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Experimental nutrition in the soft coral *Alcyonium digitatum* (Cnidaria: Octocorallia): removal rate of phytoplankton and zooplankton

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Abstract: The soft coral *Alcyonium digitatum*, a passive suspension feeder, is one of the three dominant species of the Dover Strait pebbles macrobenthic community (eastern English Channel). In order to study the exchanges between the water column and this community exposed to strong tidal currents, two sets of nutrition experiments were performed on the octocoral. A mean removal rate of phytoplankton or zooplankton organisms was first calculated through experiments conducted in small enclosures, using cultures of diatoms *Skeletonema costatum* and of *Artemia sp.* nauplii. As the removal rate (± standard deviation) of zooplankton (0.79 ± 0.48 mg C g^{-1} h^{-1}) was much higher than the removal rate of phytoplankton (0.16 ± 0.07 mg C g^{-1} h^{-1}), *Artemia sp.* nauplii were used as feeding particles in the following experiments performed in a flume under a controlled flow. Three experiments are presented here under average condition of food availability and current speed. The mean removal rate was 0.64 ± 0.16 mg C g^{-1} h^{-1}. These experiments clearly show the efficiency of this type of approach to characterize the nutrition of this benthic species as a function of the nutritive particle flow. They allow an evaluation of the transfer of organic carbon from the water column to the benthic population.

Résumé: *Nutrition expérimentale du corail mou* Alcyonium digitatum *(Cnidaria : Octocorallia): taux de prélèvement de phytoplancton et de zooplancton.* Le corail mou *Alcyonium digitatum*, un suspensivore passif, est l'une des trois espèces dominantes du peuplement macrobenthique des cailloutis du détroit du Pas de Calais (Manche orientale). Deux séries d'expériences sur la nutrition de *A. digitatum* ont été réalisées dans le cadre de l'étude des échanges entre la colonne d'eau et ce peuplement soumis à des courants de marée intenses. Un taux moyen de prélèvement d'organismes issus de cultures phytoplanctoniques (*Skeletonema costatum*) ou zooplanctoniques (nauplii d'*Artemia sp.*) a d'abord été calculé au cours d'expériences réalisées en petit volume. Le taux de prélèvement (± écart-type) de zooplancton (0.79 ± 0.48 mg C g^{-1} h^{-1}) étant beaucoup plus élevé que celui de phytoplancton (0.16 ± 0.07 mg C g^{-1} h^{-1}), les nauplii d'*Artemia sp.* ont ensuite été utilisés dans des expériences réalisées sous courant contrôlé en canal hydrodynamique. Trois expériences, réalisées sous des conditions moyennes de disponibilité de nourriture et de courant, sont présentées. Un taux moyen de prélèvement de 0.64 ± 0.16 mg C g^{-1} h^{-1} a été observé. Ces expériences montrent l'adéquation de ce type d'approche pour caractériser la nutrition de cette espèce benthique en fonction du flux de particules nutritives et permettent d'évaluer le transfert de carbone organique de la colonne d'eau vers la population benthique.

Keywords: Flow experiment, Octocoral, Removal rate, Suspension-feeding

Introduction

The soft coral *Alcyonium digitatum* (Linnaeus, 1758) is a widespread temperate colonial species occurring from

