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FOOD WEB STRUCTURE OF A MEDITERRANEAN CORALLIGENOUS ECOSYSTEM

Abstract

The coralligenous ecosystem is one of the biodiversity hotspots in the Mediterranean Sea. This study aims at determining (i) the organic matter (OM) sources at the base of the food web in a coralligenous ecosystem near Marseille (Cap Caveau, Frioul Island) and (ii) the global functional structure of its community. For that purpose, C and N stable isotope analyses were performed on 78 compartments or species collected in this habitat between 30 and 40 m depth. Results suggested that the pelagic particulate organic matter (POM), mainly composed of phytoplankton, was the main OM source fuelling coralligenous food webs, followed by sedimented organic matter (SOM) and some macrophytes. At least three level of consumers were identified from plankton-feeding invertebrates to piscivorous teleosts. Coralligenous food webs seemed to be characterized by a high abundance and trophic diversity of plankton and filter feeders. Among them numerous sessile invertebrates, such as cnidarians, bryozoans and ascidians, were poorly directly consumed, but played an important role in POM transfer. Further studies on spatial and temporal variations of coralligenous communities would be necessary for providing a general trophic functioning model of this highly diversified ecosystem.

Key-words: food webs, coralligenous ecosystem, stable isotopes, carbon, nitrogen.

Introduction

Coastal areas shelter important marine ecosystems both in terms of production and biodiversity (Ray, 1988). They are subjected to high anthropogenic pressures related to fishing activities, urbanization of coastline and sewage outfalls leading to inputs of continental organic and inorganic matter. Other threats affect these marine ecosystems due to the global change affecting the oceans, warming and acidification of seawater in particular (e.g. Doney *et al.*, 2012). In the Mediterranean Sea, two coastal ecosystems constitute "hotspots" of biodiversity: *Posidonia oceanica* meadows (Boudouresque *et al.*, 2012) and coralligenous bioconstructions (Ballesteros, 2006). The latter is a natural biogenic hard substrate (bioherm) built, under dim light conditions, by the accumulation of calcareous organisms, mainly calcareous algae (Corallinales and Peyssonneliaceae). Since its description by Marion (1883), numerous studies have described the structure and dynamics of these bioconcretions and listed the associated biodiversity (see Ballesteros, 2006). More recently, studies focused on the impact of global warming on large sessile invertebrates present on coralligenous bottoms (Garrabou *et al.*, 2009; Lejeusne *et al.*, 2010; Rivetti *et al.*, 2014). By contrast, compared to other benthic ecosystems such as *Posidonia oceanica* meadows, few data is available on the functioning aspects of coralligenous bioconstructions, particularly their trophic structure (McClanahan & Sala, 1997). To fill this gap, using C and N stable isotope analyses we tracked the sources of organic matter (OM) at the base of the food web in a coralligenous ecosystem located close to Marseille (France) and describe its trophic structure.

Materials and methods

The study area is located in the southern Bay of Marseille (France) at Cap Caveau on the south-west part of Pomègues Island, Frioul archipelago (43°15'36.7" N; 5°17'23.4" E). The geomorphology of this coastline presents steep rocky cliffs extending underwater down to 47 m depth. Coralligenous concretions are well developed from 25 m to 45 m depth, with an erected facies of gorgonians and sponges. The sources of OM considered in this coralligenous ecosystem include the particular organic matter (POM) of seawater, the sedimented organic matter (SOM), all macrophytes and settled *Posidonia oceanica* detritus. These sources, plus a number of invertebrate and fish species belonging to several trophic functional groups, were collected by SCUBA diving between 30 and 40 m depth from October to December 2015 (Tab. 1). Large and high level vagrant piscivores (moronids, carangids) could not be sampled due to the high fishing pressure in this area.

