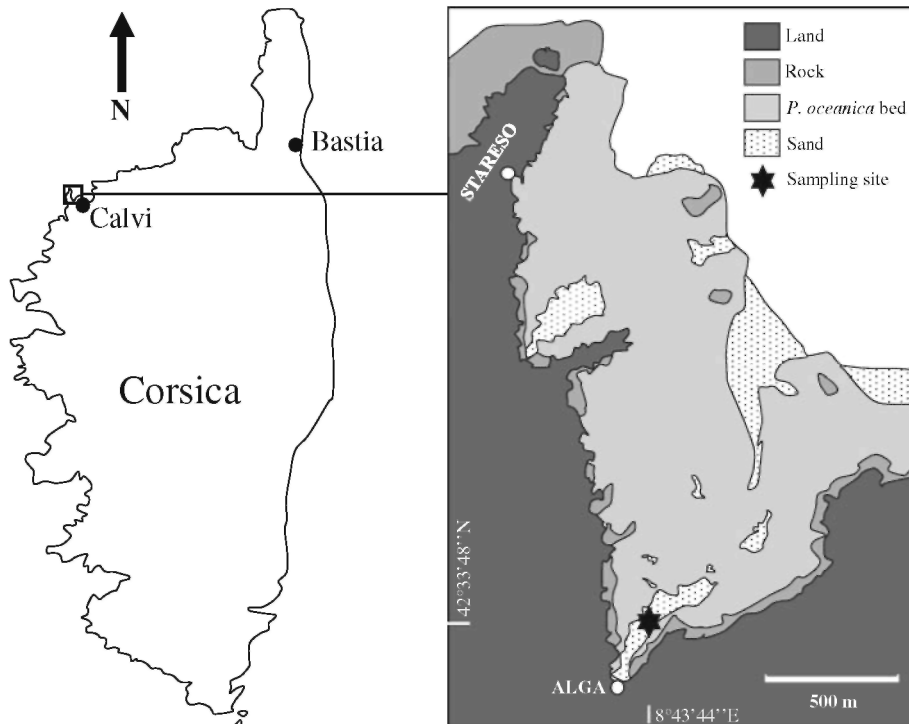
The study was carried out in the Revellata Bay (Gulf of Calvi, Western Corsica, France) (8° 43' 44"E; 42° 33' 48"N) near the oceanographic station STARESO, on a large central sand patch (~2.6 ha) surrounded by *P. oceanica* seagrass beds and rocky shore biota (Fig. 1). The seagrass *P. oceanica* covers 40% of the bay sea bottom, reaching a depth of 40 m (Janssens 2000), and annual leaf primary production was estimated to be 849 g dry wt m<sup>-2</sup> at 2 m depth (Vela 2006). The main epilithic macroalgae are *Halogetis* spp. and *Dictyota* spp. and, to a lesser extent, *Cystoseira* spp., *Udotea petiolaris*, *Sphaerococcus* sp. and some erect corallines, growing on adjacent rocks or as epiphytes of *P. oceanica* rhizomes. Some of these species appear in litter accumulations as drift macroalgae. The studied sand patch is an accumulation zone for the litter, defined in this study as fragmented *P. oceanica* leaf material, sometimes mixed with intact leaves, drift macroalgae, living and dead *P. oceanica* roots and rhizomes, which forms aggregates of ~10 m.

### Sample collection

Samples of *P. oceanica* litter were collected during the daytime by SCUBA diving between 4 and 6 m depth in March 2004 and 2005. SCUBA divers placed the leaf litter material, together with the associated macrophytes debris and macrofauna, inside 30-l plastic bags and closed them to limit fauna escape. According to a simple random sampling, seven replicate samples were taken in the study area from the top layer of different litter accumulation zones, each separated by 1-10 m. Macrofaunal species were carefully sorted, and specimens of *Idotea balthica basteri*, *Idotea hectica* sensu Charfi-Cheikhrouha (2000) and *Cleantis prismatica* sensu Poore and Lew Ton (1990) (junior synonym *Zenobiana prismatica*) were caught and transferred to the freezer at -18°C within a few hours, until further analysis. Before dissection, the sex, body length (anterior border of the cephalon to the end of the telson) ( $\pm 0.1$  mm), body colour (brown or green) and colour morph (i.e., melanophore pattern) of each individual was determined (classification according to Tinturier-Hamelin 1963; Salemaa 1978). The different potential food sources used for isotopic analysis were collected in the study area: *P. oceanica* dead leaves (i.e., senesced leaves from *P. oceanica*, detached and exported to litter accumulations), *P. oceanica* leaf epiphytes (both algae and fixed animals) that were separated from *P. oceanica* dead leaves in the laboratory by scraping them off with a razor blade, drift macroalgae species found in litter (six species of sciaphilous algae and

eight species of photophilous algae) and crustaceans (the amphipod *Gammarus aequicauda*, the most abundant species in the study area, representing >70% of litter fauna; Cox 2004).

