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THE TROPHIC ROLE OF THE MACROPHYTE *CYMODOCEA NODOSA* (UCRIA) ASCH. IN A MEDITERRANEAN SALTWORKS: EVIDENCE FROM CARBON AND NITROGEN STABLE ISOTOPE RATIOS

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ABSTRACT

A multiple stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) was used to determine the trophic role of the seagrass *Cymodocea nodosa* (Ucria) Asch. for consumers in a Mediterranean saltworks. Stable carbon and nitrogen isotope ratios performed on primary producers and consumers in February and July 1999 showed that *C. nodosa* is not a direct dietary source via grazing. No animal presented carbon values as enriched as the seagrass (−7.8‰). The trophic role of *Cymodocea* occurs through the detritus route via SOM. Sedimentary organic matter (SOM) ($\delta^{13}C$ = −16.5‰) seems to be a mixture of particulate organic matter ($\delta^{13}C$ = −19.0‰), algae ($\delta^{13}C$ = −18.6‰) and seagrass detritus ($\delta^{13}C$ = −7.7‰). The results of a mixing model suggest that *Cymodocea* detritus contribution to SOM varied temporally, a greater role in February than in July. In July the enriched values of both stable carbon and nitrogen isotopes of several primary producers and consumers in comparison with February (about +2‰ for primary producers, +3.5‰ for invertebrates and +1‰ for fish) suggest that less depleted carbon and nitrogen (probably from seagrass detritus) influence food web structure. *Cymodocea* has an important structuring role as seagrass blades are extensively colonised by a complex vegetal community which provides food and habitats for invertebrates. The $\delta^{13}C$ of the animals suggests that epiphytes may represent an important ultimate organic matter source together with SOM.

In seagrass ecosystems the energy supply for consumers generally originates from different organic matter sources, mainly seagrass living tissues and detritus, phytoplankton and benthic algae (Livingston, 1982). The relative contribution of each source can change over time. Indeed available food sources for consumers are characterised by temporal variability as a result of the seasonal changes in production, hydrodynamic conditions and allochthonous sources (Livingston, 1984; Pérez and Romero, 1994). In particular, only about 10% of the net aboveground production in seagrasses seems to be directly channelled into upper trophic levels by grazing (Pergent et al., 1994). This is due to their low nitrogen and high cellulose content and the presence of phenolic compounds (Mazzella et al., 1992). In contrast, seagrass detritus seems to be the ultimate food source for consumers in coastal environments (Mann, 1988; Cebrián et al., 1997). Given the marked seasonality in seagrass production and biomass (Duarte, 1989), above all in fast-growing 'pioneer' species such as *Cymodocea nodosa* (Cebrián et al., 1997), it is possible that the trophic importance of phanerogames is a function of different temporal scales.

Although a good understanding of trophic relationships in seagrass ecosystems is difficult to assess, the analysis of stable carbon and nitrogen isotope composition in the last decades has provided insight into the organic matter flow and food web structure, particularly in detrital food webs (Fry, 1984; Marguillier et al., 1997). The utility of such measurements lies in the fact that the transfer of carbon and nitrogen isotopes throughout the food web undergoes expected variations due to predictable patterns in metabolic isotopic fractionation (Michener and Schell, 1994). Accordingly, the carbon isotope ratios

of animals reflect those of their food sources plus a slight enrichment (about 1‰), while nitrogen undergoes a greater fractionation, increasing by about 3.5‰ (Michener and Schell, 1994).

In this paper we report the stable isotope signatures of several primary producers (phytoplankton, benthic algae, seagrass) and consumers in a *C. nodosa* flat of a Sicilian saltworks (southern Mediterranean). Despite the fact that *C. nodosa* is a dominant seagrass along Mediterranean coasts (Den Hartog, 1970), to our knowledge little information exists concerning either its incorporation into food webs or its trophic importance. The aims of this study were (i) to determine food web features and their temporal fluctuations and (ii) to assess the trophic role of the seagrass *C. nodosa* and its fluctuation on a temporal scale.