Tab. 1: List of abbreviations used for the taxa analysed

Macrophytes		<i>Astrospartus mediterraneus</i>	Ame	<i>Schizoretepora serratimargo</i>	Sser
<i>Caulerpa cylindracea</i>	Ccy	<i>Echinaster sepositus</i>	Ese	<i>Myriapora truncata</i>	Mtr
<i>Codium bursa</i>	Cbu	<i>Marthasterias glacialis</i>	Mgl	<i>Salmacina sp.</i>	Salm
<i>Codium coralloides</i>	Cco	<i>Hacelia attenuata</i>	Hat	<i>Eunice sp.</i>	Eunice sp.
<i>Flabellia petiolata</i>	Fpe	<i>Arbacia lixula</i>	Ali	Lumbrineridae	} detritivorous
<i>Pseudochlorodesmis furcellata</i>	Pfu	<i>Paracentrotus lividus</i>	Pli	<i>Syllis sp.</i>	
<i>Halimeda tuna</i>	Htu	<i>Sphaerechinus granularis</i>	Sgr	<i>Harmothoe sp.</i>	Harmothoe
<i>Palmophyllum crassum</i>	Pcra	<i>Holothuria tubulosa</i>	Htub	<i>Goniadia sp.</i>	goniadia
<i>Posidonia oceanica</i>	Pocea	<i>Lithophaga lithophaga</i>	Llith	<i>Bonellia viridis</i>	Bvi
<i>Pseudolithophyllum cabiochae</i>	Pcab	<i>Lima lima</i>	Llim	<i>Halocynthia papillosa</i>	Hpa
<i>Peyssonnelia squamaria</i>	Psqua	<i>Hexaplex trunculus</i>	Htru	Teleosts	
<i>Peyssonnelia bornetii</i>	Pbor	<i>Cantharus sp.</i>	Cantha	<i>Anthias anthias</i>	Aan
<i>Sphaerococcus coronopifolius</i>	Sco	<i>Bittium reticulatum</i>	Bret	<i>Chromis chromis</i>	Cchr
<i>Cystoseira zosteroides</i>	Czo	<i>Clanculus corallinus</i>	Ccora	<i>Spicara maena</i>	Smae
<i>Halopteris filicina</i>	Hfi	<i>Jujubinus exasperatus</i>	Jex	<i>Apogon imberbis</i>	Aim
Dyctyotales	Dyct	<i>Felimare picta</i>	Fpic	<i>Coris julis</i>	Cjul
<i>Padina pavonica</i>	Ppav	<i>Felimare tricolor</i>	Ftri	<i>Symphodus mediterraneus</i>	Smed
Invertebrates		Hydrozoa	Hydr	<i>Labrus mixtus</i>	Lmi
Decapoda	Decapo	<i>Cribrinopsis crassa</i>	Ccra	<i>Mullus surmuletus</i>	Msur
<i>Palinurus elephas</i>	Pele	<i>Eunicella cavolini</i>	Eca	<i>Diplodus sargus</i>	Dsar
Paguridae	Pagu	<i>Leptogorgia sarmentosa</i>	Lsar	<i>Diplodus vulgaris</i>	Dvu
Galatheidae	Gala	<i>Paramuricea clavata</i>	Pcl	<i>Scorpaena porcus</i>	Spor
<i>Leptocheirus sp.</i>	} Amphipodes détritivores	<i>Corallium rubrum</i>	Cru	<i>Scorpaena scrofa</i>	Sscro
<i>Erichthonius sp.</i>		<i>Alcyonium coralloides</i>	Aco	<i>Serranus cabrilla</i>	Scab
<i>Leucothoe sp.</i>		<i>Leptopsammia pruvoti</i>	Lpr	<i>Muraena helena</i>	Mhel
zooplankton	zooplankton	<i>Parazoanthus axinellae</i>	Pax	<i>Phycis phycis</i>	Pphy
<i>Ophiothrix fragilis</i>	Ofrag	Sipunculidae	Sipuncle	<i>Zeus faber</i>	Zfab
<i>Ophioderma longicauda</i>	Olong				

All samples were frozen, freeze-dried and ground into a fine powder using a mortar and pestle. For samples containing carbonates (*i.e.* POM, SOM, corals, bryozoans), one subsample was treated with 1 % HCl in excess. Samples were then rinsed with deionized water and dried before measurement of carbon isotope composition (expressed as $\delta^{13}\text{C}$). The raw subsample was used for the measurement of nitrogen isotope composition (expressed as $\delta^{15}\text{N}$). Stable isotope analyses were performed at the LIENSs stable isotope facility University of La Rochelle, France, using a continuous-flow isotope ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Bremen, Germany) coupled to an elemental analyser (Flash EA1112 Thermo Scientific, Milan, Italy). Results are expressed in the δ notation as deviations from international standards: Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$ values and atmospheric N_2 for $\delta^{15}\text{N}$ values (Peterson & Fry, 1987). Isotope

