

# The role and contribution of the seagrass *Posidonia oceanica* (L.) Delile organic matter for secondary consumers as revealed by carbon and nitrogen stable isotope analysis

S. Vizzini <sup>a,\*</sup>, G. Sarà <sup>a</sup>, R.H. Michener <sup>b</sup>, A. Mazzola <sup>a</sup>

<sup>a</sup>Laboratory of Marine Biology and Sea Resources, Department of Animal Biology, University of Palermo, via Archirafi 18, 90123 Palermo, Italy

<sup>b</sup>Stable Isotope Laboratory, Department of Biology, Boston University, Boston, MA 02215, USA

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## Abstract

The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of primary producers and consumers were studied to obtain information on the trophic role of *Posidonia oceanica* L. Delile, the dominant primary producer, in a Mediterranean shallow environment (the Stagnone di Marsala, western Sicily).  $\delta^{13}\text{C}$  strongly discriminated between pelagic and benthic pathways, with the former based on phytoplankton and the latter on a mixed pool of seagrass detritus, epiphytes and benthic algae as carbon sources. A particularly important trophic role appears to be performed by the vegetal epiphytic community on seagrass leaves ( $\delta^{13}\text{C} = -14.9 \pm 0.1\text{‰}$ ), which supports most of the faunal seagrass community (i.e. Amphipoda, Isopoda, Tanaidacea;  $\delta^{13}\text{C} = -14.9 \pm 0.1\text{‰}$ ,  $-12.5 \pm 0.1\text{‰}$  and  $-14.8 \pm 1.0\text{‰}$ , respectively). Although *P. oceanica* ( $\delta^{13}\text{C} = -11.3 \pm 0.3\text{‰}$ ) does not seem to be utilised by consumers via grazing (apart from a few Palaemonidae species with  $\delta^{13}\text{C}$  value of  $-10.8 \pm 1.8\text{‰}$ ), its trophic role may be via detritus. *P. oceanica* detritus may be exploited as a carbon source by small detritivore invertebrates, and above all seems to be exploited as a nitrogen reservoir by both bottom and water column consumers determining benthic–pelagic coupling. At least three trophic levels were detected in both the pelagic (mixture of phytoplankton and cyanobacteria, zooplankton, juvenile transient fish) and benthic (sedimentary organic matter and epiphytes, small seagrass-associated invertebrates, larger invertebrates and adult resident fish) pathways. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

**Keywords:** Stable isotopes; *Posidonia oceanica*; Food webs; Mediterranean

## 1. Introduction

*Posidonia oceanica* is a common vascular marine plant in Mediterranean coastal waters and supports highly complex and productive ecological systems (Den Hartog, 1977; Pergent and Pergent-Martini, 1991). Much attention has been focused on the architectural role of the seagrass canopy in the structuring of rich faunal assemblages (Bell and Westoby, 1987; Klumpp et al., 1992). It has been widely demonstrated that animal abundance in vegetated habitats is greater than in unvegetated areas due to both increased food supply and reduced predation risks (Heck et al., 1989; Ferrell and Bell, 1991).

Despite the extent of *P. oceanica* meadows, little is known about its trophic role, in particular with respect to secondary consumers. Literature data report that *Posidonia* living tissue is not readily utilised by herbivores, mainly as a consequence of its poor nutritional value and high lignocellulose content (Ott and Maurer, 1977). Indeed, it has been estimated (Pergent et al., 1994) that less than 10% of annual net above-ground production enters the near-shore food webs via grazing, as only a few species of consumers are able to exploit the photosynthetic leaves [e.g. *Idotea baltica* Pall. (Idoteidae), *Paracentrotus lividus* Lam. (Echinidae), *Sarpa salpa* L. (Sparidae) and some decapod species] (Ott and Maurer, 1977; Mazzella et al., 1992). In contrast, it has been suggested that the main transfer route of seagrass organic matter is the detrital pathway (Benner et al., 1988; Mann, 1988; Cebrián et al., 1997).

\* Corresponding author.

E-mail address: vizzini@unipa.it (S. Vizzini).



Experimental studies have highlighted that macroconsumers meet their nutritional needs by feeding on microfauna and meiofauna associated with detritus rather than directly on poor nutritional plant tissues (Fenchel, 1977; Tenore et al., 1984; Coull, 1990). This emphasises the importance of the indirect consumption of vascular material compared to the direct exploitation of living tissues by animals. In addition, understanding the trophic link between seagrasses and top-level consumers in coastal environments can be complicated by the presence of additional primary producers such as living phytoplankton, epiphytic and epilithic algae (Fry, 1988; Kitting et al., 1984; Klumpp et al., 1992).

