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Relative impact of a seagrass bed and its adjacent epilithic algal community in consumer diets

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Abstract The aim of this work was to identify and compare, using nitrogen and carbon stable isotope data, the food sources supporting consumer communities in a Mediterranean seagrass bed (Gulf of Calvi, Corsica) with those in an adjacent epilithic alga-dominated community. Isotopic data for consumers are not significantly different in the two communities. Particulate matter and algal material (seagrass epiflora and dominant epilithic macroalgae) appear to be the main food sources in both communities. Generally, the $\delta^{13}C$ of animals suggests that the seagrass *Posidonia oceanica* (L.) Delile represents only a minor component of their diet or of the diet of their prey, but the occurrence of a mixed diet is not excluded. *P. oceanica* dominates the diet of only of few species, among which holothurians appear as key components in the cycling of seagrass material.

Introduction

In seagrass ecosystems, food webs are often described as detritus food webs (Ott and Maurer 1977; Pergent et al. 1994; Mateo and Romero 1997) and the consumption of living seagrass seems to be generally restricted to few animal species (Mazzella et al. 1992). However, in the *Posidonia oceanica* (L.) Delile community, as in many seagrass ecosystems, it is difficult to identify the sources of primary organic matter assimilated by different consumers (Fry 1988). Indeed, seagrass material (dead or alive), suspended particulate organic matter (SPOM) and leaf epiphytes coexist as potential food sources within the ecosystem (Dauby 1989).

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The aim of this work was to identify and compare, using nitrogen and carbon stable isotope data, the food sources supporting consumer communities in a Mediterranean seagrass bed (Gulf of Calvi, Corsica) with those in an adjacent epilithic alga-dominated community, from which seagrasses are absent.

Measurements of carbon and nitrogen stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$, respectively) have been proposed as a potentially powerful method to access food web structure in marine and, particularly, in seagrass ecosystems (Fry 1988; Jennings et al. 1997; Marguillier et al. 1997). For the Revellata Bay seagrass ecosystem, previous carbon isotope studies have been performed by Cooper and DeNiro (1989), Dauby (1989) and Havelange et al. (1997), and a nitrogen isotope study focused on fish by Pinnegar and Polunin (2000). In Dauby (1989) and Havelange et al. (1997), ^{13}C values of some consumers (e.g. *Sabella pavonina*, *Echinaster sepositus*, *Sarpa salpa*, *Scorpaena scrofa*) could be ambiguously related to direct or indirect seagrass material assimilation. In this work, the additional use of N isotope ratios, which are more related to the trophic level of consumers, should help to interpret such ambiguities.

Materials and methods

All samples were collected in the Revellata Bay (Gulf of Calvi, Corsica) (8°45′E; 42°35′N) (Fig. 1) between 5 and 10 m depth in February, June and October 1996 and in February and June 1997. Sampling was conducted in the *Posidonia oceanica* seagrass meadow, described by Bay (1984) and Gobert et al. (1995), and in an adjacent epilithic algal settlement. The photophilous brown algae *Halopteris scoparia* and *Dictyota* spp. were the characteristic species of this settlement, representing 90% of the algal biomass. Small invertebrates associated with the *Posidonia* meadow were caught with a hand-towed net (adapted from Russo et al. 1985). Fish were caught by net or by crossbow just above the seagrass meadow or rocks.

The *Posidonia oceanica* leaves were scraped with a razor blade under a binocular microscope to remove and separate the epifauna and epiflora (Lepoint et al. 1999). Epilithic macroalgae were