MATERIALS AND METHODS

STUDY AREA.—Samples for stable isotope analysis were collected in a 'cooling vat' of a saltworks in western Sicily (37°52′N, 12°28′E). The saltworks is adjacent to and communicates with the 'Stagnone di Marsala', a shallow and oligotrophic semi-enclosed marine system. The surface area of the vat is approximately 6 ha with an average depth of 0.8 m. The phytoplankton biomass is quite low, with chlorophyll-a concentrations on average 1 μg l^{-1} (Sarà et al., 2000). Frequent wind-induced cycles of resuspension-sedimentation-accumulation in the sediments occur (Sarà et al., 2000). The sand-muddy bottoms are covered with *Cymodocea nodosa*, the dominant primary producer.

SAMPLING.— Sampling was carried out on two different dates: 02-08-1999 (temperature 10°C; salinity 38‰) and 07-16-1999 (temperature 29°C; salinity 57‰). Samples of seawater, collected in each period at the same distance from the bottom, were filtered through precombusted glass fibre filters (Whatman GF/F) (450°C, 4 h) for the isotopic analysis of particulate organic matter (POM). Handle corers were used to sample sedimentary organic matter (SOM). Common terrestrial halophytes (*Arthrocnemum glaucum* and *Atriplex portulacoides)*, dominant in the edge of the saltworks, were picked by hand together with macroalgae and *C. nodosa*. Vagile fauna was caught by means of a hand-towed net (mesh size: 400 μm). Other benthic invertebrates were sorted from mud sampled with a handle corer. A hand-towed trawl net (mesh size: 3 mm) was used to catch fish.

STABLE ISOTOPE MEASUREMENTS.—In the laboratory, after acidification in 2N HCl (at least for 10 min) all samples were dried at 60°C for several hours and ground. Due to the wide variation in the isotopic composition of plants (Michener and Schell, 1994) and to avoid within- and among-individual variability, each plant sample consisted of five to ten individuals. All invertebrate and fish samples were a composite of a variable number of individuals to meet mass requirements for isotopic analysis. Invertebrate specimens were analysed whole, while only the muscle of fish was analysed after dissection. Samples were run at Boston University using continuous flow and a Finnigan Delta-S isotope ratio mass spectrometer. Isotopic values were expressed in parts per thousand as deviations from standards (Vienna Pee Dee Belemnite for δ^{13}C and nitrogen in air for δ^{15}N) according to the following formula:

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

Experimental precision based on the standard deviation of replicates of internal standards was 0.2‰ for both δ^{13}C and δ^{15}N. Temporal differences in the isotopic composition (δ^{13}C and δ^{15}N) were tested using t-test (Sokal and Rohlf, 1995) on data presented in Table 1.

Table 1. Carbon and nitrogen isotope ratios of the main organic matter sources, invertebrates and fish collected in the study area. Values are expressed in per mil (‰). ACR: acronyms; N: number of specimens pooled; n: number of replicates.

