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Feeding of the Sparid Fish *Sarpa salpa* in a Seagrass Ecosystem: Diet and Carbon Flux

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With 3 figures and 2 tables

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Abstract. In Revellata Bay (Gulf of Calvi, Corsica, France), the sparid fish *Sarpa salpa* L. is the main macro-consumer of *Posidonia oceanica* (L.) DELILE leaf. Stomach contents were analysed and $^{13}C/^{12}C$ isotopic ratios were measured in fish muscle and potential food sources (algae, *P. oceanica* leaf and its epiphytes) to determine their relative contribution to the fish diet. *S. salpa* has an age-related mixed diet: juveniles are plankton feeders, young, sub-adults and adults are herbivorous, and, the older the individuals, the higher the relative contribution of *P. oceanica* to the diet. Our results and former studies of carbon stocks and fluxes in the *P. oceanica* bed of Revellata Bay have enabled an estimation of the general impact of *S. salpa* grazing on infralittoral communities: the studied species consumes 24 g $C \cdot m^{-2} \cdot a^{-1}$ from *P. oceanica* leaf, 4.8 from epiphytes and 13 from epilithic algae. The fish net production and biomass turnover in that zone have been estimated to be 1.2 g $C \cdot m^{-2} \cdot a^{-1}$ and 1.5 a^{-1}, respectively.

Problem

The meadows of the seagrass *Posidonia oceanica* (L.) DELILE cover more than $2 \cdot 10^4$ km^2 in the Mediterranean Sea (PERGENT, 1993) and thus are considered as a key component in the ecology of its coastal zone. The ecology of this temperate seagrass species had been well studied (*e.g.*, KERNEIS 1960; GIRAUD, 1979; BAY, 1984; LIBES, 1985; FRANKIGNOULLE & BOUQUEGNEAU, 1987; MEINESZ *et al.*, 1988; VELIMIROV & WALENTA-SIMON, 1992, 1993; PERGENT *et al.*, 1994; ROMERO *et al.*, 1994), but the role of macro-consumers in the recycling of *P. oceanica* production remains insufficiently investigated (MAZZELLA *et al.*, 1992). Potential consumers include the sparid fish *Sarpa salpa* L. (VELIMIROV, 1984; VERLAQUE, 1990), the echinid *Paracentrotus lividus* LAM. (OTT & MAURER, 1977; TRAER, 1980; NEDELEC & VERLAQUE, 1984; ZUPO & FRESI, 1984) and the isopod *Idotea baltica* PALL. (LORENTI & FRESI, 1983). The relative importance of these three macro-consumers displays a great variation from one meadow to another along the Mediterranean coast: *e.g.*, in Lacco Ameno meadow, Ischia, *P. lividus* is by far the main macro-consumer (TRAER, 1980), while in the Spanish Mediterranean, *S. salpa* contributes about 75% of total herbivory consumption (CEBRIEN *et al.*, 1996). However, herbivore appears to be a minor factor in the control of *P. oceanica* since it only

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accounts for about 2% of its leaf production (CEBRIAN *et al.*, 1996). In the Gulf of Calvi (Corsica), the *P. oceanica* meadow covers 10 km^2 (BAY, 1984) and its main leaf macro-consumer is *S. salpa*, grazing about 15% of the net primary production (BOUQUEGNEAU *et al.*, 1994).

WHITEHEAD *et al.* (1986) describe *S. salpa* as omnivorous, young fish mainly being carnivorous (crustaceans), while adult fishes are almost exclusively herbivorous: the species displays a highly adapted dentition: in both jaws incisors are uniserial, upper ones notched, lower ones depressed on their outer face and ending in a single triangular point; all incisors have well visible roots inside the mouth.

However, the main food sources for the various age-classes of *S. salpa* remains debatable. According to VELIMIROV (1984), *S. salpa* grazes mainly on the seagrass, while VERLAQUE (1990) claimed that *S. salpa* grazes mainly on epilithic algae; neither author takes the epiphytic covering of *P. oceanica* into account as a potential food source.

The aim of this work is to detail the trophic relationships between the sparid fish *S. salpa* and the three following potential food sources: (1) *P. oceanica* leaves, (2) epiphytic community of *P. oceanica* (both flora and fauna) and (3) adjacent epilithic algae. Our results and data from VELIMIROV (1984), BOUQUEGNEAU *et al.* (1994) and LEPOINT *et al.* (in press) have been integrated into a box-flux model of the carbon transfer towards *S. salpa* in Revellata Bay.