compositions are expressed in parts per thousand (‰) according to the equation: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where X is ^{13}C or ^{15}N and R is the isotope ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. Calibration was done using reference materials (USGS-24, IAEA-CH6, IAEA-600 for carbon; IAEA-N2, IAEA-NO-3, IAEA-600 for nitrogen). For both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, measurement precision is < 0.15 ‰ based on the analyses of acetanilide (Thermo Scientific) and peptone (Sigma-Aldrich) used as laboratory internal standards. A total of 78 compartments were analysed: 76 taxa, POM and SOM (Belloni *et al.*, 2018). For each compartment or taxon, mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were calculated from 3 to 6 replicates. The isotope compositions measured in a consumer is close to its diet, taking into account a trophic fractionation factor (mean = 1 ‰ for $\delta^{13}\text{C}$ and = 3.4 ‰ for $\delta^{15}\text{N}$) (Peterson & Fry, 1987). The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values provide information about the trophic level and the origin of the OM sources, respectively. Combining isotope analyses of C and N allows an efficient monitoring of the transfer of organic matter in food webs (Layman *et al.*, 2012). Data processing was carried out using R (v1.1.456).

Results

The food web of the coralligenous ecosystem presented a large range of $\delta^{13}\text{C}$ values (from -33.0 ± 0.2 ‰ to -10.6 ± 0.9 ‰), while $\delta^{15}\text{N}$ values ranged from 2.1 ± 0.3 ‰ to 11.4 ± 0.4 ‰ (Fig. 1).

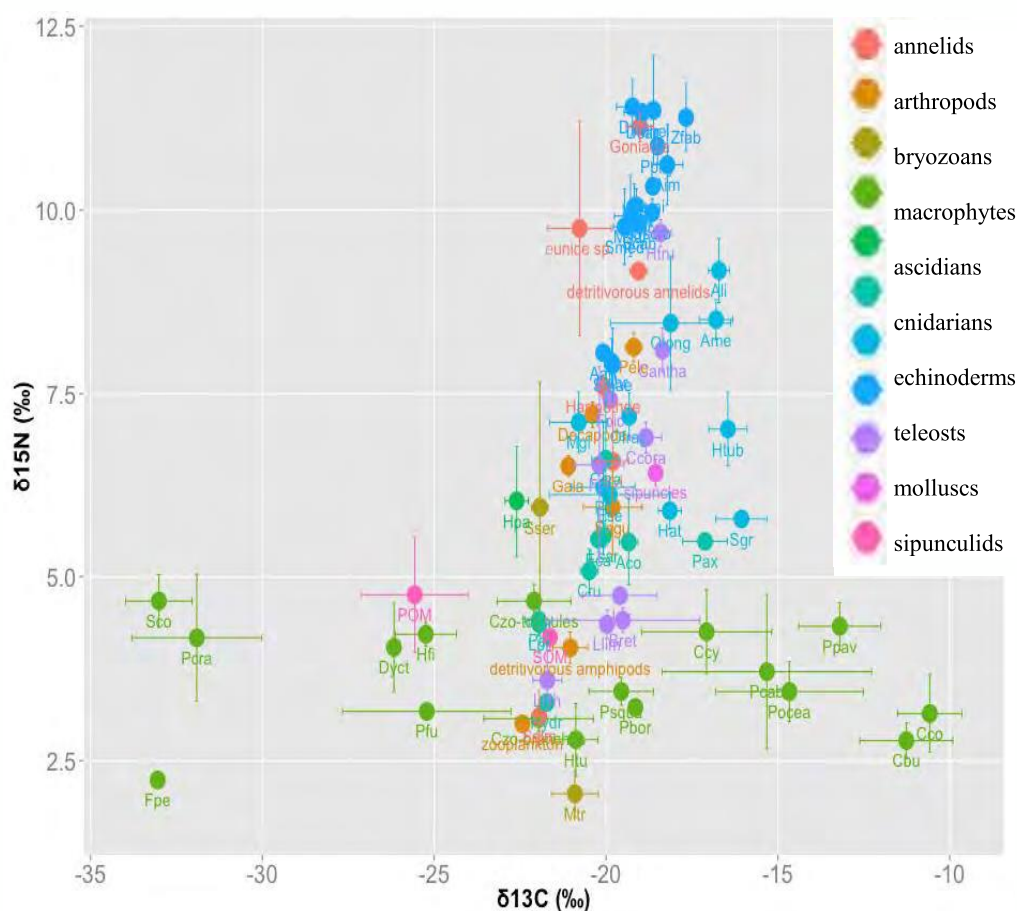


Fig. 1: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm standard deviation, ‰) of the taxa and compartments sampled in the coralligenous ecosystem. See Tab. 1 for abbreviations used.