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Iceland to western Europe, common and locally very abundant along the entire English Channel coastal zone (Cornelius et al., 1990). This species is generally found attached to rocks and boulders, in situations where strong water movements (currents or wave turbulence) prevail, on the lower shore or in the sublittoral (Manuel, 1981). This passive suspension feeder has been described as carnivorous, its food being reported as consisting mainly of small zooplankton, which it paralyses by the action of its nematocysts. This view of octocorals as carnivorous was supported by the examination of morphological features of the polyps surface (Lewis, 1982). Nevertheless, some zooxanthellae-free soft corals such as *A. digitatum* do not seem to be fully depending on animal food and may also feed on phytoplankton (Roushdy & Hansen, 1961; Tixier-Durivault, 1987; Sorokin, 1991; Fabricius et al., 1995a). *A. digitatum* is the third dominant species of the Dover Strait pebbles macrobenthic community of the eastern English Channel (Migné & Davoult, 1997a). This rich community (both in terms of diversity and biomass) accounts for 30 to 40 % of the total English Channel area (Larsonneur et al., 1982) and is largely dominated by suspension feeders (99.8 % of the total biomass; Migné & Davoult, 1997a). This trophic pathway has been shown to play a leading part in the exchanges of carbon and nitrogen between pelagic and benthic compartments in shallow temperate coastal habitats (Hily, 1991). An annual budget of carbon and nitrogen fluxes has been proposed in the Dover Strait pebbles macrobenthic community by applying the equation of conservation of matter to the three dominant populations (Migné & Davoult, 1998). Recent studies on a population of *A. digitatum* (Migné & Davoult, 1997a) and experimental measurements on the species (Migné & Davoult, 1997b, 1997c) allowed us to estimate each term of the equation with the exception of ingestion which was calculated by difference.

In this study, our aim was to estimate an order of magnitude of particles removal rate by *A. digitatum* by conducting laboratory experiments under flow conditions. As the knowledge on the feeding mechanism of *A. digitatum* is limited, e.g. the rythms and reasons of extension-retraction of polyps are not known (Roushdy, 1962; Pavans de Ceccatty et al., 1963), it was necessary, in a first step, to test the behaviour of the species and to select the particles to be used in experiments (particles must be ingested by the species and easy to obtain in large quantities).

Two sets of experiments are presented here: a first one, conducted in small enclosures, in order to compare the consumption of phyto- and zoo-plankton organisms and a second one, conducted in a flume, to control the influence of current speed on the consumption of zooplankton organisms.

Materials and methods

Sampling

Colonies of *Alcyonium digitatum*, attached to pebbles, were collected by scuba diving at a depth of 37 m in the Dover Strait (50°55’5 N; 1°34’7 E).

Nutritive particles

As in the nutrition experiments performed by Roushdy & Hansen (1961) on *A. digitatum*, cultures of diatoms (*Skeletonema costatum* Cleve, 1873) were used as phytoplankton sources. The cultures were grown with a photoperiod of 12 h light/12 h dark, in filtered and sterilized sea water, by adding growth factors following Le Borgne (1986). The diatoms concentration was determined by measuring the chlorophyll *a* content (following the Scor-Unesco method, 1966). It was expressed in terms of organic carbon according to the relationship established between the organic carbon concentration (C_{org} in µg l^{-1}) and the chlorophyll *a* concentration (Chl*a* in µg l^{-1}) of a culture of *S. costatum* (C_{org} = 45.8 Chl*a* ; Davoult et al., 1994).

As in previous studies conducted on different species of *Alcyonium* (Pratt, 1905) or other soft corals (Lewis, 1982; Sorokin, 1991), living nauplii of the brine shrimp *Artemia sp.* were used as zooplankton source. Cysts were incubated 24 h in bubbled and warmed (25 °C) sea water. Nauplii were used in experiments seven days after hatching. At this stage of development, the nauplius average size is 0.9 mm (i.e. the same size of nauplii used by Sorokin, 1991) and its average organic carbon content (determined by CHN element analyser) is 15 µg. The nauplii concentration was determined by counting (as done by Patterson, 1991 for cysts of *Artemia salina*) after filtration of samples on Whatman GF/C filters.

Experiments

Pebbles bearing colonies of *Alcyonium digitatum* were kept for three to six hours in sea water enriched with phyto- or zoo-plankton (saturating conditions). Small enclosures (capacity of 10 l) were used in the first set of experiments, a flume (capacity of 200 l) was used in the second set. In the small enclosures, water was bubbled in order to ensure the homogeneity of the plankton suspension and to allow interception of motionless prey by *A. digitatum*. In the flume, the experiments were carried out under a controlled flow speed of about 10 cm s^{-1}. Regular sampling (0.1 l in small enclosures and 1.5 l in the flume) allowed us to control the removal of plankton by the soft-coral. Controls, with pebbles only, were included to establish if the decrease of plankton concentration was due to the removal by the colonies or to a sedimentation process.