Material and Methods

Our investigation was conducted near the marine research station STARESO (Corsica, 42 35′N 8 43′E) between 5 and 15 m depth (Fig. 1). At 10 m, the *P. oceanica* shoot density ranges from 349 shoots$\cdot m^{-2}$ to 467 shoots$\cdot m^{-2}$ depending on the location and time of year (SOULLARD *et al.*, 1994).

Fig. 1. Study site; dark stippling = fish catch area.

The meadow is surrounded on its upper limit (from the surface to 7 m depth) by rocks covered by a rich macroalgae biocenosis (epilithic algae).

We used qualitative stomach content analyses and comparative measurements of the isotopic $^{13}C/^{12}C$ ratios of both the fish muscle tissue and the three above mentioned potential food sources of the fish.

Posidonia oceanica leaf distal parts (the uppermost 15 cm) and epilithic algae (*Halopteris* sp. and *Dictyota* sp.) were collected by SCUBA diving at depths of 10 and 5 m, respectively. Epiphytes were completely removed with a blade scraper, according to DAUBY & POULICEK (1995). Seventy-five fish were caught by net or speared. Each captured fish was measured (total and standard length: TL and SL) in cm and dissected; lateral muscle and stomach contents were sampled. When possible, the total digestive tract length was measured (gL) in cm. Fish were sorted into five length classes according to FAGGIANELLI & COOK (1981).

The relative length of the gut calculated as the ratio of gut to body length (RLG = gL/SL) correlates in most cases with the fish diet. RLG is generally lower than 0.1 for carnivorous fish, higher than 3 for herbivores, and intermediate for omnivores (SUYEHIRO, 1942; KLUMPP & NICHOLS, 1983). The RLG of 30 *S. salpa* specimens was calculated and averaged in the length classes.

In order to estimate the relative contributions of epilithic algae, *P. oceanica* leaves and epiphytes to the fish diet, both food sources and the fish muscle tissue $\delta^{13}C$ were measured. Samples were slightly acidified to remove inorganic carbonates (except for the fish muscle), rinsed and oven-dried at 50°C for several days. They were then ground into fine powder and combusted in the presence of copper oxide wire at 500°C in vacuum sealed Pyrex tubes (SOFER, 1980). The generated CO_2 was purified cryogenically and analysed on an Optima 540 (Micromass) IR-MS. All values are reported relative to the international PDB as

$$\delta^{13}C = [(R_{sample} - R_{standard})/R_{standard}] \times 1000,$$

where R is the $^{13}C/^{12}C$ ratio. Routine measurements are precise to within 0.1.

DE NIRO & EPSTEIN (1978) and FRY *et al.* (1987) have shown that the $\delta^{13}C$ of a consumer is slightly (about 1) enriched in ^{13}C compared to the consumer's food, and this should be subtracted from all muscle measurements in order to estimate the $\delta^{13}C$ of the food source. Thus, the relative contribution of the three potential carbon sources (rc_{algae}, rc_{leaves} and $rc_{epiphytes}$) to *S. salpa* diet has been calculated from the following three equations (modified from DAUBY, 1989):

$$rc_{algae} + rc_{leaves} + rc_{epiphytes} = 100\% \quad (1)$$

$$rc_{epiphytes}/rc_{leaves} = biomass_{epiphytes} \times Cc_{epiphytes} \times Aeff_{epiphytes}/biomass_{leaves} \times Cc_{leaves} \times Aeff_{leaves} \quad (2)$$

$$\delta^{13}C_{food} = (rc_{algae} \times \delta^{13}C_{algae}) + (rc_{leaves} \times \delta^{13}C_{leaves}) + (rc_{epiphytes} \times \delta^{13}C_{epiphytes}) \quad (3)$$

where 'biomass' is the amount of matter on leaf tips, 'Cc' is the organic carbon contents (in % of dry weight biomass), 'Aeff' is the assimilation efficiencies of food carbon by the fish (in % of ingested carbon).