**Fig. 1** Location of the sampling site and distribution of the different benthic ecosystems in Revellata Bay according to Pasqualini (1997) (Gulf of Calvi, NW Corsica)



#### Gut content analysis

Specimens were dissected under stereoscopic microscope, and the digestive tract was extracted and observed under optic microscope. The gut content analysis allowed the food sources to be separated into six components: *P. oceanica* dead leaves, crustaceans, algae (diatoms, macroalgae and *P. oceanica* vegetal epiphytes), animal epiphytes (foraminifera, bryozoans and sponges), *P. oceanica* living leaves and non-identified organic matter for each individual. Two indices were used for diet description and analysis: frequency of occurrence ( $F_i$ ) (percentage of all non-empty guts in which the component  $i$  was found) and abundance level ( $A_i$ ). For this latter, components were itemized and described with three levels of abundance: (1) absent (-): the component  $i$  was not present in the gut tract; (2) rare (+): the component  $i$  was identified 1-4 times in the gut tract and (3) abundant (++) : five items or more of the component  $i$  were identified, often in different regions of the gut tract.

#### Stable isotope analysis

Specimens and potential food sources were dried for 48 h at 50°C and ground into a homogeneous fine powder. When the individual specimen size was equal to or greater than 10 mm, it was possible to perform individual isotopic analysis. Other individuals were pooled according to the following size classes: 2 for *I. balthica*: <5 and 5-10 mm and 2 for *C. prismatica*: 5-9 and 9-10 mm. To remove carbonates, which are known to be more enriched in C than dietary organic components, the samples were acidified with 1 N HCl for 24 h and then rinsed with deionized water and oven dried at 50°C for 48 h. Stable carbon and nitrogen isotope analysis was performed with a mass spectrometer (Optima, Micromass, UK) coupled to a C-N-S elemental analyzer (Carlo Erba, Italy). All  $^{15}\text{N}/^{14}\text{N}$  ratios were measured before acidification because of the modifications of  $^{15}\text{N}/^{14}\text{N}$  after HCl addition (Bunn et al. 1995). The isotopic analysis was reported in  $\delta$  values in parts per thousand (‰) relative to the Vienna Pee Dee belemnite (vPDB) for carbon samples and atmospheric  $\text{N}_2$  for nitrogen:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left( \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right) \times 10^3$$

where  $R = \frac{^{13}\text{C}}{^{12}\text{C}}$  or  $\frac{^{15}\text{N}}{^{14}\text{N}}$ .

Reference materials from IAEA were IAEA-N2 (ammonium sulphate) ( $20.3 \pm 0.2\text{‰}$ ) and IAEA CH-6 (sucrose) ( $-10.4 \pm 0.2\text{‰}$ ). Hundreds of replicate assays of internal laboratory standards (powder of glycine) indicate measurement errors (SD) of  $\pm 0.3$  and  $\pm 0.3\text{‰}$  for stable carbon and nitrogen isotope measurements, respectively.

Jackson et al. (2009) developed a package called *SIAR* for solving linear-mixing models. This model uses Bayesian inference to solve for the most likely set of dietary proportions given the isotopic ratios in a set of possible food sources and a set of consumers. The model assumes that each target value comes from a Gaussian distribution with an unknown mean and standard deviation. The structure of the mean is a weighted combination of the food sources' isotopic values. The weights are made up of dietary proportions (which are given a Dirichlet prior distribution), and the concentration dependencies given for the different food sources. The standard deviation is divided up between the uncertainty around the discrimination corrections and the natural variability between target individuals (Jackson et al. 2009; Moore and Semmens 2008).

Animal metabolism generally leads to an increase in  $^{15}\text{N}$  abundance in animal tissue compared to its diet (i.e., isotopic fractionation). To account for this fractionation, we subtracted  $0.5\text{‰}$  from the nitrogen isotope signature of each sample as estimated for detritivorous crustaceans by Vanderklift and Ponsard (2003). No adjustment was made for carbon, because  $\delta^{13}\text{C}$  fractionation is close to zero (Peterson and Fry 1987).

### Statistics

Statistical analysis was performed using STATISTICA software (version 8.0, StatSoft Inc. 2007). Because data did not fit assumptions of normality, a non-parametric Kruskal-Wallis *H*-test was used for comparisons of isotope ratios between the different food sources and the different isopod species. Subsequently, significant differences were localized by using Mann-Whitney *U*-tests, which also allowed a comparison of differences among sexes and colour morphs. Regression analysis was carried out to examine the relationship between body length and stable isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of *I. balthica*. No regression analysis was carried out for *I. hectica* and *C. prismatica* because of the limited range of body lengths.