Recently, contextual analysis of the carbon and nitrogen stable isotope composition of producers and consumers has been used as a tool for identifying the relative incorporation of each organic matter source into food webs (see Fry and Sherr, 1984; Owens, 1987; Michener and Schell, 1994). Stable isotope tracers ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) have been used to follow the fluxes of organic matter into food webs and resolve food web structure (Fry, 1988; Dauby, 1989; Goering et al., 1990; Rau et al., 1992; Yamamuro, 1999; Vizzini, 2001; Moncreiff and Sullivan, 2001). The carbon stable isotope ratios ( $\delta^{13}\text{C}$ ) of consumers reflect those of their organic matter sources with a slight enrichment (about 1‰) (Peterson and Fry, 1987), while the nitrogen isotope ratio undergoes a major increase (about 3–5‰) with each trophic level (Minagawa and Wada, 1984).

Several isotopic studies have been carried out in complex ecosystems such as mangroves, seagrass beds and salt-marshes to assess the relative trophic role of each primary producer and the magnitude of each contribution to upper trophic levels (Fry and Parker, 1979; Mc Connaughey and Mc Roy, 1979; Fry, 1984; Peterson et al., 1985; Dauby, 1989). Such authors state that seagrass living tissues, despite their biomass, appear to be a minor organic matter source for consumers, while seagrass detritus and, to a greater extent, epiphytes on seagrass leaves seem to play the most important trophic role. However, to our knowledge, little information exists on the isotopic composition of *P. oceanica* flats (Bricout et al., 1980; Mc Millan et al., 1980; Cooper and De Niro, 1989) and on its fate in Mediterranean food webs (Dauby, 1989; Havelange et al., 1997; Jennings et al., 1997; Lepoint et al., 2000; Pinnegar and Polunin, 2000).

Consequently, the aims of this study were to investigate (i) the importance of *Posidonia* carbon and nitrogen for consumers in comparison with that of other primary producers (phytoplankton, macroalgae, epiphytes) and (ii) the food web structure in a *P. oceanica* meadow in the western Mediterranean Stagnone di Marsala where *P. oceanica* represents, above all in the central part, one of the most abundant primary producers.

## 2. Materials and methods

### 2.1. Study site

The Stagnone di Marsala is a shallow basin in western Sicily (37° 52' north; 12° 28' east) (Fig. 1) with a surface area of about 2000 ha and an average depth of 1.5 m. It is separated from the open sea by a calcarenite platform (Isola Longa). A northern (Bocca S. Teodoro) and a southern (Bocca Grande) mouth allow water exchange. Water temperatures (min. 11.2 °C, max. 29.1 °C) and salinities (min. 32.8‰, max. 47.1‰) have larger annual amplitudes than in the surrounding sea (temperature: min. 14.1 °C and max. 26.4 °C; salinity close to 37‰) (Sarà et al., 1999). The basin is oligotrophic with chlorophyll-a values ranging around 1.0  $\mu\text{g l}^{-1}$  (Sarà et al., 1999). Seagrasses (*P. oceanica* in the central-southern area and *Cymodocea nodosa* Ucria Asch. in the northern) cover the sand-muddy bottom. *Cystoseira barbata* C. Ag., *C. ercegovicii* Giaccone and *C. spinosa* Sauvageau are generally found on the calcarenite blocks. In the sheltered and muddy areas, *Caulerpa prolifera* (Forssk) Lam. becomes another important primary producer (Scilipoti, 1998). No freshwater input is present (Sarà et al., 1999). The phytoplankton community is dominated by phytoflagellates (Campolmi, 1998). Zooplankton constitutes a quantitatively scant group and Copepoda Harpacticoida

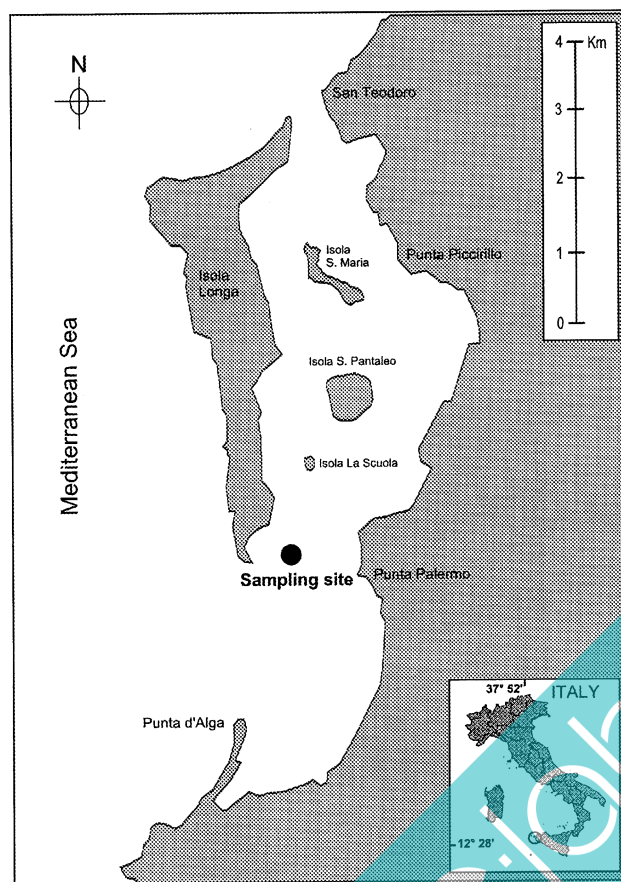


Fig. 1. The study site.