	ACR	02-08-1999			07-16-1999		
		N	$\delta^{13}C$ ± s.d. (n)	$\delta^{15}N$ ± s.d. (n)	N	$\delta^{13}C$ ± s.d. (n)	$\delta^{15}N$ ± s.d. (n)
Organic matter sources							
Chaetomorpha linum	–	–	−21.4 ± 0.1 (2)	5.8 ± 0.5 (2)	–	−19.4 ± 0.0 (2)	6.9 ± 0.0 (2)
Cymodocea nodosa	–	10	−8.7 ± 0.1 (2)	5.2 ± 0.3 (2)	10	−7.1 ± 0.1 (2)	7.9 ± 0.2 (2)
Cymodocea nodosa detritus	–	–	−7.8 ± 0.5 (2)	5.9 ± 0.1 (2)	–	−7.7 ± 0.1 (2)	8.3 ± 0.5 (2)
Cystoseira sp.	–	5	−17.8 ± 0.1 (2)	7.1 ± 0.1 (2)	5	−15.8 ± 0.1 (2)	9.8 ± 0.1 (2)
Epiphytes	–	–	–	–	–	−14.6 ± 0.0 (2)	7.2 ± 0.2 (2)
Halophytes	–	5	−24.7 ± 0.2 (2)	8.0 ±1.5 (1)	5	−24.0 ± 0.3 (2)	7.8 ± 0.7 (2)
Laurencia sp.	–	–	−19.6 ± 0.2 (2)	5.9 ± 0.1 (2)	–	−17.8 ± 0.3 (2)	7.4 ± 0.2 (2)
Particulate organic matter	POM	–	−22.2 ± 1.0 (3)	5.9 ± 0.3 (3)	–	−15.7 ± 0.2 (3)	3.8 ± 0.8 (3)
Sedimentary organic matter	SOM	–	−15.3 ± 1.8 (3)	1.3 ± 1.1 (3)	–	−17.7 ± 0.7 (3)	4.9 ± 0.2 (3)
Invertebrates							
Amphipoda	Amp	>100	−17.6 ± 0.5 (2)	3.6 ± 0.1 (2)	>100	−15.4 ± 0.1 (3)	8.6 ± 0.3 (2)
Harpacticoida	Harp	>200	−20.5 ± 0.4 (2)	3.4 ± 0.3 (2)	>200	−14.5 ± 0.5 (2)	9.9 ± 0.4 (2)
Mysidacea	Mys	>50	−12.5 ± 0.6 (2)	9.5 ± 0.0 (2)	>50	−10.1 ± 0.1 (2)	12.2 ± 0.2 (2)
Nematoda	Nem	>200	−22.0 ± 0.1 (2)	2.8 ± 0.4 (2)	>200	−16.1 ± 0.4 (2)	8.6 ± 0.1 (2)
Polychaeta	Pol	>100	−13.9 ± 0.4 (2)	8.0 ± 0.3 (2)	>100	−14.5 ± 0.1 (2)	10.5 ± 0.5 (2)
Tanaidacea	Tan	>100	−21.3 ± 0.4 (2)	3.5 ± 0.3 (2)	>100	−16.5 ± 0.0 (2)	9.2 ± 0.1 (2)
Fishes							
Aphanius fasciatus	Af	20	−11.2 ± 0.3 (4)	13.4 ± 0.6 (4)	20	−10.5 ± 0.3 (4)	12.7 ± 0.4 (4)
Atherina boyeri	Ab	20	−12.0 ± 0.5 (7)	12.2 ± 0.2 (7)	20	−11.8 ± 0.4 (7)	13.2 ± 0.2 (7)
Liza aurata (juvenile)	La	12	−19.8 ± 0.1 (2)	7.5 ± 0.5 (2)	8	−19.9 ± 0.1 (2)	7.5 ± 0.2 (2)
Pomatoschistus tortonesei	Pt	18	−13.1 ± 0.3 (2)	12.8 ± 0.1 (2)	8	−11.6 ± 0.4 (2)	13.2 ± 0.2 (2)
Sparus aurata (juvenile)	Sa	10	−21.5 ± 0.3 (2)	7.4 ± 0.4 (2)	–	–	–
Syngnathus abaster	Sya	20	−12.3 ± 0.8 (6)	11.8 ± 0.1 (6)	12	−11.0 ± 0.8 (6)	12.4 ± 0.4 (6)
Syngnathus typhle	Syt	11	−12.7 ± 0.3 (2)	10.7 ± 0.1 (2)	12	−11.2 ± 0.1 (2)	11.9 ± 0.0 (2)
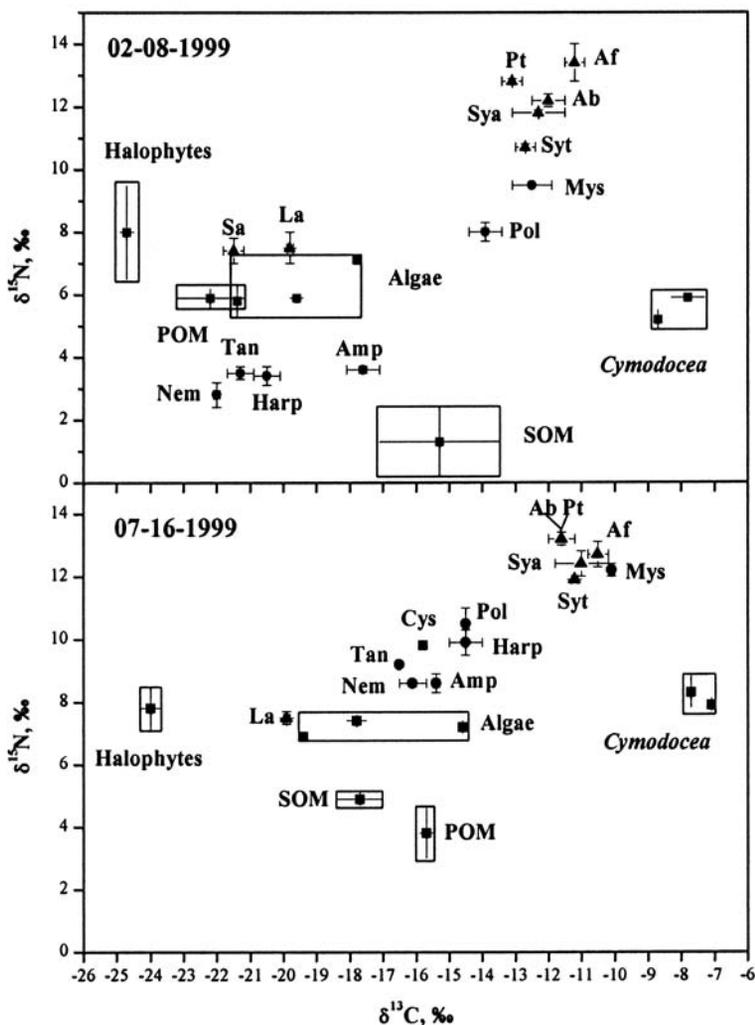
Figure 1. Plot of $\delta^{13}C$ versus $\delta^{15}N$ for organic matter sources (■), invertebrates (●) and fish (▲) from a Mediterranean saltworks, expressed as parts per mil (‰). For acronyms see Table 1.