### Results

A total of 70 individuals were sampled: *I. balthica* ( $n = 45$ : 5 males, 25 females and 15 juveniles), *I. hectica* ( $n = 15$ : 10 males and 5 females) and *C. prismatica* ( $n = 10$ : 3 males and 7 females). Isopod species showed little variation in size except in *I. balthica*, where individuals measuring less than 7 mm were classified as juveniles (Salemaa 1979; Guarino et al. 1993). *I. balthica* ranged from 2.6 to 25.9 mm (avg. 4.1 and 11.2 mm for juveniles and adults, respectively), *I. hectica* from 10.7 to 21.9 mm (avg. 14.8 mm) and *C. prismatica* from 5.5 to 10.4 mm (avg. 8.4 mm). All individuals were brown except in *I. hectica* where two specimens were green. Six colour morphs were identified for *I. balthica* specimens: *uniformis*, *bilineata*, *maculata*, *pseudolineata*, *bilineatalineata* and *albafusca-bilineata*. The morph *uniformis* largely dominates among sampled individuals (81%).

### Gut contents

From a total of 45 *I. balthica* guts analyzed, four were empty. Gut contents of adult *I. balthica* were dominated by *P. oceanica* dead leaves (88% of occurrence), crustaceans (46%) and non-identified organic matter (100%). Animal epiphytes and *P. oceanica* living leaves occurred, respectively, in 17 and 10% of gut contents and were rare in terms of abundance (Table 1).

Of the 15 *I. hectica* guts analyzed, four were empty. Gut contents of *I. hectica* were dominated by *P. oceanica* dead leaves, algae and non-identified organic matter (>90% of occurrence for these last food sources). Gut contents of this species also include large amounts of *P. oceanica* living leaves (25% of occurrence) and rare amounts of crustaceans (33%) and animal epiphytes (45%).

From the 10 *C. prismatica* guts analyzed, seven were empty. *C. prismatica* had gut contents dominated by *P. oceanica* dead leaves and non-identified organic matter (100% of occurrence). Crustaceans (33%), algae (100%) and animal epiphytes (33%) were rare.

Generally, *P. oceanica* dead leaves and non-identified organic matter dominated the gut contents of the three species. Crustaceans were more abundant in *I. balthica* than in *I. hectica* and *C. prismatica*, while algae and *P. oceanica* living leaves were more abundant in *I. hectica* than in *I. balthica* and *C. prismatica* gut contents. Hence, according to gut content analysis, four potential food sources were distinguished for isotopic analysis: *P. oceanica* dead leaves, crustaceans of the litter, drift sciaphilous algae and a mixed food source composed of drift photophilous algae and *P. oceanica* leaf epiphytes.

**Table 1** Gut content analysis (GCA) on individuals with full guts of *Idotea balthica* ( $n = 41$ ), *Idotea hectica* ( $n = 11$ ) and *Cleantis prismatica* ( $n = 3$ )

| Food sources                     | <i>Idotea balthica</i> |    | <i>Idotea hectica</i> |    | <i>Cleantis prismatica</i> |    |
|----------------------------------|------------------------|----|-----------------------|----|----------------------------|----|
|                                  | F (%)                  | A  | F (%)                 | A  | F (%)                      | A  |
| <i>P. oceanica</i> dead leaves   | 88                     | ++ | 92                    | ++ | 100                        | ++ |
| Crustaceans                      | 46                     | ++ | 33                    | +  | 33                         | +  |
| Algae                            | 29                     | ++ | 92                    | ++ | 100                        | +  |
| Animal epiphytes                 | 17                     | +  | 45                    | +  | 33                         | +  |
| <i>P. oceanica</i> living leaves | 10                     | +  | 25                    | ++ | 0                          | -  |
| Non-identified organic matter    | 100                    | ++ | 100                   | ++ | 100                        | ++ |

F (%) frequency of occurrence and A abundance of fragments of each food source (-: absent, +: <5, ++: ≥5)

#### Stable isotope values

Drift macroalgae were separated into two ecological groups (sciaphilous and photophilous algae), with drift sciaphilous algae lower in  $\delta^{13}\text{C}$  ( $-29.7 \pm 4.5\text{‰}$ ) than drift photophilous algae ( $-19.8 \pm 2.3\text{‰}$ ). Drift photophilous algae and *P. oceanica* leaf epiphytes had very similar  $\delta^{13}\text{C}$  and were aggregated into one potential food source ( $-20.1 \pm 2.6\text{‰}$ ), because it was not possible to differentiate between them with isotopic models (Caut et al. 2008; Table 2; Fig. 2). *P. oceanica* dead leaves and crustaceans of the litter had significantly more enriched  $\delta^{13}\text{C}$  values than other potential food sources, with *P. oceanica* dead leaves higher in  $\delta^{13}\text{C}$  ( $-13.3 \pm 0.8\text{‰}$ ) than crustaceans ( $-16.4 \pm 0.8\text{‰}$ ). The  $\delta^{15}\text{N}$  values of the four potential food sources ranged from 1.3 to 3.0‰. Stable isotope values of the four potential food sources were generally well separated using both carbon and nitrogen.