represent the main taxon followed by Copepoda Calanoida as a consequence of the shallowness and hydrodynamic processes (sediment and bottom organism resuspension) (Campolmi, 1998). As regards the ichthyofauna, *Atherina boyeri* Risso (Atherinidae), *Syngnathus typhle* L. and *S. abaster* Risso (Syngnathidae), *Pomatoschistus tortonesei* Mill. and *Gobius niger* L. (Gobiidae) are the main resident fish, while *Liza aurata* Risso (Mugilidae), *Sarpa salpa* L. and *Diplodus puntazzo* Cetti (Sparidae) are the most abundant transient fish (Scilipoti, 1998).

## 2.2. Sampling methods and isotopic analyses

Samples were collected in September 1998 from a *P. oceanica* meadow in the central part of the Stagnone di Marsala (Fig. 1). Particulate organic matter (POM) samples were obtained by filtering 10 l of seawater onto prewashed and precombusted (450 °C, 4 h) Whatman GF/F filters (0.70 µm nominal pore size) under moderate vacuum within 2 h of collection. The POM samples were then stored frozen until laboratory analysis. The dominant in situ primary producers were collected by hand and treated for carbon and nitrogen isotopic analysis. The procedure of Couch (1989) was tentatively used to extract diatoms from sediments. This procedure did not lead to an effective collection of diatoms in terms of dry weight for use in isotopic analysis. Consequently, we do not report microphytobenthic signatures but extracted isotopic data from the current literature (Couch, 1989). Benthic invertebrates were collected with a hand-towed net (400 µm mesh size), while zooplankton was sampled using a mesh net (125 µm mesh size). Sediments were collected using hand corers in order to determine the isotopic composition of the first centimetre of sedimentary organic matter (SOM). Finally, fish were caught by means of a hand-towed trawl net (3 mm mesh size) and only muscle tissue was analysed.

All samples were acidified with 1 N HCl for 10 min or till bubbling stopped to remove carbonates (Goering et al., 1990) and then rinsed with distilled water and oven dried for variable times between 24 and 72 h depending on species. The samples, ground into a fine powder with a mortar and pestle, were loaded into tin capsules and combusted in a Fisons NA1500 elemental analyser. Using continuous flow, the samples were introduced into a Finnigan Delta S isotope ratio mass spectrometer for isotopic analysis.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were obtained in parts per thousand (‰) relative to Vienna Pee Dee Belemnite (vPDB) and atmospheric  $\text{N}_2$  standards, respectively, according to the following formula:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3 \text{ where } R = {}^{13}\text{C}/{}^{12}\text{C} \text{ or } {}^{15}\text{N}/{}^{14}\text{N}.$$

Instrumental precision based on the S.D. of replicates of internal standards was 0.2‰ for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

Bonferroni's corrected *t*-test allowed comparison between taxa within plants and fish (Sokal and Rohlf, 1995).

## 3. Results

### 3.1. Carbon and nitrogen isotopic ratios in primary producers and SOM

Primary producers collected at the study site, apart from *P. oceanica* and its undetermined vegetal epiphytic component, included 14 species of macroalgae. Among the large number of potential food sources analysed, a great variability in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  was observed (Table 1). Macroalgae  $\delta^{13}\text{C}$  ranged from -13.0‰ [*Padina pavonica* (L.) Gail.] to -19.5‰ (*C. ercegovicii*), the  $\delta^{15}\text{N}$  from 1.1‰ (*Polysiphonia* sp.) to 9.5‰ [*Anadyomene stellata* (Wulf.) C. Ag.], while the C:N ratio ranged from 9 (*Halimeda tuna* Lam.) to 46.5 (*C. barbata*). *P. oceanica* showed the most enriched  $\delta^{13}\text{C}$  value (-11.3‰) and among the most depleted  $\delta^{15}\text{N}$  value (2.8‰). The vegetal portion (diatoms, calcareous encrusting, soft encrusting and filamentous erect algae) of seagrass epiphytes showed a value of -14.9‰ for  $\delta^{13}\text{C}$ , 5.2‰ for  $\delta^{15}\text{N}$  and a low C:N value (7.4). Since the POM carbon signal was relatively light (-21.5‰) with a low C:N ratio (7.2), this may be representative of a phytoplankton isotopic signature (Harrigan et al., 1989; McClelland and Valiela, 1998). In contrast, SOM showed an isotopic signature of -11.8 and 2.4‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively. Bonferroni test results (Table 2) confirmed a great variability in the isotopic composition of plants. In particular, *P. oceanica*  $\delta^{13}\text{C}$  values differed significantly from other plant  $\delta^{13}\text{C}$ .