As the biomass of epiphytes equals that of leaf tissue on *P. oceanica* leaf tips (averaged measurement on the upper 15 cm, annual basis; HAVELANGE, unpubl.), it was assumed that $biomass_{epiphytes}/biomass_{leaves} = 1$. Dried *P. oceanica* leaves contain 34% organic carbon (GOBERT *et al.*, 1995); *S. alpa* assimilates 20% of the ingested organic matter (VELIMIROV, 1984); dried epiphytes (non-decalcified) contain 7% of organic carbon (GOBERT *et al.*, 1995); *S. salpa* assimilates 40% of that organic carbon: averaged value estimated from MONTOGOMERY & GERKING (1980), LOBEL & OGDEN (1981), EDWARDS & HORN (1982) and GERKING (1984). Thus, as *S. salpa* only grazes on the leaf tips, $rc_{epiphytes}/rc_{leaves}$ can be estimated from equation (2) to be 0.4 (*i.e.*, $1 \times 7 \times 40/34 \times 20$).

Results

There were no significant differences between the mean RLG of the different length classes (Table 1, cross *t*-test, $P > 0.05$ in all cases). All values were higher than 3, ranging from 4.5 to 5.0. Stomach contents comprised a mixture of epilithic algae – most often *Halopteris* and *Dictyota* – and *P. oceanica* leaf pieces and epiphytes

Table 1. *S. salpa*: length classes, mean relative length of gut = RLG (standard deviation and sample size in parentheses) and qualitative information on the main diet components for each age-class based on *in situ* observations and direct analysis of stomach contents.

age group	total length [cm]	RLG	diet
juveniles	<5		plankton (+few fragments of seaweed)
young	5–15	4.5 (0.7; n = 5)	turf epilithic algae (mainly small *Halopteris*)
sub-adults	15–23	5.0 (0.7; n = 17)	erect epilithic algae (mainly *Halopteris* and *Dictyota*), + *P. oceanica* leaf and epiphytes
adults	>23	4.7 (0.1; n = 8)	*P. oceanica* leaf and epiphytes (+erect *Halopteris* and *Dictyota*)

(Table 1). Vagile fauna, gastropods (*Gibbula* spp., *Rissoa* spp.) and crustaceans (isopods, mysids), were rarely recorded in digestive contents. Pieces of *P. oceanica* leaves were generally well-preserved and were often covered with epiphytes, even in the distal part of the intestine or in the faeces. Some leaves showed small grinding marks by pharyngeal teeth. Note that we rarely observed large specimens of *S. salpa* grazing on epilithic algae.

The average *P. oceanica* leaf $\delta^{13}C$ was -14.3 (Fig. 2). Mean values for epiphytes (-17.7) and epilithic alge $\delta^{13}C$ (-21.7 to -19.1) were lower than those for seagrass leaves. Considering the relative abundance of *Dictyota* and *Halopteris* in the study site – 15 and 85% of substrate cover, respectively (JANSSENS, pers. comm.) – the mean $\delta^{13}C$ of the epilithic algal community has been calculated to be -21.4. The fish muscle $\delta^{13}C$ varies from -20.4 to -16.1 among the different length classes. Mean $\delta^{13}C$ of the general fish population (-16.8) has been calculated, taking into account all length classes, except the juvenile one, because they are not true benthic

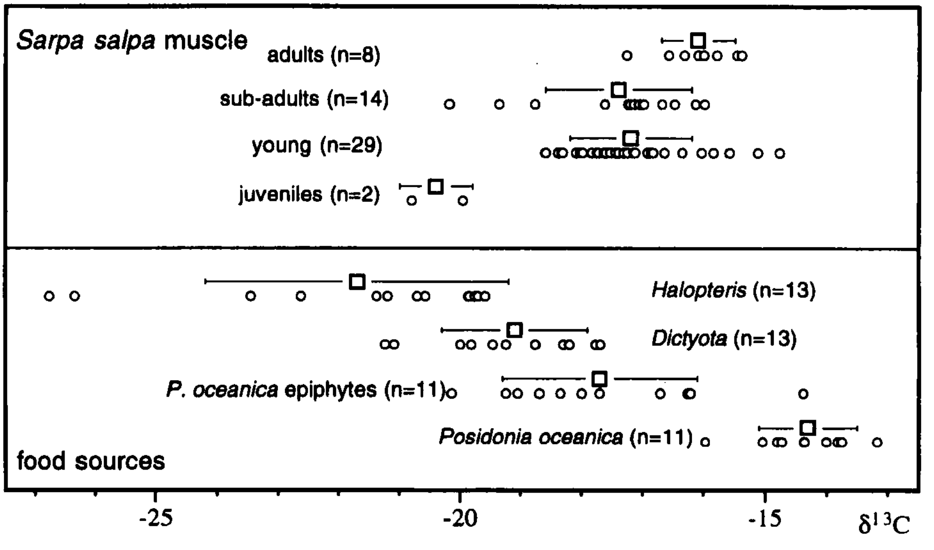

Fig. 2. $\delta^{13}C$ measurements and mean values in *Sarpa salpa* muscle and food sources (n = sample size; error bars = standard deviation).