The  $\delta^{13}\text{C}$  values of the isopod species ranged from  $-23.4\text{‰}$  to  $-18.6\text{‰}$  (Table 2; Fig. 2). *I. balthica* and *C. prismatica* ( $-19.3 \pm 0.5\text{‰}$  and  $-20.0 \pm 0.9\text{‰}$ , respectively) had higher  $\delta^{13}\text{C}$  values than *I. hectica* ( $-22.3 \pm 0.8\text{‰}$ ) ( $P = 0.0001$ ). The three species had very similar  $\delta^{15}\text{N}$  values for adult specimens: *I. balthica* ( $3.0 \pm 0.7\text{‰}$ ), *I. hectica* ( $2.6 \pm 0.5\text{‰}$ ) and *C. prismatica* ( $2.7 \pm 0.3\text{‰}$ ), and there were no significant differences among them ( $P = 0.236$ ). For all specimens of *I. balthica* (all size categories),  $\delta^{15}\text{N}$  values ranged from 1.6 to 4.1‰ (Fig. 2). There was a significant correlation between body length and  $\delta^{15}\text{N}$  values for *I. balthica* ( $r^2 = 0.36$ ,  $P = 0.003$ ; Fig. 3), while no significant relationship was observed between body length and  $\delta^{13}\text{C}$  values ( $P = 0.815$ ). Further, we did not detect any differences between delta values of the *uniformis* and the other five colour morphs for *I. balthica* ( $P > 0.300$ ) and between delta values of males and females for *I. balthica* and *I. hectica* ( $P > 0.270$ ).

#### Food source contributions

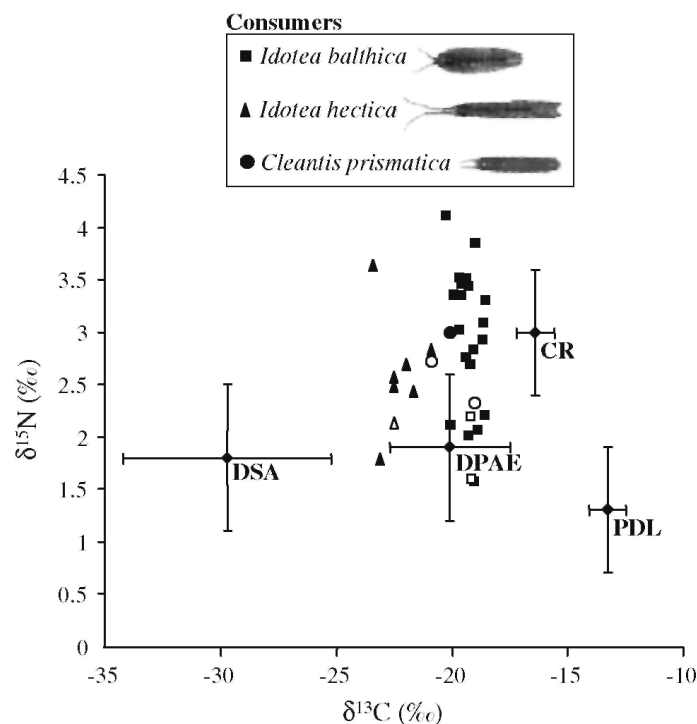
The ranges of feasible contributions for each food source to the three species are shown in Fig. 4. For *I. balthica*, the model suggested that crustaceans appeared to constitute the majority of the diet with a mean of 31%. Drift sciaphilous algae and drift photophilous algae and epiphytes were both potentially significant contributors to the diet of *I. balthica* (mean of 23 and 26%, respectively). The latter two food sources were likely to be major contributors to the diet of *I. hectica* (40 and 32%, respectively), while crustaceans had a smaller dietary contribution (mean of 10%). For the last consumer *C. prismatica*, drift photophilous algae and epiphytes was a potentially significant contributor (27%), but the range of potential contribution was wide. The contribution of crustaceans to the food source was also relatively important (20%), while the other potential food sources made up the remainder of the diet. *P. oceanica* dead leaves accounted for a medium dietary contribution to all three species (20, 18 and 25% for *I. balthica*, *I. hectica* and *C. prismatica*, respectively).

**Table 2** Mean values (SD) of  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , %C and %N for potential food sources and consumers with different size categories