### 3.2. Carbon and nitrogen isotopic ratios in consumers

The isotopic composition of consumers showed a wide range of values (Table 1). Invertebrate carbon isotopic ratios ranged from -10.8‰ (Palaemonidae) to -22.7‰ (Copepoda Calanoida) and nitrogen isotopic ratios were between 2.5‰ (Nematoda) and 8.9‰ (*Carcinus aestuarii* Nardo). The  $\delta^{13}\text{C}$  of fish collected in the Stagnone di Marsala ranged from -11.6‰ (*P. tortonesei* and *S. typhle*) to -20.0‰ (*L. aurata*) and  $\delta^{15}\text{N}$  from 6.4‰ (*Symphodus ocellatus* Forssk.) to 16.1‰ (*P. tortonesei*). Bonferroni test outcomes (Table 2) showed a smaller variability in the isotopic composition of consumers compared with that of plant. Transient fish  $\delta^{13}\text{C}$  values were significantly different from those of resident species. As regards  $\delta^{15}\text{N}$  values, *P. tortonesei* was significantly different from all the other fish species.

## 4. Discussion

### 4.1. Carbon and nitrogen isotopic ratios in primary producers and SOM

The isotopic signatures of the primary producers in the Stagnone di Marsala showed a very wide variation in the

Table 1

Carbon and nitrogen stable isotopic values and C:N elemental ratios in primary producers, particulate and sedimentary organic matter and consumers collected in the study area in September 1998. ACR: acronyms; N: number of specimens pooled; n: number of replicates

		ACR	N	n	$\delta^{13}\text{C}$	$\pm\text{S.D.}$	$\delta^{15}\text{N}$	$\pm\text{S.D.}$	C:N	$\pm\text{S.D.}$	
Organic matter sources	<i>Anadyomene stellata</i>	Anad	–	3	–14.3	2.5	9.5	1.0	19.5	1.2	
	<i>Caulerpa prolifera</i>	Cau	–	3	–13.3	1.0	4.0	2.2	12.7	1.1	
	<i>Chaetomorpha</i> sp.	Chae	–	3	–17.9	0.1	5.6	0.4	14.9	0.4	
	<i>Chondria</i> sp.	Chon	–	3	–17.5	2.0	5.4	5.0	24.1	10.7	
	<i>Cystoseira barbata</i>	Cys1	5	3	–16.3	0.1	1.8	0.2	46.5	0.1	
	<i>Cystoseira ercegovicii</i>	Cys2	5	3	–19.5	0.1	5.4	0.1	25.1	0.8	
	<i>Cystoseira spinosa</i>	Cys3	5	3	–16.0	0.2	2.2	0.8	26.4	9.8	
	<i>Dasycladus vermicularis</i>	Dasy	–	3	–18.8	0.6	8.9	0.8	12.0	1.1	
	<i>Halimeda tuna</i>	Hal	–	3	–16.3	0.8	5.0	0.7	9.0	0.6	
	<i>Laurencia</i> sp.	Lau	–	3	–18.1	1.1	5.3	0.2	19.8	0.6	
	<i>Padina pavonica</i>	Pad	5	3	–13.0	2.5	2.5	5.6	26.2	2.4	
	<i>Polysiphonia</i> sp.	Pol	–	3	–18.4	0.1	1.1	0.1	25.7	0.8	
	<i>Posidonia oceanica</i>	Pos	5	3	–11.3	0.3	2.8	0.4	27.4	5.0	
	<i>Posidonia</i> vegetal epiphytes	Epiph	–	3	–14.9	0.1	5.2	0.4	7.4	1.5	
	<i>Rytiphloea tinctoria</i>	Ryt	5	3	–17.3	0.4	9.5	0.2	13.1	0.8	
	<i>Valonia utricularis</i>	Val	–	3	–15.7	0.2	10.4	0.8	12.8	1.9	
	Particulate organic matter	POM	–	3	–21.5	0.8	6.0	0.8	7.2	1.0	
	Sedimentary organic matter	SOM	–	3	–11.8	0.9	2.4	1.6	–	–	
	Invertebrates	Actinaria	Act	6	2	–14.5	0.3	4.6	0.6	–	–
		Amphipoda	Amp	>100	2	–14.9	0.1	4.5	0.5	–	–
<i>Asterina gibbosa</i>		Ag	15	2	–13.1	0.6	6.5	1.0	–	–	
<i>Carcinus aestuarii</i>		Ca	8	2	–13.0	0.3	8.9	0.1	–	–	
<i>Cerastoderma glaucum</i>		Cg	10	2	–15.0	0.7	6.3	0.9	–	–	
Copepoda Calanoida		Cal	>100	2	–22.7	0.4	5.3	0.8	–	–	
Copepoda Harpacticoida		Har	>100	2	–20.6	0.4	3.7	0.8	–	–	
Isopoda		Iso	12	2	–12.5	0.1	5.2	1.7	–	–	
Nematoda		Nem	>100	2	–22.0	0.8	2.5	1.0	–	–	
<i>Ophiura</i> sp.		Op	5	2	–13.7	0.6	6.6	1.2	–	–	
Ostracoda		Ostr	>100	2	–15.9	0.8	8.5	0.6	–	–	
Palaemonidae		Pal	10	2	–10.8	1.8	7.2	0.6	–	–	
Pantopoda		Pan	20	2	–17.4	0.2	3.4	0.4	–	–	
Polychaeta		Pol	>100	2	–13.1	0.0	6.3	0.1	–	–	
Tanaidacea		Tan	>100	2	–14.8	1.0	4.9	1.1	–	–	
Fish		<i>Aphanius fasciatus</i>	Af	10	2	–12.6	0.3	12.9	0.0	–	–
		<i>Atherina boyeri</i>	Ab	20	2	–12.4	0.1	10.3	0.0	–	–
	<i>Gobius niger</i>	Lb	10	2	–11.9	0.8	14.1	0.6	–	–	
	<i>Lipophrys basiliscus</i>	Gn	8	2	–12.0	0.5	13.1	0.5	–	–	
	<i>Liza aurata</i>	La	15	2	–20.0	0.6	6.9	0.8	–	–	
	<i>Pomatoschistus tortonesei</i>	Pt	15	2	–11.6	0.2	16.1	0.0	–	–	
	<i>Sarpa salpa</i>	Ss	7	2	–18.4	0.9	9.6	0.9	–	–	
	<i>Symphodus ocellatus</i>	So	8	2	–12.8	0.1	6.4	0.1	–	–	
	<i>Syngnathus abaster</i>	Sa	10	2	–11.8	0.7	11.4	0.4	–	–	
	<i>Syngnathus typhle</i>	St	10	2	–11.6	0.6	10.7	1.1	–	–	