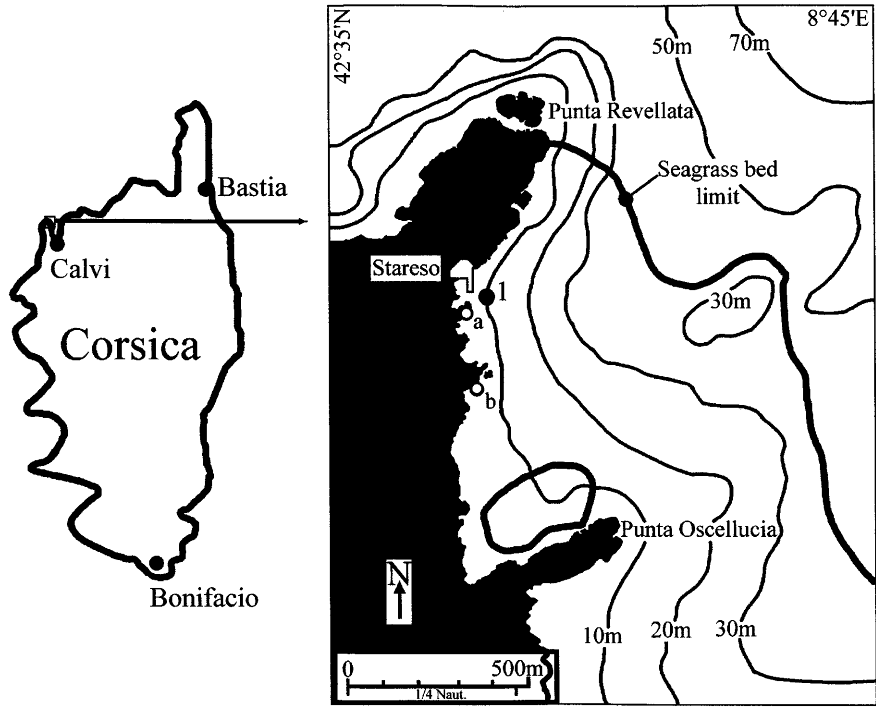

Fig. 1 Sampling locations and extent of *Posidonia oceanica* meadow in the Revellata Bay (Gulf of Calvi, Corsica) adjacent to the oceanographic station Stareso (8°45′E; 42°35′N) *a to b* portion of the coast sampled in the epilithic community; *1* location of 10 m depth site for sampling within the seagrass bed

collected in plastic bags and sorted to remove small fauna. SPOM was obtained by filtering 1.5 litre of seawater on pre-ignited GF/F Whatman filters, after pre-filtering on a 50 μm sieve. Mesozooplankton was trapped using a net with a mesh of 200 μm, towed near the shore. All samples were oven-dried for 48 h at 50 °C and ground to a fine powder. After grinding, samples containing inorganic carbonates were acidified with HCl (1 *N*).

Measurements were performed with a mass spectrometer (Optima, Micromass, UK) coupled to a C-N-S elemental analyser (Carlo Erba, Italy) for combustion and automated analysis. As recommended by Pinnegar and Polunin (1999), when samples were acidified, $^{15}N/^{14}N$ ratios were measured before acidification due to significant modifications of $^{15}N/^{14}N$ after HCl addition (Bunn et al. 1995). Ratios are presented as δ values (‰), expressed relative to the vPDB (Vienna Peedee Belemnite) standard and to atmospheric N_2 for carbon and nitrogen, respectively. Reference materials were IAEA-N1 ($\delta^{15}N = +0.4 \pm 0.2$‰) and IAEA CH-6 (sucrose) ($\delta^{13}C = -10.4 \pm 0.2$‰). Experimental precision (based on the standard deviation of replicates of an atropina standard) was 0.5 and 0.4‰ for carbon and nitrogen, respectively.

Results and discussion

Three food sources were distinguished in terms of mean $\delta^{13}C$ for the Revellata Bay food web (Table 1; Fig. 2): SPOM, algae (dominant epilithic macroalgae plus *Posidonia* leaf epiflora) and seagrass (dead and living *P. oceanica* leaves). The $\delta^{13}C$ of *Halopteris scoparia* and *Dictyota* spp., which represented 90% of the algal biomass, were used as the average of epilithic algae. On the other hand, the $\delta^{15}N$ signatures of macroalgae and SPOM did not differ significantly from the *P. oceanica* (Table 1; Fig. 2).

Delta ^{13}C values of particulate suspended matter and benthic macrophytes match the values reported by Dauby (1989) and Cooper and DeNiro (1989) in the same study site. They are lower than the data of Jennings et al. (1997), probably because we acidified samples to remove carbonates for ^{13}C measurements. The extended range we measured for the macroalgae $\delta^{13}C$ has been described and discussed by various authors (e.g. Kerby and Raven 1985; Hecky and Hesslein 1995; Raven et al. 1995) who consider it is mainly related to the range of abilities of algae to use HCO_3^- or to rely on CO_2 diffusion for photosynthesis (Raven et al. 1995).