Among the potential sources of OM, macrophytes encompassed all the range of $\delta^{13}\text{C}$ values, from the most ^{13}C -depleted *Flabellia petiolata* to the most ^{13}C -enriched *Codium coralloides*, while their $\delta^{15}\text{N}$ values ranged from 2.2 ± 0.1 ‰ to 4.7 ± 0.2 ‰. *Posidonia oceanica* detritus had a high $\delta^{13}\text{C}$ value (-14.7 ± 2.2 ‰) and an intermediate $\delta^{15}\text{N}$ value (3.4 ± 0.4 ‰), while SOM and POM presented intermediate $\delta^{13}\text{C}$ value (-21.6 ± 0.1 ‰ and -24.5 ± 1.5 ‰, respectively) and $\delta^{15}\text{N}$ value (4.2 ± 0.2 ‰ and 4.8 ± 0.8 ‰, respectively). To determine which sources fuelled the food web, an ascending hierarchical classification clustered the potential OM sources in five groups with similar isotope composition (Fig. 2). Based on their extreme $\delta^{13}\text{C}$ values and the discrepancy between these values and those of the first consumers of the food web, two groups of macrophytes could be excluded as important OM sources in this ecosystem: *Flabellia petiolata*, *Palmophyllum crassum* and *Sphaerococcus coronopifolius* with low $\delta^{13}\text{C}$ values (from -33.1 ‰ to -31.9 ‰) and the two *Codium* species with high $\delta^{13}\text{C}$ values (-11.3 ‰ and -10.6 ‰). Three groups could probably contribute to the coralligenous food web functioning. The first one gathered *Padina pavonica*, *Posidonia oceanica*, *Pseudolithophyllum cabiochae* and *Caulerpa cylindracea*. The second one contained Dictyotales, *Halopteris filicina*, *Pseudochlorodesmis furcellata* and POM. A third group gathered *Peyssonnelia squamata*, *Peyssonnelia bornetii*, *Halimeda tuna*, *Cystoseira zosteroides* and SOM.

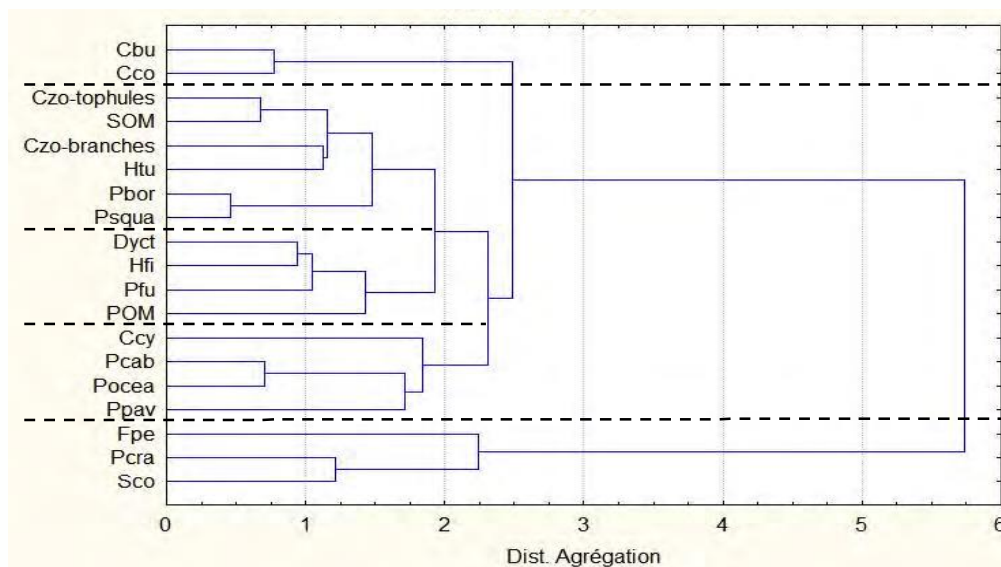


Fig. 2: Hierarchical clustering (minimum jump, Euclidean distance) of OM sources based on their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. See Tab. 1 for abbreviations used.