$^{13}\text{C}$  content. Indeed, the carbon isotope ratios between seagrass, algae and phytoplankton-POM were markedly distinct (Fig. 2). *P. oceanica* leaves and detritus had the most enriched  $\delta^{13}\text{C}$  and among the lowest  $\delta^{15}\text{N}$  values. Algae exhibited a great range of variability for both isotopic signatures showing significant differences between taxa (Table 2). This may be explained by physiological factors (enzymatic discrimination during photosynthesis) and the ability to use different carbon ( $\text{HCO}_3^-$  or dissolved  $\text{CO}_2$ ) and nitrogen ( $\text{NO}_3^-$  or  $\text{NH}_4^+$ ) sources (Zieman et al., 1984; Cifuentes et al., 1988; Fry, 1991; Hemminga and Mateo, 1996). Size of algae can also affect their metabolism, biochemical composition and, consequently, their isotopic composition. It has been demonstrated that the relative surface area (i.e. SA:V) can influence gas exchanges be-

tween the plant and external environment (Hein et al., 1995). As a consequence, also the SA:V ratios of algae can play a not negligible role in determining differences of the isotopic composition between algae.

POM  $\delta^{13}\text{C}$  was the most depleted and was similar to values reported for phytoplankton samples in other Mediterranean areas (Dauby, 1989; Mazzola et al., 1999; Vizzini, 2001; Mazzola et al., 2001), indicating that seagrass detritus contributed little to the suspended bulk. Accordingly, the low C:N atom ratios of POM (7.2) may highlight the contribution of phytoplankton to POM. In addition, the SOM carbon isotopic composition fell well within the *P. oceanica* isotopic range. The role of microphytobenthos (literature data [Coull, 1990] at about  $-12.8$  and  $3.8\text{‰}$ , respectively, for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ), *P. oceanica*





Table 2  
The significance levels of the Bonferroni's corrected *t*-test to evaluate differences in the isotopic composition ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) among plants (a) and fish (b). Each cell of the table includes the results for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ( $\delta^{13}\text{C}/\delta^{15}\text{N}$ , respectively). \*:  $P \leq 0.05$ ; \*\*:  $P \leq 0.01$ ; \*\*\*:  $P \leq 0.001$ ; ns: not-significant difference ( $P > 0.05$ ). For acronyms, see Table 1