The ^{15}N values of plants presented in this paper are in the range reported by Jennings et al. (1997) for the Balearic Islands and Pinnegar and Polunin (1999) in this ecosystem. In temperate estuarine ecosystems, McClelland et al. (1997) and Fourqurean et al. (1997) found higher ^{15}N values related either to wastewater loads, or to river inputs (Mariotti et al. 1984) in which inorganic nitrogen (particularly NO_3^-) is ^{15}N enriched. In the Revellata Bay, as in Balearic Islands, the $\delta^{15}N$ of plants is relatively low and could reflect the negligible impact of wastewater and river inputs on the nitrogen budget of the primary producers.

The $\delta^{15}N$ values increased in the food web from plants to invertebrates and fishes (Fig. 2). However, some animals exhibited $\delta^{15}N$ lower than producers (Tables 2, 3). Macko et al. (1982) have reported that, in laboratory and field measurements, the fractionation (i.e. differential use of ^{15}N vs ^{14}N) displayed a great species to species variation. This fractionation could sometimes result in a depletion of ^{15}N (Pinnegar and Polunin 2000). On the other hand, most of the animals with low $\delta^{15}N$ are known to be micrograzer or microfilter species. The micro-organisms, which have not been sampled in this study, could have lower $\delta^{15}N$ values than other producers, particularly N_2-fixing Cyanobacteria,

Table 1 Mean values (± SD) of δ^{13}C and δ^{15}N (‰) of benthic primary producers, organic suspended particulate matter and leaf epifauna of *Posidonia oceanica*, collected in the Revellata Bay (Gulf of Calvi, Corsica) between 5 and 15 m depth (*n* number of samples). δ^{13}C and δ^{15}N of "dominant algae" are weighted averages, considering that *Halopteris scoparia* and *Dictyota* spp. constituted respectively 80 and 10% of the total algal biomass (g_{dw} m^{-2}) in the sampled algal settlement

Biota	Groups	Species	*n*	δ^{15}N	δ^{13}C
Rocks	Macroalgae				
	Green algae	*Acetabularia acetabulum*	3	2.1 ± 1.1	−11.1
		Cladophora proliphera	1	4.0	−17.5
		Codium bursa	6	3.1 ± 1.2	−10.3 ± 0.7
		Halimeda tuna	3	1.3 ± 0.3	−19.3 ± 1.7
		Udotea petiolata	16	1.8 ± 0.9	−32.6 ± 1.1
	Brown algae	*Dictyota* spp.	30	3.6 ± 1.7	−17.4 ± 1.4
		Halopteris scoparia	43	1.8 ± 1.2	−20.7 ± 1.7
		Nematochrisopsis sp.	2	4.0 ± 0.3	−25.4 ± 0.6
		Padina pavonica	5	4.3 ± 0.8	−11.9 ± 1.1
	Red algae	*Corallina* sp.	4	3.8 ± 0.4	−18.1 ± 2.6
		Peysonelia sp.	8	3.2 ± 0.9	−21.7 ± 2.6
		Sphaerococcus coronopifolius	3	2.4 ± 0.4	−33.4 ± 1.3
	Dominant algae	Weighted averages		1.8	−18.3
Seagrass bed	Phanerogam	*Posidonia oceanica* (living leaves)	28	2.6 ± 1.0	−13.9 ± 1.0
		Posidonia leaf epifauna (fixed epifauna)	6	3.4 ± 0.6	−19.4 ± 0.8
	Epiphytic algae	*Posidonia* leaf epiflora	6	3.0 ± 0.9	−18.6 ± 1.9
Water column		Organic suspended particulate matter	19	1.9 ± 0.5	−22.5 ± 0.8