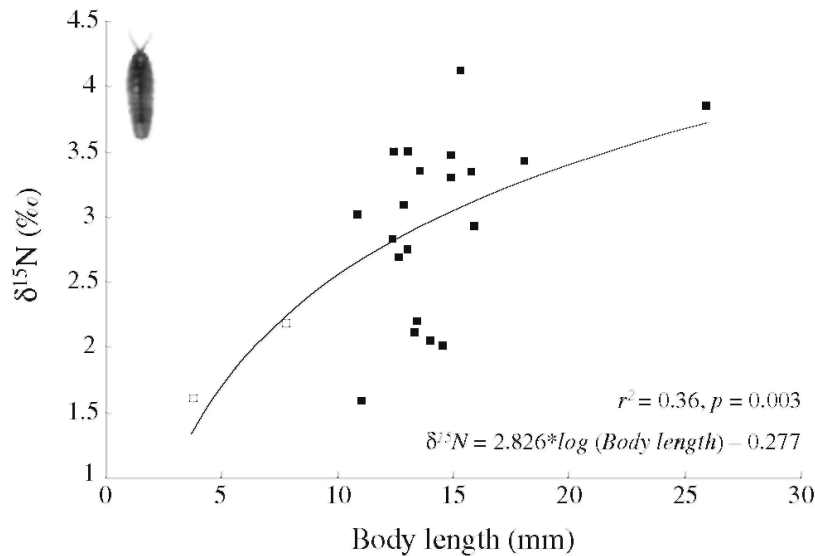
|                                   | <i>n</i> | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ | %C         | %N        |
|-----------------------------------|----------|-----------------------|-----------------------|------------|-----------|
| <b>Potential food sources</b>     |          |                       |                       |            |           |
| <i>P. oceanica</i> dead leaves    | 20       | -13.3 (0.8)           | 1.3 (0.6)             | 27.4 (1.4) | 0.5 (0.1) |
| Crustaceans                       | 30       | -16.4 (0.8)           | 3.0 (0.6)             | 48.7 (0.9) | 7.8 (1.1) |
| Drift sciaphilous algae           | 6        | -29.7 (4.5)           | 1.8 (0.7)             | 28.0 (2.9) | 2.9 (0.4) |
| Drift photophilous algae          | 8        | -19.8 (2.3)           | 1.9 (0.9)             | 25.2 (2.6) | 1.3 (0.1) |
| <i>P. oceanica</i> leaf epiphytes | 9        | -20.3 (0.6)           | 1.9 (0.5)             | 38.7 (4.0) | 1.4 (0.4) |
| <b>Consumers</b>                  |          |                       |                       |            |           |
| <i>Idotea balthica</i>            |          | -19.3 (0.5)           | 2.9 (0.7)             | 47.8 (2.8) | 7.9 (1.0) |
| <5 (mm)*                          | 10       | -19.2                 | 1.6                   |            |           |
| 5-10 (mm)*                        | 27       | -19.2                 | 2.2                   |            |           |
| >10 (mm)                          | 20       | -19.3 (0.5)           | 3.0 (0.7)             |            |           |
| <i>Idotea hectica</i>             |          | -22.3 (0.8)           | 2.6 (0.5)             | 47.8 (1.4) | 9.1 (0.6) |
| 10-12 (mm)*                       | 5        | -22.5                 | 2.1                   |            |           |
| >12 (mm)                          | 7        | -22.3 (0.9)           | 2.6 (0.6)             |            |           |
| <i>Cleantis prismatica</i>        |          | -20.0 (0.9)           | 2.7 (0.3)             | 48.9 (1.1) | 7.8 (0.9) |
| 5-9 (mm)*                         | 7        | -19.1                 | 2.3                   |            |           |
| 9-10 (mm)*                        | 2        | -20.9                 | 2.7                   |            |           |
| >10 (mm)                          | 1        | -20.0                 | 3.0                   |            |           |

*n* for potential food sources: number of samples and *n* for consumers: number of individual specimens  
 \* Pooled specimens

**Fig. 2**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures of *Idotea balthica*, *Idotea hectica* and *Cleantis prismatica* (black and white colours indicate isotope values for individual and pooled specimens, respectively) and of their potential food sources (mean  $\pm$  SD). DSA drift sciaphilous algae, DPAAE drift photophilous algae and epiphytes of *Posidonia oceanica*, CR crustaceans and PDL *Posidonia oceanica* dead leaves



**Fig. 3** Correlation between body length and  $\delta^{15}\text{N}$  values of *Idotea balthica*. Black and white colours indicate values for individual and pooled specimens, respectively



## Discussion

Gut content observations indicate that *P. oceanica* dead leaves are an important part of the ingested food of the three species, although their tissues contain only a small to medium fraction of *P. oceanica* carbon. Furthermore, despite the common food supply (i.e., *P. oceanica* dead leaves, crustaceans, drift sciaphilous and photophilous algae), we showed that there were considerable inter- and intra-specific differences in diet composition.