(a)														
	Anad	Cau	Chae	Chond	Cys1	Cys2	Cys3	Epiph	Dasy	Hal	Lau	Ryt	Val	Pos
Anad	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cau	****/****	—	—	—	—	—	—	—	—	—	—	—	—	—
Chae	****/****	****/****	—	—	—	—	—	—	—	—	—	—	—	—
Chond	****/****	****/****	ns/ns	—	—	—	—	—	—	—	—	—	—	—
Cys1	ns/****	****/ns	****/****	****/****	—	—	—	—	—	—	—	—	—	—
Cys2	****/****	****/ns	ns/ns	ns/ns	****/****	—	—	—	—	—	—	—	—	—
Cys3	****/****	****/ns	****/****	****/****	ns/ns	****/****	—	—	—	—	—	—	—	—
Epiph	ns/****	****/****	****/ns	****/ns	ns/****	****/ns	ns/****	—	—	—	—	—	—	—
Dasy	****/****	****/****	ns/ns	ns/ns	****/****	ns/ns	****/****	****/ns	—	—	—	—	—	—
Hal	****/ns	****/****	ns/****	****/ns	ns/****	****/****	ns/****	ns/ns	****/ns	—	—	—	—	—
Lau	****/****	****/ns	ns/****	ns/****	****/ns	ns/****	****/ns	****/****	ns/****	****/****	—	—	—	—
Ryt	****/ns	****/****	ns/****	ns/****	****/****	****/****	ns/****	****/****	ns/****	ns/ns	ns/****	—	—	—
Val	****/****	****/****	ns/****	ns/****	****/ns	****/****	ns/ns	****/****	ns/****	ns/****	ns/ns	ns/****	—	—
Pos	****/****	****/ns	****/****	****/****	****/ns	****/****	****/ns	****/****	****/****	****/****	****/ns	****/****	****/ns	—
(b)														
	Af	Ab	Lb	Gn	La	Pt	Ss	So	St					
Af	—	—	—	—	—	—	—	—	—					
Ab	ns/****	—	—	—	—	—	—	—	—					
Lb	ns/ns	ns/****	—	—	—	—	—	—	—					
Gn	ns/ns	ns/****	ns/ns	—	—	—	—	—	—					
La	****/****	****/ns	****/****	****/****	—	—	—	—	—					
Pt	ns/****	ns/****	ns/ns	ns/****	****/****	—	—	—	—					
Ss	****/****	****/ns	****/ns	****/****	ns/ns	****/****	—	—	—					
So	ns/****	ns/****	ns/****	ns/****	****/ns	ns/****	****/****	—	—					
St	ns/ns	ns/ns	ns/ns	ns/ns	****/ns	ns/****	****/ns	ns/****	—					

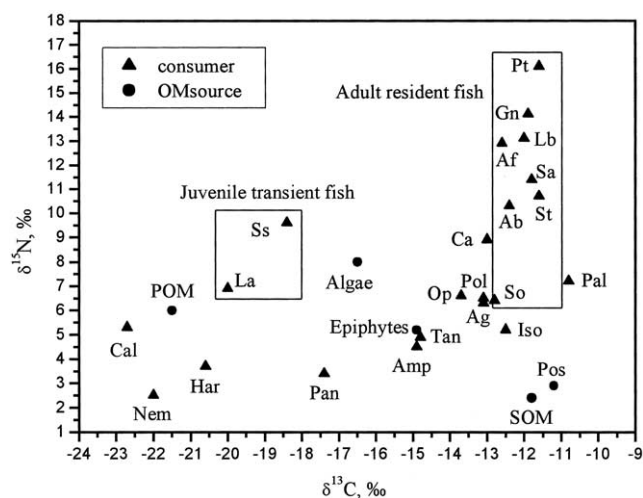


Fig. 2.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of primary producers (●) and consumers (▲) in a *P. oceanica* meadow of the Stagnone di Marsala. For acronyms, see Table 1.

( $\delta^{13}\text{C} = -11.3\text{‰}$ ;  $\delta^{15}\text{N} = 2.8\text{‰}$ ) and, to a lesser extent, macroalgae ( $\delta^{13}\text{C}$  range from  $-19.5$  to  $-13.0\text{‰}$ ;  $\delta^{15}\text{N}$  range from  $1.1$  to  $11.3\text{‰}$ ) may not be negligible in the mixed SOM isotopic signature ( $\delta^{13}\text{C} = -11.8\text{‰}$ ;  $\delta^{15}\text{N} = 2.4\text{‰}$ ).

#### 4.2. Carbon and nitrogen isotopic ratios in consumers

The carbon stable isotope ratios differed markedly between three invertebrate categories (Table 1). The animals

clustered independently of their size and trophic guilds, suggesting that there were at least three ultimate carbon sources in the study area. First, the exclusive use of *P. oceanica* would seem to be possible for only some Palaemonidae taxa whose  $\delta^{13}\text{C}$ , the most enriched, overlapped with that of the seagrass plus a small enrichment (Fig. 2). Accordingly, it has been demonstrated that some decapods feed on *Posidonia* (Mazzella et al., 1992). Second, Copepoda Calanoida, Copepoda Harpacticoida and Nematoda were the most depleted in  $^{13}\text{C}$  and showed great similarity to the POM signatures, suggesting the exploitation of pelagic resources in the water column by Calanoida and during settling by the other taxa living in association with vegetation and sediments. Lastly,  $\delta^{13}\text{C}$  in the remaining invertebrate taxa fell into the range from  $-17.4$  to  $-12.5\text{‰}$ , suggesting a mixed diet, the ultimate carbon sources of which might be living vegetal tissues (i.e. microphytobenthos and the epiphytic community) and/or vegetal detritus (algae and seagrass). According to some authors (Kitting et al., 1984; Klumpp et al., 1992), the animal community associated with *Posidonia* (e.g. Amphipoda and Tanaidacea) is an important trophic link in the food web between primary producers and consumers and appears to feed on vegetal epiphytes.