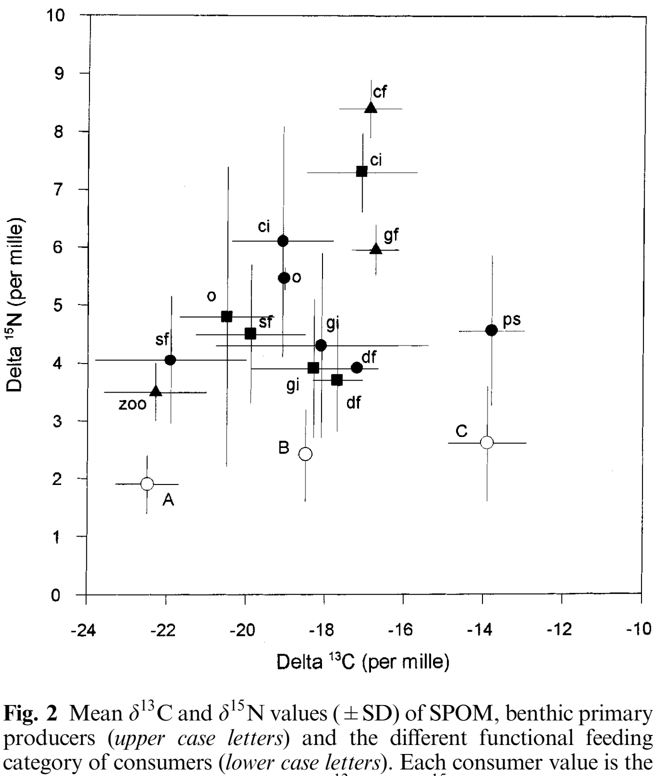

Fig. 2 Mean δ^{13}C and δ^{15}N values (± SD) of SPOM, benthic primary producers (*upper case letters*) and the different functional feeding category of consumers (*lower case letters*). Each consumer value is the unweighted mean (± SD) of the δ^{13}C and δ^{15}N mean values of all the species belonging to the same functional feeding category and the same biota (as listed in Tables 2 and 3) [*A* suspended particulate matter; *B* algal material, averaged from dominant epilithic algal values and epiflora of *Posidonia oceanica* leaf (Table 1); *C P. oceanica* leaves; *cf* carnivorous fish; *ci* carnivorous invertebrates; *df* deposit feeders; *gi* grazers (invertebrates) (this category groups "true" grazers and fauna feeding on plant detritus); *gf* grazers (fish); *o* omnivorous invertebrates; *ps* psammivorous; *sf* suspension feeders; *zoo* zooplankton; *white circles* primary producers; *black circles* seagrass fauna; *black squares* epilithic fauna; *black triangles* water column fauna]

which generally display δ^{15}N close to atmospheric N_2 (i.e. 0‰: e.g. Wada and Hattori 1976). These primary producers are very abundant as epiphytes on *Posidonia* leaves or algae (Wilmotte and Demoulin 1988; Mazzella and Russo 1989).

Kolmogorov–Smirnov two-samples tests were performed to test the differences between the delta values of fauna of seagrass and epilithic communities. For this purpose, animals were classified in functional feeding groups (Tables 2, 3). This non-parametric test was chosen because of the small number of species in each functional feeding category ($n < 25$) and the non-normal distribution of δ^{13}C and δ^{15}N data. Results exhibited no significant differences between the same functional feeding groups within the two communities, with the exception of the suspension feeders ($p < 0.01$). The main food sources would appear therefore to be similar in the two communities (i.e. algal material and SPOM). Suspension feeders of the seagrass bed displayed more depleted δ^{13}C values than epilithic ones (Fig. 2), this implies that *Posidonia* material represents only a very minor component in their diet. Dauby et al. (1995) have performed an extensive study in the Revellata Bay seagrass meadow showing that suspended matter is sometimes mainly composed by seagrass detritus. From our data, we cannot argue that suspension feeders are selective for a particular type of particles but only that seagrass detritus is not assimilated by these organisms.

For many grazers in the seagrass bed, δ^{13}C results were intermediate between algal and seagrass values (Tables 2, 3; Fig. 2). These values were not significantly different from those for grazers in the epilithic algal community, although we cannot totally exclude the

Table 2 Functional feeding groups (*FFG*), number of samples (*n*) (independent from date samplings), $\delta^{15}N$ and ^{13}C (‰) ± SD of consumers sampled in the epilithic algal community in the Revellata Bay (Gulf of Calvi, Corsica) [Functional feeding groups: *cf* carnivorous fish; *ci* carnivorous invertebrates; *df* deposit feeders; *gi* grazer (invertebrates) (this category groups "true" grazers and fauna feeding on plants detritus); *gf* grazer (fish); *o* omnivorous invertebrates; *ps* psammivorous; *sf* suspension feeders]