A mixing model equation (see Dauby, 1989 for details), used for the identification of the origin of sedimentary organic matter (SOM), derives the range of the possible contribution from three main sources (seagrass detritus, algae and POM) to total SOM.

Results

The isotopic composition of several organic matter sources, invertebrates and fish were analysed and are presented in Table 1 and Figure 1. Considering the mean values of the two sampling dates, the carbon and nitrogen isotopic ratios varied respectively between –24.3 ± 0.5‰ (halophytes) and –7.8 ± 0.4‰ (*C. nodosa* detritus) and between 3.1 ± 2.5‰ (SOM) and 13.1 ± 0.5‰ (*Aphanius fasciatus*). $\delta^{13}C$ showed a wider variation in sources (ranging from –24.3 ± 0.5‰ in halophytes to –7.8 ± 0.4‰ in *C. nodosa* detritus) than in

invertebrates (ranging from -19.1 ± 4.2‰ in Nematoda to -11.3 ± 1.7‰ in Mysidacea) or fish (ranging from -21.5‰ in *Sparus aurata* to -10.9 ± 0.5‰ in *A. fasciatus*). $\delta^{15}N$ ranged from 3.1 ± 2.5‰ in SOM to 8.5 ± 1.9‰ in *Cystoseira sp.* in organic matter sources, from 5.7 ± 4.1‰ in Nematoda to 10.9 ± 1.9‰ in Mysidacea in invertebrates and from 7.4‰ in *S. aurata* to 13.1 ± 0.5‰ in *A. fasciatus* in fish.

In looking at the temporal differences in isotopic composition, a general trend towards $\delta^{13}C$ and $\delta^{15}N$ enrichment was detected in both producers and consumers from February to July (Table 1, Fig. 1). Organic matter sources and fish have closer variations than invertebrates. In particular $\delta^{13}C$ temporal differences were not evident in *Cymodocea* both living tissue (P >0.05, n = 2) or detritus (P >0.05, n = 2), while significant differences were observed in the ^{15}N content (P <0.01, n = 2 and P < 0.05, n = 2 respectively) (Table 2). The particulate and sedimentary organic matter presented significant variations in both $\delta^{13}C$ (POM P < 0.001, n = 3; SOM P < 0.05, n = 3) and $\delta^{15}N$ (POM P < 0.01, n = 3; SOM P < 0.05, n = 3). Apart from the $\delta^{13}C$ of Polychaeta (P > 0.05, n = 2), all the invertebrate taxa showed significant differences (Table 2). The largest temporal variations (Δ‰) were shown by Copepoda Harpacticoida ($\delta^{13}C$ $\Delta6$‰, P < 0.01, n = 2; $\delta^{15}N$ $\Delta6.5$‰, P < 0.01, n = 2), Nematoda ($\delta^{13}C$ $\Delta5.9$‰, P < 0.01, n = 2; $\delta^{15}N$ $\Delta5.8$‰, P < 0.01, n = 2) and Tanaidacea ($\delta^{13}C$ $\Delta4.8$‰, P < 0.05, n = 2; $\delta^{15}N$ $\Delta5.7$‰, P < 0.001, n = 2). Regarding the ichthyofauna, *A. fasciatus*, *P. tortonesei*, *Syngnathus abaster* and *S. typhle* showed marked temporal variations in their carbon isotope ratios (P < 0.01, n = 4; P <0.05, n = 2; P < 0.01, n = 6 and P < 0.05, n = 2 respectively), while the same was true for only *Liza aurata* and *S. abaster* in ^{15}N content (P < 0.001, n = 2 and P < 0.01, n = 6, respectively) (Table 2).