Invertebrates, which constituted the largest part of the consumers in the coralligenous ecosystem, presented isotope composition ranging from -22.6 ± 0.3 ‰ to -16.1 ± 0.8 ‰ for $\delta^{13}\text{C}$ values, and between 2.1 ± 0.3 ‰ and 11.1 ± 0.2 ‰ for $\delta^{15}\text{N}$ values. Among them, zooplankton feeders (cnidarians, bryozoans, ascidians, bivalves and the annelid *Salmacina* sp.) presented low mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (4.7 ± 0.4 ‰ and -20.9 ± 0.3 ‰), while carnivorous invertebrates (annelids, actinians, gastropods and echinoderms) presented high mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (8.1 ± 0.4 ‰ and -18.9 ± 0.5 ‰). Herbivores (gastropods and echinoids), detritivores (sipunculids, molluscs, arthropods and echinoderms) and omnivores (annelids, arthropods and echinoderms) had intermediate stable isotope

composition (from 5.8 ± 0.4 ‰ to 8.0 ± 0.6 ‰ for mean $\delta^{15}\text{N}$ values, and from -19.9 ± 1.0 ‰ to -18.9 ± 0.6 ‰ for mean $\delta^{13}\text{C}$ values). The isotope composition of teleost fishes presented narrower ranges of $\delta^{15}\text{N}$ values (from 7.9 ± 0.5 ‰ to 11.4 ± 0.4 ‰) and $\delta^{13}\text{C}$ values (from -20.1 ± 0.1 ‰ to -17.7 ± 0.2 ‰). The zooplankton feeders, *Chromis chromis*, *Spicara maena* and *Anthias anthias*, had low $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (from 7.9 ± 0.3 ‰ to 8.1 ± 0.1 ‰, and from -19.8 ± 0.2 ‰ to -20.1 ± 0.1 ‰, respectively). Four species had the highest $\delta^{15}\text{N}$ values: two macrocarnivorous species, *Zeus faber* and *Muraena helena*, and two mesocarnivores: *Diplodus vulgaris* and *D. sargus* (from 11.3 ± 0.5 ‰ to 11.4 ± 0.4 ‰). The other teleost species, whether meso- (labrids, mullids) or macrocarnivores (scorpaenids, serranids), were characterized by intermediate $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

Discussion and conclusions

The stable isotope values recorded for coralligenous species, particularly teleost fishes, were close to those obtained by Cresson *et al.* (2014a, b) on nearby artificial reefs in the Bay of Marseille. The range of $\delta^{13}\text{C}$ values measured in this study was much wider for the potential food sources than for consumers, thereby indicating that not all sources were used in the food web. Among the macrophytes, some are well known to be not palatable, such as *Pseudolithophyllum* or *Peysonnelia* spp., which have calcareous thallus or *Pseudochlorodesmis*, which is an encrusting species. The major food sources susceptible to fuel the food web of the coralligenous habitat were some macrophytes, such as the Dictyotales and *Cystoseira zosteroides* consumed by the herbivores, the POM, highly consumed by filter feeders, and the SOM, ingested by the detritivores. The range of $\delta^{13}\text{C}$ values of invertebrates supported the fact that different sources of OM were at the base of this food web. The coralligenous ecosystem included numerous filter-feeding species, which increased the flux of OM from pelagic to benthic habitats. However, a large part of sessile filter-feeding invertebrates (bryozoans, ascidians, cnidarians), while playing a crucial role in the construction and architecture of the coralligenous ecosystem (Ballesteros, 2006), were poorly palatable and hardly consumed by other organisms. This trophic pathway could be considered therefore as a dead end for the coralligenous food web because of a lack of direct transfer of their organic matter up in the food web. The main trophic pathway of OM transfer seemed to be constituted by mobile invertebrates and soft-bodied filter feeders up to carnivorous species. This trophic way fuelled the entire food web up to the highest trophic levels and was the major way of transfer of the organic matter from the lowest to the highest trophic levels. The high range of $\delta^{15}\text{N}$ values between OM sources and carnivorous teleosts indicated that at least three trophic levels of consumers were present. The low $\delta^{15}\text{N}$ values of filter-feeding invertebrates placed them as primary consumers, followed by herbivorous and detritivorous invertebrates. Higher in the food web, one found zooplankton-feeding teleosts, then omnivorous invertebrates and mesocarnivorous teleosts. Carnivorous annelids and the macrocarnivorous teleosts, which prey mainly on fish, were found at the top of this coralligenous food web. After this first attempt of an isotopic characterization of the coralligenous food webs, it would be interesting to analyse their spatial and temporal variations and to compare their functional structure with that observed on other coralligenous ecosystem or on the highly diversified coral reefs (Behringer & Butler, 2006).

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