As regards  $\delta^{15}\text{N}$  values, the depleted signatures in most of invertebrate taxa, often lower than that of the organic matter sources, might indicate the assimilation of  $\text{N}_2$ -fixing blue-green algae, which usually exhibit  $\delta^{15}\text{N}$  values very



close to atmospheric  $N_2$  (Wada and Hattori, 1976). Indeed, it is well known that cyanobacteria is an important component of the epiphytic community on *Posidonia* leaves (Mazzella and Russo, 1989). On the other hand, due to the low  $^{15}N$  content, SOM could be another nitrogen source for some consumers. Other hypotheses can explain the depleted nitrogen isotopic signatures in several invertebrates. It is well known that different biochemical components in plants and animals exhibit different isotopic signatures (Gannes et al., 1998). As a consequence, a selective assimilation of depleted biochemical fractions from the bulk ingested can be a mechanism at the base of low  $^{15}N$  content in invertebrates. In addition, the acidification of samples before the isotopic analysis could alter the original isotopic signature. It has been suggested that the acidification process, which provides a more accurate measure of  $\delta^{13}C$  values, may affect  $\delta^{15}N$  values (Bunn et al., 1995). However, while acidification is a procedure that is still used, at present it is not well understood how and to what extent it affects the isotopic composition.

Analysis of stomach contents of juvenile transient and resident fish demonstrated that transient species are usually planktivorous, feeding on microzooplankton and POM detritus (Ferrari and Chiericato, 1981; Gisbert et al., 1996), while resident species are carnivorous on epibenthic and vagile fauna associated with vegetation (Zander and Berg, 1984; Tipton and Bell, 1988; Barry et al., 1996).  $\delta^{13}C$  data confirm the different feeding strategies of the two fish categories as demonstrated by the significant differences in the carbon isotopic composition between fish belonging to the two groups (Table 2). Juvenile transient species (*L. aurata*, *S. salpa*) were significantly different in terms of both  $\delta^{13}C$  and  $\delta^{15}N$  from each other species. *L. aurata* and *S. salpa* juveniles showed depleted  $\delta^{13}C$  values (mean  $\delta^{13}C = -19.2 \pm 1.1\%$ ), suggesting a feeding preference for Copepoda Calanoida and Harpacticoida (mean  $\delta^{13}C = -21.7 \pm 1.5\%$ ). However, an unexpected positive fractionation (2.5‰) leads us to hypothesise a mixed diet, consisting, apart from Copepoda, of Crustacea Peracarida (mean  $\delta^{13}C = -14.8 \pm 0.1\%$ ) and/or resuspended detritus. This unusual feeding behaviour may be a result of the environmental features of the study site. As previously demonstrated (Campolmi, 1998), a true zooplankton community is not present in the Stagnone di Marsala. Although Copepoda Calanoida represent a large proportion of the community, a significant part was due to Copepoda Harpacticoida and other benthic organisms as a consequence of the shallow water, resuspension events, large fluctuations in physico-chemical variables and the oligotrophy of the study area. In contrast, resident fish species (*Aphanius fasciatus* Nardo, *A. boyeri*, *Lipophrys basiliscus* Val., *G. niger*, *P. tortonesei*, *S. ocellatus*, *S. abaster* and *S. typhle*), which spend their entire life cycle inside the Stagnone, showed matching  $\delta^{13}C$  values (mean  $\delta^{13}C = -12.1 \pm 0.4\%$ ), highly enriched in comparison with migrant species shown to feed exclusively on benthic fauna. Such feeding preferences have been

reported for most resident species in the study site (Scilipoti, 1998), being microcarnivores on phytal preys. The only exceptions were the Gobiidae (*P. tortonesei* and *G. niger*), which, according to the literature (Vesey and Langford, 1985; Hamerlynck and Cattrijsse, 1994; Scilipoti, 1998), feed mainly on sediment-associated prey and faecal pellets. Their highest  $^{15}N$  content, significantly different from other species values (Table 2), may indicate feeding preferences, which include decomposing material with an active associated microbial community. Similar findings have never been obtained from gut content analysis. Although a close correspondence has generally been observed between literature dietary data and the isotopic composition of fish (Pinnegar and Polunin, 2000), the exception of the Gobiidae indicates the utility of stable isotope analysis as a tool for investigating trophic relationships. In contrast with gut content analysis,  $\delta^{13}C$  and  $\delta^{15}N$  yield information on digested and unidentifiable material (i.e. detritus) and provide relatively long-term and time-integrated measurements of feeding preferences and what is actually assimilated (Harrigan et al., 1989; Vander-Zanden, 1997).