Table 2. The significance levels of the t-test to evaluate temporal differences in the isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) of organic matter sources and consumers in a Mediterranean saltworks. *: P ≤ 0.05; **: P ≤ 0.01; ***: P ≤ 0.001; Ns: non-significant difference (P > 0.05).

	P-level	
	$\delta^{13}C$	$\delta^{15}N$
Chaetomorpha linum	0.0532 (Ns)	0.1293 (Ns)
Cymodocea nodosa	0.0766 (Ns)	0.0044 (**)
Cymodocea nodosa detritus	0.4000 (Ns)	0.0109 (*)
Cystoseira sp.	0.0012 (**)	0.0007 (***)
Halophytes	0.0555 (Ns)	0.4400 (Ns)
Laurencia sp.	0.0097 (**)	0.0055 (**)
POM	0.0002 (***)	0.0065 (**)
SOM	0.0489 (*)	0.0058 (**)
Amphipoda	0.0129 (*)	0.0010 (**)
Harpacticoida	0.0028 (**)	0.0015 (**)
Mysidacea	0.0153 (*)	0.0323 (*)
Nematoda	0.0012 (**)	0.0013 (**)
Polychaeta	0.1190 (Ns)	0.0131 (*)
Tanaidacea	0.0121 (*)	0.0004 (***)
Aphanius fasciatus	0.0082 (**)	0.0501 (Ns)
Atherina boyeri	0.2351 (Ns)	0.0621 (Ns)
Liza aurata (juvenile)	0.2113 (Ns)	0.0001 (***)
Pomatoschistus tortonesei	0.0257 (*)	0.0636 (Ns)
Syngnathus abaster	0.0092 (**)	0.0026 (**)
Syngnathus typhle	0.0108 (*)	0.1167 (Ns)

DISCUSSION

FOOD WEB FEATURES AND THEIR TEMPORAL CHANGES.—Stable carbon ratios distinguished the main vegetal sources, making analysis of their relative trophic importance to consumers possible. Halophytes had the most depleted $\delta^{13}C$ values (−24.3 ± 0.5‰) and the seagrass *C. nodosa* the most enriched (−7.8 ± 0.4‰), while algae showed intermediate values (-18.6 ± 1.9‰). In looking at *Cymodocea* detritus, changes in carbon isotope ratios in comparison with living tissues were of the order of ~1‰ (Table 1), as reported for other marine plants (Zieman et al., 1984). This fact substantiates the hypothesis that the transformation of living tissues into detritus may produce a slight isotopic discrimination. POM from the first sampling date had a clear phytoplankton isotopic signature (−22.2 ± 1.0‰) which overlapped the values that the literature generally ascribes to pelagic microalgae (Dauby, 1989; Mazzola et al., 1999) and seemed to be independent of the sedimentary compartment. In contrast, the POM from July had a benthic isotopic signature (−15.7 ± 0.2‰) (France, 1995), probably due to sediment resuspension. Such a finding agrees with the environmental features of the study site, where frequent resuspension events occur as a consequence of wind forcing and shallowness independently on seasons (Sarà et al., 2000). Overall SOM isotopic composition showed a benthic organic matter signature (France, 1995). The SOM mean $\delta^{13}C$ value suggests that the organic matter in the sediments may be a mixture of POM, algae and seagrass. The outcome result of the mixing model (Dauby, 1989) highlighted a different composition of SOM from the two sampling dates. The contribution of algae was quite similar in the two sampling dates (about 40%, Table 3). On the other hand, *Cymodocea* detritus and phytoplankton seem to play a similar role in winter (about 30%), while phytoplankton seems to be dominant in summer (52%) (Table 3).

When looking at the incorporation of primary organic matter into the food web, both halophytes (the most depleted primary source) and *Cymodocea* (the most enriched primary source) don't appear to be channelled into the upper trophic levels (Fig. 1). On the contrary, POM and SOM seem to be the main organic matter sources for consumers.