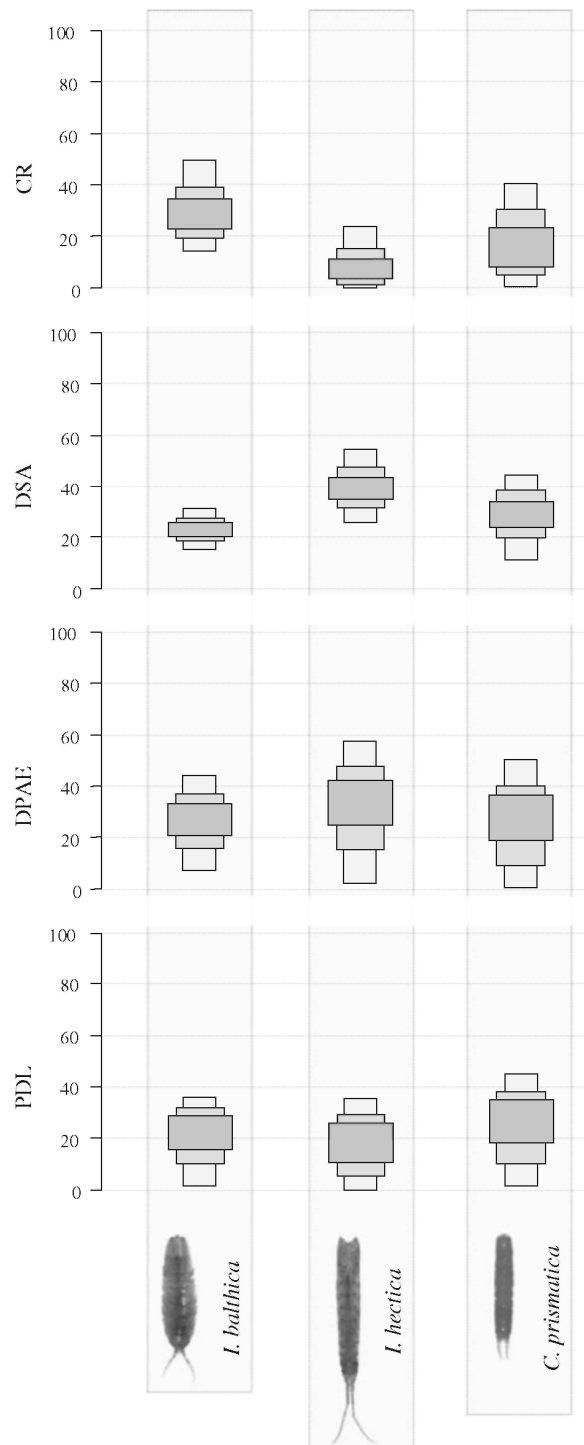
### Importance of *P. oceanica*

The present study shows that the three isopod species ingest considerable quantities of *P. oceanica* dead leaves.

For all the species, dead leaf material was very fragmented and altered. This fragmentation is possible because isopods possess mouthparts characterized by the presence of large molar processes on each mandible that slide across each other to crush the food and heavily chitinized structures for biting or scraping the food material (Naylor 1955). As previously underlined by Wittmann et al. (1981), these species may play a key role in the degradation process of *P. oceanica* litter.

However, the contribution of *P. oceanica* dead leaves to the diet of isopods is moderate, representing an average of 20, 18 and 25% of the assimilated carbon for *I. balthica*, *I. hectica* and *C. prismatica*, respectively. The apparent lack of *P. oceanica* carbon in the diet of isopods can be explained by the tough consistency of the leaves (even when dead) due to their high fibre content and high amount of poorly digestible structural carbohydrates (mainly lignin and cellulose) (Buia et al. 2000; Klap et al. 2000). In addition, *P. oceanica* dead leaves are highly encrusted by calcareous epiphytes (*Melobesia*) and have high C/N ratios, indicating resistance to mechanical factors (fragmentation by animals) and making assimilation more difficult (Pirc and Wollenweber 1988). Thus, the assimilation of *P. oceanica* carbon could only occur in the presence of cellulose and/or lignin digestion. The ability of these species to assimilate such material appears to be affected by the nature and variety of digestive enzymes. The ability to digest cellulose was already demonstrated in some marine isopods (Zimmer et al. 2002). But as for the parent species *Idotea wosnesenskii*, this ability is weakly developed. Moreover, the use of hepatopancreatic endosymbionts that contribute to cellulose digestion appears absent in marine isopods (Zimmer et al. 2002).

**Fig. 4** Dietary contributions (%) of the four potential food sources for *Idotea balthica*, *Idotea hectica* and *Cleantis prismatica*. Histograms show the distribution of feasible contributions from each food source to the three isopod species diet resulting from the application of the SIAR isotopic model. Values shown are 5-95% ranges for these distributions. CR crustaceans, DSA drift sciaphilous algae, DPAE drift photophilous algae and epiphytes of *Posidonia oceanica* and PDL *Posidonia oceanica* dead leaves



However, some other crustacean detritivores showed evidence of being capable of more efficiently digesting residual plant material (Zimmerman et al. 1979). Lepoint et al. (2006) showed that *P. oceanica* dead leaves could contribute up to 50% of the total assimilated carbon for the amphipod *Gammarus aequicauda*, living in the *P. oceanica* litter. Vizzini et al. (2002) also suggested that seagrass material is assimilated by some detritivorous



amphipods. This assimilation could be mediated through an intestinal symbiosis with bacteria for *G. aequicauda* (A. Genin, unpublished data) or a production of endogenous cellulases for other aquatic amphipods (McGrath and Matthews 2000; Zimmer and Bartholmé 2003). Overall, we cannot exclude the fact that low digestibility of *P. oceanica* leaf litter, when compared to higher digestibility of algal and animal matter, will result in an increase in relative amount of detrital material in the gut contents, leading to an over-estimation of its nutritive significance.