Table 2. Literature data on *P. oceanica* carbon stocks and fluxes in the Bay of Calvi (10 m depth).

stocks [g C·m^{-2}], fluxes [g C·m^{-2}·a^{-1}] and ratios		source
stocks		
S. salpa biomass	0.8	Houziaux, 1993
fluxes		
P. oceanica leaf net primary production	155	Bouquegneau *et al.*, 1994
P. oceanica epiphytes net primary production	82	Bouquegneau *et al.*, 1994
leaf consumption by *S. salpa*	24	Houziaux, 1993
S. salpa net production	1.2	Velimirov, 1984
ratios		
fauna vs flora epiphytic biomass	0.4	Lepoint *et al.*, in press
S. salpa carbon assimilation efficiency	0.2	Velimirov, 1984

grazers. Combining these values ($\delta^{13}C = -14.3$, -17.7, -21.4 and -16.8 for seagrass, epiphytes, epilithic algae and fishes, respectively) in the equations (1) to (3), the relative contributions of seagrass, epiphytes and algae to *S. salpa* carbon uptake have been calculated to be 40, 17 and 43%, respectively.

A box-flux model of carbon transfer through the *S. salpa* compartment can be constructed from our results and previous data on the same site (Table 2). The model obtained (Fig. 3) indicates that *S. salpa* ingests 41.8 g C·m^{-2}·a^{-1} from benthic communities, with a faeces production of 29.9 g C·m^{-2}·a^{-1}. The sec-

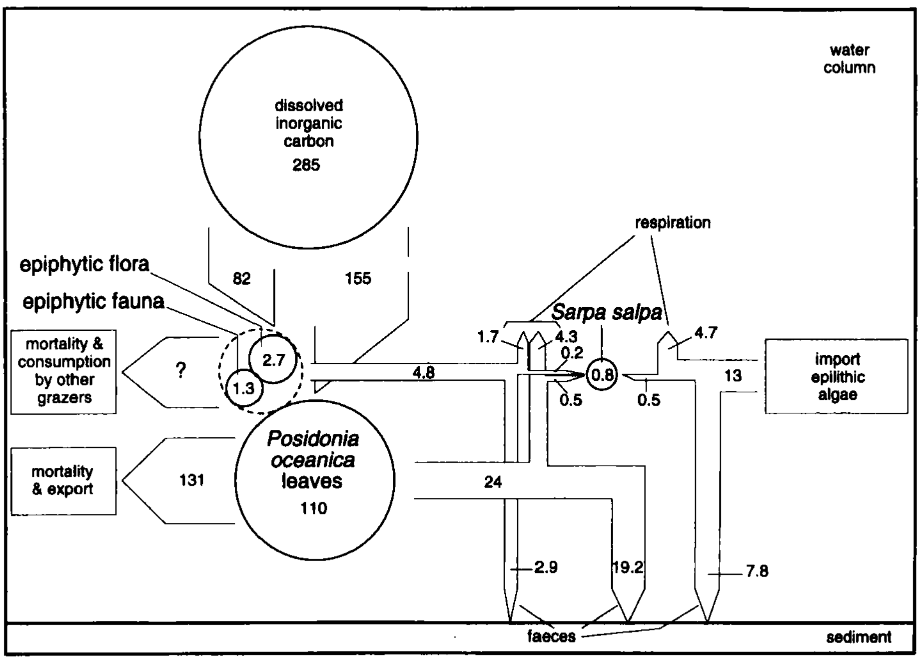

Fig. 3. Box-flux model of carbon transfer towards *Sarpa salpa* at 10 m depth in the Bay of Calvi. Arrows are carbon fluxes [g C·m^{-2}·a^{-1}], spheres are stocks [g C·m^{-2}].

ondary net production of *S. salpa* in Revellata Bay is estimated to be 1.2 g $C \cdot m^{-2} \cdot a^{-1}$ (sum of three energy fluxes displayed in Fig. 3).