Primary consumers belonging to the vagile and meiobenthic invertebrates associated with *Cymodocea* showed large temporal variations in stable carbon and nitrogen isotope ratios. With the exception of Polychaeta and Mysidacea, all taxa collected in February were depleted in ^{13}C and ^{15}N, and seem to depend on POM as a food source. However, the depleted $\delta^{15}N$ signatures (from 2.8 to 3.6‰), lower than that of the producers, might be explained by the assimilation of N_2-fixing blue-green algae, which usually exhibit $\delta^{15}N$ values very close to atmospheric N_2 (Wada and Hattori, 1976). On the other hand, it is well known that Cyanobacteria is an important component of the epiphytic community on seagrass blades (Mazzella and Russo, 1989). In July invertebrates were significantly enriched in ^{13}C and ^{15}N in comparison with winter, suggesting that they feed mainly on organic carbon originating from SOM.

On both sampling dates, POM seem to be the ultimate carbon reservoir for juvenile transient fish (*Liza aurata* and *Sparus aurata*) and SOM plus *Cymodocea* epiphytes for adult resident fish. Accordingly, $\delta^{13}C$ and $\delta^{15}N$ differentiated ichthyofauna into juvenile transient and resident fish, with the latter enriched in both carbon and nitrogen (Fig. 1). The higher values of $\delta^{13}C$ and $\delta^{15}N$ in resident fish leads us to hypothesize that their ultimate carbon sources may be epiphytes and/or an enriched fraction of SOM (i.e., seagrass detritus). Furthermore, the isotopic ratios of the resident ichthyofauna are consistent with

Table 3. Mixing model (Dauby, 1989) results indicating the percentage contribution of each main carbon source to sedimentary organic matter (SOM) in the study area. Reference signature was used for phytoplankton (−21.4‰; Dauby, 1989). Algae and *Cymodocea* detritus signatures are those measured in our study.

	SOM $\delta^{13}C$	% *Cymodocea* detritus	% Algae	% Phytoplankton
02-08-1999	−15.3	30	43	27
07-16-1999	−17.7	13	35	52
Mean ± S.D.		22 ± 12	39 ± 6	39 ± 20

the assumption that these fishes have a different trophic niche in comparison with juvenile transients (Livingston, 1982; Barry et al., 1996). Such findings lead us to define resident fish as microcarnivores on detritus-consuming mobile fauna and highlight the importance of the plant detritus-based system in the study area. In contrast, juveniles of the species, which occupy the saltworks seasonally, may feed in the water column. Analysis of stomach contents has demonstrated that juvenile transient species are usually planktivores, feeding on microzooplankton and POM detritus (Ferrari and Chieregato, 1981; Gisbert et al., 1996). Although in this study we did not consider zooplankton, the isotopic signatures extrapolated from the literature ($\delta^{13}C$ = −22.3‰, $\delta^{15}N$ = 3.5‰, Pinnegar and Polunin, 2000) may justify its assimilation by juvenile fish.

In looking at the temporal variations in the isotopic composition of fish, the ichthyofauna generally showed slight differences. The range of variation was very small compared with that of invertebrates and plants. Such a discrepancy may suggest that different physiological and ecological factors are involved in fish isotopic composition. Indeed, it is likely that a certain role may be played also by both the integration of isotopic composition from different prey resources and higher turnover rates in fish in comparison with invertebrates.