Two main hypotheses have been proposed to explain why *P. oceanica* dead leaves account for a small to medium fraction of the assimilated carbon, although it is a major component of the gut contents. The first one is that microorganisms (bacteria, fungi, cyanobacteria and diatoms) found at the surface of *P. oceanica* dead leaves constitute the real food source (Mazzella et al. 1992; Lepoint et al. 2006). The *P. oceanica* leaf litter is massively colonized by diatoms, bacteria and marine filamentous fungi (Lepoint et al. 2006), with bacteria reaching densities as high as  $4 \times 10^4$  cells  $\text{mm}^{-2}$  (Velimirov et al. 1981). Microorganisms can provide essential fatty acids, amino acids, sterols, vitamins and other growth factors to detritivores (Phillips 1984). They contain more protein than decaying seagrass fragments with which they are associated (Zimmerman et al. 1979). The work of Fenchel (1970) has indicated that in at least some cases microorganisms constitute the real food source for the detritivores associated to the detritus derived from turtle grass *Thalassia testudinum*. In the seagrass *Syringodium isoetifolium* bed, isotopic data suggest that herbivorous heterotrophs depend significantly on epiphytic cyanobacteria (high nitrogen content with  $\delta^{13}\text{C}$  of approximately  $-13.5\text{‰}$ ) rather than seagrass leaves and its detritus (Yamamuro 1999). Holmer et al. (2004) also identified that bacteria  $\delta^{13}\text{C}$  ratios in pristine sediments vegetated by the seagrass *P. oceanica* were similar to the seagrass signal or slightly enriched (approximately  $-13\text{‰}$ ). In our study, we cannot exclude the possibility that microbial biofilm may contribute partially to the isotopic signature of detritus. Undoubtedly, detritivores can receive nourishment by assimilating microorganisms inhabiting seagrass litter (Fenchel 1970), although it is unlikely that they rely solely on microorganisms as an energy source (Blum et al. 1988). The second hypothesis proposes that species benefit from *P. oceanica* dead leaves to assimilate the brown pigments that they incorporate into their carapace. In *Idotea* sp., pigments of the cuticle are derived from the food sources of the animals (Lee 1966a, b). Certain parts of the plant material may have different  $\delta\text{C}$  than the bulk tissue, which could lead to the variation in  $\delta^{13}\text{C}$  in these species (Crawley et al. 2007). The colouration may act as a camouflage against predation. Indeed, *Idotea* species are subject to severe predation by fish (Wallerstein and Brusca 1982; Vesakoski et al. 2008), and may play a major role in the aquatic food webs, representing a major link among producers and secondary consumers.

Relatively little is known about foraging patterns of these species and underlying mechanisms of food choice and food preference. Laboratory observations of M. Zimmer and K. Lunau (unpublished data) showed that some species of terrestrial isopod respond positively to extracts of microbially inoculated litter but not to extracts of sterilized litter. From this, we could expect that these species search for specific food items such as microbial colonization of the food. However, Jormalainen et al. (2001) suggested that in *I. balthica*, habitat structure, in terms of predation avoidance, and the spatiotemporal stability of the habitat are more important factors selecting for feeding preferences than the quality of the food.

#### *Inter-specific trophic segregation*

The clear differences in  $\delta^{13}\text{C}$  between *P. oceanica* dead leaves and idoteid species which live in *P. oceanica* litter suggest that idoteids do not digest *P. oceanica* dead leaves to any great extent, but rather digest drift photophilous algae, *P. oceanica* leaf epiphytes (both macro and micro epiphytes) and crustaceans, which have a more similar  $\delta^{13}\text{C}$  to that of the idoteids. *I. balthica* and *C. prismatica* had very close  $\delta^{13}\text{C}$  values ( $-19.3$  and  $-20.0\text{‰}$ , respectively), suggesting that assimilated matter for these two species is very similar. However, *I. hectica* had a significantly different  $\delta^{13}\text{C}$  value ( $-22.3\text{‰}$ ), reflecting a difference in its diet. A previous study has found a similar  $\delta^{13}\text{C}$  for *Idotea* sp. sampled in the epilithic algal community of the Mediterranean coast ( $-19.2\text{‰}$ ) and a different  $\delta^{13}\text{C}$  for a green individual of *Idotea* sp. collected in a *P. oceanica* bed ( $-15.1\text{‰}$ ) (Lepoint et al. 2000). This last value is very close to the isotopic signature of *P. oceanica* living leaves ( $-13.9\text{‰}$ ), suggesting, as observed by Lorenti and Fresi (1983b), that this species is able to nourish itself principally on *P. oceanica* living leaves. However, in our study,  $\delta^{13}\text{C}$  for green individuals of *I. hectica* ( $-21.4 \pm 0.6\text{‰}$ ) were not distinctly different from brown individuals ( $-22.6 \pm 0.6\text{‰}$ ).