#### 4.3. Food web implications

$\delta^{13}C$  and  $\delta^{15}N$  were used to identify the transfer route of carbon and nitrogen into the food web of a *P. oceanica* bed in the Stagnone di Marsala. Consumer  $\delta^{13}C$  values in general were more negative than those of the dominant seagrass. This suggests the dominance of alternative or mixed carbon sources. Only a few true herbivores belonging to Palaemonidae showed a carbon isotope ratio, which markedly overlapped that of living *P. oceanica*, confirming the poor contribution of seagrasses to the upper trophic level via grazing. In contrast, carbon from epiphytes, algae and seagrass detritus appeared to dominate the benthic food web. The important trophic role of the vegetal community growing on seagrass leaves, as a consequence of the elevated production, often equivalent or greater than that of the seagrasses, and the high nutritional value of epiphytes has been stressed (Fry, 1984; Kitting et al., 1984; Gambi et al., 1992). When we consider the functioning of the entire *P. oceanica* ecosystem in the study site, the intermediate values of most consumers between epiphytes and *Posidonia*-SOM let us hypothesise a use of mixed sources for the benthic pathway. POM carbon may be an alternative carbon source available exclusively to planktonic invertebrates and planktivorous fish. Consequently, in terms of carbon uptake, plant detritus and epiphytes were more important for benthic organisms and phytoplankton was more important for pelagic organisms indicating an uncoupling between bottom-associated and pelagic resources. Our results are in agreement with findings reported in other Mediterranean *Posidonia* ecosystems by means of stable isotope analysis. *P. oceanica* seems to be a minor organic matter source for consumers in the Revellata Bay (Gulf of Calvi, Corsica, FR) (Dauby, 1989; Lepoint et al., 2000).



Pinnegar and Polunin, 2000). The only transfer route for *P. oceanica* into the food web is through decomposition. Seaweeds, phytoplankton and epiphytes on seagrass leaves supply an elevated proportion of organic matter for consumers. Similar findings have been found in other geographical areas with other seagrass species (Fry and Parker, 1979; Mc Connaughey and Mc Roy, 1979; Fry, 1984; Paterson and Whitfield, 1997). However, herbivore pressure shows high variability among seagrass species. Fast-growing plants (high leaf turnover rate) due to their low lignin content are more used by herbivores than slow-growing ones (low leaf turnover rate), which have a greater lignin content (Cebrián et al., 1997). In particular, in the Mediterranean, the loss of organic matter to herbivores is greater in *C. nodosa* and *Zostera noltii* Hornem. (fast-growing plants) than in *P. oceanica* (slow-growing plant) (Cebrián et al., 1997). Such finding can be involved in the poor herbivore pressure on *P. oceanica* in the study site.

Using the assumption of a  $\delta^{15}\text{N}$   $3.4 \pm 1.1\text{‰}$  enrichment per trophic level (Minagawa and Wada, 1984), we can quantify the number of trophic steps present in the pelagic and benthic systems of the study site (Fig. 3). Both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  indicated a pelagic food web of at least three levels, from a mixture of phytoplankton and cyanobacteria at the base to juvenile transient fish (*L. aurata* and *S. salpa*), with zooplankton as the intermediate level. The benthic organic matter transfer also undergoes at least three trophic steps: SOM and epiphytes at the base, small seagrass-associated invertebrates which consume detritus and/or epiphytes at the second level, while at the upper trophic levels are found invertebrates plus some fish species (*A. boyeri*, *S. ocellatus*, *S. abaster* and *S. typhle*) which feed on phytal prey and carnivorous-detritivores feeding on a mixture of living resources and decomposed and rearranged organic material (*A. fasciatus*, *L. basiliscus*, *G. niger*, *P. tortonesei*).

At present not many isotopic data exist, to our knowledge, about food web structure in Mediterranean coastal environments. The isotopic analyses of carbon and nitrogen presented here suggest interesting features regarding the trophic role of the seagrass *P. oceanica*, a key component in the infralittoral Mediterranean, for higher trophic levels. The overall picture that has emerged is of trophic impor-

tance of seagrass detritus and epiphytes rather than seagrass living tissues and provides suggestive evidence regarding the benthic–pelagic coupling in marine coastal areas.

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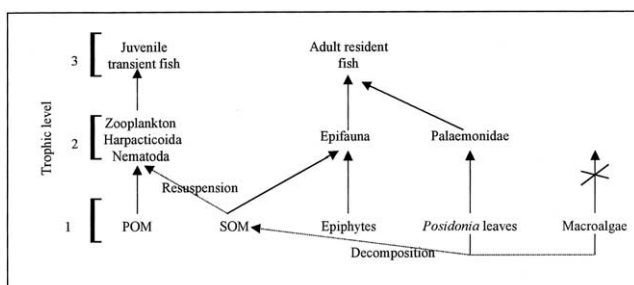


Fig. 3. Food web structure in a *P. oceanica* meadow of the Stagnone di Marsala as revealed by  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. Dot arrow: physical or chemical events. Solid arrow: organic matter fluxes. SOM: sedimentary organic matter.



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