Biota, group	Species	FFG	*n*	$\delta^{15}N$	$\delta^{13}C$
Rocks					
Sponge	*Anchinoe tenacitor*	sf	1	5.9	−18.4
	Axinella verucosa	sf	1	7.1	−20.3
	Clatherina clathrus	sf	1	4.7	−16.0
	Crambe crambe	sf	8	4.5 ± 1.0	−21.0 ± 1.1
	Hemimycale collumella	sf	3	5.1 ± 2.6	−21.7 ± 1.7
	Ircinia sp.	sf	3	4.7	−18.6 ± 0.9
	Petrosia ficiformis	sf	2	4.8 ± 0.9	−20.2 ± 0.4
Cnidarian	Hydrozoans (indet.)	sf	2	5.2 ± 2.0	−20.5 ± 0.7
	Sertularia sp.	sf	1	2.4	−19.6
	Eudendra sp.	sf	1	3.7	−18.7
	Anemona sulcata	ci	2	7.7 ± 0.8	−15.7 ± 0.7
	Parazoanthus axinellae	sf	3	4.9 ± 1.2	−20.1 ± 0.4
	Eunicella cavolinii	sf	2	4.9 ± 1.8	−19.5 ± 0.4
Siponculian	Siponculian (indet.)	df	1	3.0	−18.1
Echiurian	*Bonellia veridis*	df	1	4.3	−17.2
Annelid	Aphroditidae (indet.)	ci	1	7.0	−17.4
	Nereidae (indet.)	ci	1	7.3	−17.5
	Protula sp.	sf	1	3.3	−21.7
	Sabella pavonina	sf	2	2.5 ± 0.1	−20.5 ± 0.6
	Serpula vermicularis	sf	2	5.1 ± 1.0	−19.8 ± 0.1
	Syllidae (indet.)	ci	1	8.1	−19.1
Mollusc	*Acanthochitona communis*	gi	1	4.2	−16.9
	Chiton olivaceus	gi	2	4.1 ± 0.6	−17.7 ± 1.3
	Haliotis lamellosa	gi	2	2.6 ± 0.8	−16.2 ± 0.8
	Cerithium vulgatum	gi	5	4.9 ± 1.5	−17.3 ± 0.6
	Collumbella rustica	gi	1	2.9	−19.6
	Bittium reticulatum	gi	3	6.6	−18.5
	Rissoidae (mixed species)	gi	3	2.7 ± 0.9	−17.5 ± 0.8
	Trochidae (mixed species)	gi	1	4.8	−16.5
	Barbatia barbata	sf	2	3.0 ± 0.4	−19.6 ± 0.2
	Lima lima	sf	3	3.4 ± 0.9	−19.7 ± 0.5
Crustacean	Amphipods (mixed species)	gi	3	2.6	−21.9 ± 2.1
	Isopods (mixed species)	gi	1	3.3	−17.8
	Idotea sp.	gi	1	5.2	−19.2
	Alpheus sp.	gi	2	4.5 ± 2.5	−20.6
	Maiidae (mixed species)	o	3	3.5 ± 1.0	−19.6 ± 0.9
	Paguridae (mixed species)	o	3	3.0 ± 0.2	−21.9 ± 0.5
	Caprellidae (indet.)	o	1	7.8	−20.0
Echinoderm	*Echinaster sepositus*	ci	2	6.3 ± 1.3	−15.8
	Paracentrotus lividus	gi	12	3.6 ± 1.0	−18.2 ± 1.1
	Sphaerechinus granularis	gi	3	2.9 ± 0.7	−17.8 ± 0.3
Tunicate	*Halocynthia papillosa*	sf	4	5.7 ± 1.0	−22.0 ± 0.6

possibility that seagrass material was present. Our results suggest the occurrence of a mixed diet, predominated by epiphyte material, as also suggested by Havelange et al. (1997) for the sparid fish *Sarpa salpa*. The leaf epiphytes appear to be a major food source for the fauna associated with the *Posidonia oceanica* canopy, which is in agreement with findings in other temperate seagrass systems (Kitting et al. 1984; Mazzella and Russo 1989; Jernakoff et al. 1996). The grazing of epiphytes seems to be among the important factors controlling the variations of epiphyte biomass (Alcoverro et al. 1997).