Discussion

Based on the relative gut length measurements, *S. salpa* is to be considered as a true herbivore. Juvenile *S. salpa*, however, are considered to be plankton feeders (FAGGIANELLI & COOK, 1981; WHITFIELD, 1985), although some seaweed fragments have been found in the stomach contents. Consumption of epilithic algae varies within the young, sub-adult and adult groups: the young specimens graze on turf algae (mainly small *Halopteris* spp.), while sub-adults and adults graze on erect algae (large *Halopteris* spp. for more than 75%, mainly *Dictyota* for the rest). No data were available on large adults (TL > 35 cm), but VERLAQUE (1990) noted that some large adult specimens had stomachs filled with seagrass leaves and epiphytes. As, in addition, we never observed large specimens grazing on epilithic algae, we consider large adults as generally feeding on *P. oceanica* leaves only.

Our $\delta^{13}C$ measurements are in good agreement with previous data on both *P. oceanica* collected at the same depth (BRICOUT *et al.*, 1980; COOPER & DE NIRO, 1989) and algae (FRY *et al.*, 1982; KITTING *et al.*, 1984).

The variability of fish muscle $\delta^{13}C$ reflects the above-mentioned heterogeneity in diet. A similarity is more evident for adult specimens, whose mean $\delta^{13}C$ is quite close to that of *P. oceanica* leaves, indicating that the diet of large animals is probably dominated by seagrass.

Sarpa salpa ingests huge amounts of living *P. oceanica* leaf tissue in response to the relatively poor digestibility of seagrass material with high ligno-cellulose fibre content (OTT & MAURER, 1977). However, it displays a diversified feeding strategy-mixed diet of seaweed, epiphytes and seagrass leaves – as described for most seagrass grazers in tropical waters (OGDEN, 1976; LOBEL & OGDEN, 1981; KLUMPP & NICHOLS, 1983). A spatio-temporal study of *P. oceanica* leaf-epiphyte communities of Revellata Bay showed that the animal biomass accounts for about 30% of the total epiphytic biomass at 10 m depth (LEPOINT *et al.*, in press). So, given that epiphytes contribute up to 17% of diet, and assuming a similar digestion efficiency between fauna and flora, assimilation of animal matter could reach 5% of the total assimilated carbon. This animal organic matter probably represents an essential source of animal nitrogen in the *S. salpa* diet, as already shown for tropical fish species (KLUMPP & NICHOLS, 1983; KLUMPP *et al.*, 1989).

The present study reveals the variability of the *S. salpa* diet between the different fish length classes. Small amounts of seaweed found in the stomach of some juvenile specimens could stem from ingestion of small pieces of floating algae as well as from grazing small erect epiphytes of *P. oceanica* (CHRISTENSEN, 1978; HARMELIN-VIVIEN *et al.*, 1995; B. VELIMIROV, pers. comm.); however, this carbon uptake could be minor as muscle $\delta^{13}C$ (−20.4, Fig. 2) and is similar to that of plankton which is about −21 according to DAUBY *et al.* (1990). $\delta^{13}C$ measurements, stomach content analysis and *in situ* observations showed that the grazing of larger individuals on phytobenthos could range from full algal to mixed algal-seagrass-epiphytes consumption and finally to only seagrass uptake. This age-dependent diet shift is consistent with an adaptative grazing on the epilithic algae biocenosis according to territory range, food availability and grazing capacity (mouth aperture), as suggested by VERLAQUE (1990).

Finally, *S. salpa* ingests 15% of primary production of *P. oceanica* leaf and 4% of epiphytic algae, which is in good accordance with herbivore rates compiled by CYR & PACE (1993). From secondary net production and mean biomass, one can calculate the turn-over of fish biomass as $1.5 \cdot a^{-1}$, which is in agreement with conclusions drawn for other fish species of similar size range (SHELDON *et al.*, 1972).

Summary

The use of stable carbon isotopes determination – in *S. salpa* and in its potential food sources – definitively answers the question whether *S. salpa* does or does not assimilate the large amounts of ingested *P. oceanica* leaf tissue. *Sarpa salpa* clearly has an age-related mixed diet: juveniles are plankton-feeders, young, sub-adults and adults are herbivorous (algae, *P. oceanica* leaf and its epiphytes) and, the older the individual, the higher the relative contribution of assimilated *P. oceanica* leaf tissue.

Owing to its large-spectrum herbivory, its large biomass, its important faeces production, which is available to meso- and micro-grazer activity and ultimately to remineralization by the microbial compartment, it appears that *S. salpa*, in Revellata Bay where it dominates the macro-grazer community, plays an important role in the regulation and transformation of primary production.

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