In assessing the contribution of food sources from *P. oceanica* litter, we showed that macroalgae and epiphytes appeared likely to be a substantial contributor for the three isopod species studied. Similar results were also observed by Lepoint et al. (2006) for the amphipods *Gammarus aequicauda* and *Gammarella fucicola*, showing that macroalgae and epiphytes contribute up to 50 and 80% of the total assimilated carbon, respectively. Moreover, the study confirmed that some of these species are omnivores, in particular *I. balthica*, currently seen

as one of the main herbivores of many ecosystems (e.g., shallow rocky shores in the Baltic Sea) (Svensson et al. 2004). Fragments of crustaceans were recorded in 46% of individuals of *I. balthica* in large quantities and contribute up to 31% of the total assimilated carbon. *I. hectica* specimens show a tendency towards an herbivorous diet, with algae contributing to 40% of the assimilated carbon. The idoteid-like valviferan *C. prismatica* has an intermediate diet composed of an equitable mix of the different food sources. The patterns of trophic segregation observed in this study may not be explained by the variety of the structure of the feeding apparatus of these species. Indeed, comparative information between the morphology of *Idotea* species mouthparts studied by Naylor (1955) and the description of *I. hectica* by Charfi-Cheikhrouha (2000) did not show major differences.

#### *Intra-specific trophic segregation*

The variation of  $\delta^{15}\text{N}$  values for *I. balthica* was high (from 1.6 to 4.1‰) and was explained by differences in body size. This pattern indicates a gradual shift in the diet with increasing size and suggests a trend towards increasing carnivory with maturity. Relationships between body length and stable isotopic signatures have already been found for mysids (Gorokhova and Hansson 1999; Branstrator et al. 2000; Lesutiene et al. 2007), crabs (Dittel et al. 2006) and fish (Renones et al. 2002; Melville and Connolly 2003; Quan et al. 2007). The significant changes in stable isotopic signatures with increasing size are often attributable to ontogenetic diet shifting of animals (Branstrator et al. 2000; Renones et al. 2002; Quan et al. 2007; Lesutiene et al. 2007). In our study, this hypothesis is consistent with gut content analysis, which showed that greater body size admits *I. balthica* to a more diversified diet including macroalgae and crustaceans. However, other studies support that differential metabolic fractionation of nitrogen with age also influences the correlation between body length and  $\delta^{15}\text{N}$  values, especially when there is no correlation between body length and  $\delta^{13}\text{C}$  values (Melville and Connolly 2003). Our results showed no correlation between body length and  $\delta^{13}\text{C}$  values of *I. balthica*. However, elucidating  $^{15}\text{N}$  accumulation with age and estimating the rate of enrichment due to accumulation require specific laboratory experiments (Gannes et al. 1997; Caut et al. 2009), which are beyond the aim of our study. Thus, caution must be exercised in interpreting the isotopic values. We agree with Melville and Connolly (2003) and Quan et al. (2007) that interpretations of diet based on stable isotope analysis should be limited to individuals of similar size to avoid any potential confounding effects.

This study confirms the importance of combining stable isotope and gut contents information to evaluate the diet of a species. The conjoint analysis allowed us to identify that, while *P. oceanica* dead leaves were ingested in large quantities, they were assimilated only to a small to moderate extent. Probable reasons for this include the presence of a dense microorganisms population on decaying leaf litter (easy digestible food and richer in nutrients) and the assimilation of brown pigments of the leaf litter by idoteids that they incorporate into their carapace. On the other hand, the good agreement found between gut content and stable isotope data for other food sources allowed us to establish that *I. balthica* is the more generalist species and is characterized by an omnivorous diet in which crustaceans are the principal component. *I. hectica* indicated a major contribution of algae material, while *C. prismatica* showed an intermediate diet. The data obtained demonstrated an important trophic diversity, at both intra and inter-specific levels, of the idoteid species living in *P. oceanica* litter. Although these species live in the same biotope, they appear to occupy different microhabitats within the litter and share their food resources. Therefore, habitat heterogeneity and trophic diversity of idoteids are probably the factors that reduce competition and make coexistence possible. As reported by Lepoint et al. (2006), for amphipods, the results also underline the potential role of the isopod species in the degradation of *P. oceanica* litter by mechanically fragmenting the litter and by directly assimilating a fraction of *Posidonia* carbon. Further investigation of the processes involved in litter breakdown, including the quantification of the role of detritivores and microbial activity, is needed to improve the understanding of *P. oceanica* carbon dynamics and food webs in Mediterranean coastal zones.

#### **Acknowledgments**

The authors would like to thank the staff of the oceanographic research station STARESO (Calvi, Corsica) for valuable help during field work. We would like to thank A. L. Jackson, R. Inger and A. Parnell for their help in the isotopic model, and two anonymous referees for their helpful comments on the manuscript. We wish to thank Jacqueline Minett for improvement of the English. NS receives a doctoral grant from the Belgian Fund for Research for the Industry and Agriculture (FRIA), and GL is a Research Associate at the Belgian National Science Foundation (FRS-FNRS). This study was also funded by the Belgian National Fund for Scientific Research (FRFC 2.45.69.03). This paper is MARE publication number 177. The authors declare that the experiments performed comply with the current laws of France and Belgium.

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