Results confirm the observation that *Posidonia oceanica* dominates the diet of only a few species (Dauby 1989; Mazzella et al. 1992), among which psammivorous holothurians are very abundant in the meadow and appear, therefore, to be a key component in seagrass material recycling.

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Table 3 Functional feeding groups (*FFG*), number of samples (*n*) (independent from date samplings), $\delta^{15}N$ and ^{13}C (‰) ± SD of consumers sampled in the seagrass bed and in the water column of the Revellata Bay (Gulf of Calvi, Corsica) (functional feeding group abbreviations, see Table 2)

Biota, group	Species	FFG	*n*	$\delta^{15}N$	$\delta^{13}C$
Seagrass bed					
	Fixed leaf epifauna	sf	15	3.4 ± 1.3	−19 ± 1.7
Sponge	*Crambe crambe*	sf	1	4.2	−22.2
Cnidarian	*Cerianthus* sp.	ci	1	8.5	−18.0
Echiurian	*Bonellia veridis*	df	1	3.9	−17.2
Annelid	*Sabella pavonina*	sf	1	3.4	−20.9
Mollusc	*Pecten* sp.	sf	2	5.3 ± 0.3	−19.5 ± 1.4
	Bittium reticulatum	gi	2	3.2 ± 0.3	−18.0 ± 1.2
	Calliostoma sp.	gi	1	5.1	−14.6
	Emarginula sp.	gi	1	4.1	−16.2
	Gibbula sp.	gi	1	3.3	−16.5
	Jujubinus sp.	gi	1	2.9	−18.3
	Rissoa auriscalpium	gi	2	3.6 ± 0.1	−19.2 ± 3.5
	Tricolia sp.	gi	2	3.4 ± 1.3	−14.2
	Aplysia punctata	gi	2	2.5 ± 1.8	−24.2 ± 5.9
	Nudibranch (mixed species)	ci	1	3.7	−20.0
Crustacean	Amphipods (mixed species)	gi	2	3.5 ± 0.2	−20.1 ± 1.0
	Isopods (mixed species)	gi	1	8.7	−17.2
	Idotea sp.	gi	2	4.1	−15.1 ± 1.3
	Sphaeroma sp.	gi	1	3.7	−19.1
	Mysidiacae (mixed species)	sf	2	6.0	−23.1 ± 1.4
	Paguridae (mixed species)	o	7	5.3 ± 1.1	−19.1
	Galatheidae (mixed species)	o	1	5.6	−19.0
	Thoralus cranchii	gi	2	4.6 ± 0.4	−18.6 ± 0.6
	Hippolyte inermis	gi	2	6.4 ± 0.3	−18.3 ± 0.1
	Palaemon sp.	ci	3	7.8 ± 1.2	−17.5 ± 0.7
Bryozoan	*Electra posidoniae* (leaf epiphytes)	sf	2	4.7 ± 1.6	−22.6
Echinoderm	*Asterina gibbosa*	ci	2	5.0 ± 1.3	−20.1 ± 0.4
	Holothuria stellati	ps	1	3.6	−14.4
	Holothuria tubulosa	ps	8	5.5 ± 1.0	−13.2 ± 1.7
	Sphaerechinus granularis	gi	2	5.3 ± 2.4	−22.1 ± 1.1
Tunicate	Didemnidae (leaf epiphytes)	sf	1	3.5	−25.3
	Botryllus schlosserii (leaf epiphytes)	sf	1	2.5	−22.3
Water column					
Crustacean (mainly)	Zooplankton	sf	20	3.5 ± 0.5	−22.3 ± 1.3
Fish	*Cantharus cantharus*	cf	1	8.5	−17.0
	Coris julis	cf	2	9.1 ± 0.4	−17.0 ± 0.4
	Diplodus anularis	cf	2	8.2 ± 0.4	−17.9 ± 1.5
	Mullus surmulletus	cf	1	8.6	−15.2
	Oblada melanura	cf	3	8.5 ± 0.9	−17.6 ± 1.3
	Sarpa salpa (young)	gf	8	5.4 ± 0.4	−17.4 ± 0.6
	Sarpa salpa (adult)	gf	3	6.5 ± 0.5	−16.1 ± 0.6
	Scorparia porcus (young)	cf	2	7.5 ± 0.1	−16.6 ± 0.1

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