THE TROPHIC ROLE OF *CYMODOCEA NODOSA* AND ITS TEMPORAL VARIATION.—The overall outcome of our study leads us to define at least two main energy transfer paths in the *Cymodocea* flat food web (Fig. 2). The first, which includes juvenile transient fish as secondary consumers (i.e., zooplanktivores), relies on pelagic organic matter as the main carbon source. The second, which terminates with resident fish, showed a close dependence on detrital sources in which *Cymodocea* provided a contribution which varied over time, and also on vegetal epiphytes. None of the consumers studied subsisted primarily on *Cymodocea* despite its availability, while the seagrass detritus seemed to be channelled into the upper trophic levels via SOM (Fig. 2). The variable temporal contribution of *Cymodocea* to sedimentary organic matter may be ascribed to its annual cycle as it reaches the maximum biomass and production in summer and the minimum in winter when dead leaves accumulate into the sediments (Pérez and Romero, 1994). Similarly, seagrass detritus isotopic contribution to sediment $\delta^{13}C$ is greater in February than in July (Table 3). Moreover, the shift towards heavier carbon values in all the taxa (primary producers and consumers) in July may highlight the importance of enriched carbon (possibly from *C. nodosa*) in structuring the food web. In addition, while the isotopic composition of several primary and secondary consumers presented statistical differences between February and July, *Cymodocea* $\delta^{13}C$ and $\delta^{15}N$ showed respectively no and marginal significant changes. This finding, together with the enrichment in ^{13}C in July, sug-
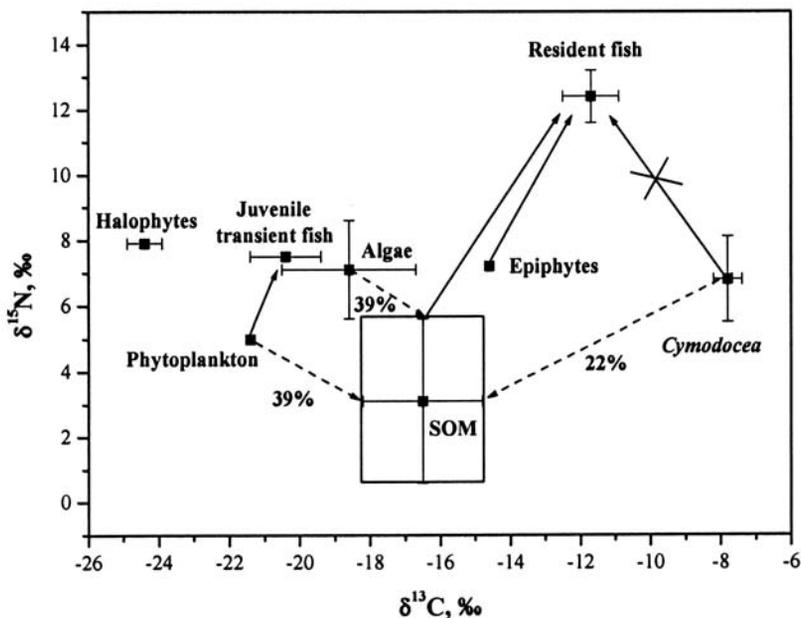
Figure 2. Ultimate organic matter sources for fish in a Mediterranean saltworks as inferred by the carbon and nitrogen stable isotope composition. Dashed arrows show the contribution of the main organic matter reservoir to SOM, the solid ones indicate the direct and/or indirect organic matter fluxes to resident and juvenile transient fish. Percentage values are calculated according to Dauby (1989). For further details see text.

gests the hypothesis of a greater *Cymodocea* detrital flow during the warmer period than in February.

In addition, an important, although indirect, role of *Cymodocea* is to increase the spatial complexity by means of the epiphyte community on seagrass blades (Cyanobacteria, diatoms, crustose and ephemeral algae) (Mazzella et al., 1992). Epiphytes increase the heterogeneity of seagrass ecosystems by supplying food and habitats for the associated fauna. Despite the common assumption that epiphytes are a negligible food source for herbivores due to their low biomass (Penhale, 1977; Borum et al., 1984), recent studies suggest that their production may be elevated to exceed even that of seagrasses (Morgan and Kitting, 1984; Moncreiff et al., 1992). Epiphyte communities can thus play a central role in seagrass food webs. Since epiphyte biomass is low in February (Gambi et al., 1992; Mazzella et al., 1992), SOM was probably the main food source for consumers. However, our results from July cannot provide a reliable indication of the relative trophic contribution of epiphytes and SOM (a mixing of phytoplankton, seagrass detritus and algae), as these sources showed very similar isotopic signatures. Thus we merely suggest that both sources can play an important role.

Several stable isotope studies have focused on the relative role of each vegetal source in seagrass ecosystems (Fry et al., 1984; Jennings et al., 1997; Lepoint et al., 2000; Pinnegar and Polunin, 2000), indicating that benthic plants, not phytoplankton, are the main organic matter reservoir for consumers. Moreover, in comparing seagrass and epiphyte trophic role in different temperate seagrass ecosystems, seagrass detritus and leaf epiphytes appear to be an important food source for the fauna associated with the canopy

(Fry, 1984; Lepoint et al., 2000). Although our findings are consistent with literature data and suggest that the benthic pathway support a large number of consumers, we would emphasize the need to collect and analyse samples at several times of a year to assess the exact role of seasonal effects in the structuring the food webs.

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