A prey removal rate by the soft-coral was calculated (in µg Chl*a* g^{-1} h^{-1} and ind g^{-1} h^{-1}) by regressing prey concentration against time for each experiment where a linear trend was observed. It was then expressed in terms of mass of organic carbon removed from water by unit of *A. digitatum* biomass and unit of time (mg C_{org} g^{-1} h^{-1}).

Six experiments (E1 to E6) plus two controls (C1 and C2) were conducted in small enclosures with *Skeletonema costatum* (Table 1). The initial concentration in phytoplankton (about 18 µg Chl*a* l^{-1}) was as high as the maximum concentration measured in the sampling area during spring phytoplanktonic blooms (Quisthoudt, 1987 ; Davoult et al., 1998 ; Gentilhomme & Lizon, 1998). Five experiments (E7 to E11) plus two controls (C3 and C4) were conducted in small enclosures with nauplii of *Artemia sp.* (Table 2). Three experiments (E12 to E14) plus one control (C5) were conducted in the flume with nauplii of *Artemia sp.* (Table 3). The initial concentration in nauplii varied from 23 to 500 ind l^{-1} but was always higher than the maximum concentration of zooplankton estimated in the area (≈ 10 ind l^{-1}, Le Fèvre-Lehöerff et al., 1983). This high concentration of nauplii allowed a determination by counting.

Table 1. Characteristics of the nutrition experiments of *Alcyonium digitatum* carried out in small enclosures with *Skeletonema costatum* (afdw = ash free dry weight).

Tableau 1. Caractéristiques des expériences de nutrition d'*Alcyonium digitatum* avec *Skeletonema costatum* en petit volume (afdw = poids sec libre de cendres).

	Initial volume of water (l)	*A. digitatum* Biomass (g afdw)	Temperature (°C)	*S. costatum* Initial concentration (µg Chla l^{-1})	(mg C l^{-1})
Experiments					
E1	8.0	1.83	17.0	16.0	0.73
E2	8.0	1.61	10.0	15.6	0.71
E3	8.3	3.84	8.0	18.5	0.85
E4	8.5	3.58	7.5	20.2	0.93
E5	8.0	5.17	9.5	18.2	0.83
E6	10.0	7.25	13.0	19.3	0.88
Controls					
C1	8.0	0	8.0	19.0	0.87
C2	10.0	0	13.0	19.8	0.91

Results

In none of the experiments, except for the first one realized with nauplii (E7), an expansion of the colony was observed in response to the presence of nutritive particles. A complete expansion of colonies during our experiments has never been observed and duration and intensity of polyp expansions varied from one colony to the other. The expansion duration was therefore not controlled and was always variable in the different experiments.

Table 2. Characteristics of the nutrition experiments of *Alcyonium digitatum* carried out in small enclosures with nauplii of *Artemia sp.* (afdw = ash free dry weight).

Tableau 2. Caractéristiques des expériences de nutrition d'*Alcyonium digitatum* avec *Artemia sp.* en petit volume (afdw = poids sec libre de cendres).

	Initial volume of water (l)	*A. digitatum* Biomass (g afdw)	Temperature (°C)	*Nauplii* Initial concentration (ind l^{-1})	(mg C l^{-1})
Experiments					
E7	8.0	7.25	13.8	60	0.90
E8	10.0	7.25	14.1	90	1.35
E9	8.0	8.41	15.3	200	3.00
E10	8.0	2.66	9.0	130	1.95
E11	8.0	6.01	9.0	500	7.50
Controls					
C3	10.0	0	14.1	110	1.65
C4	8.0	0	9.0	40	0.60

Control

In the small enclosure, as in the flume, the nutritive particles concentration remained constant along each control (Table 4). Therefore the decrease in chlorophyll *a*, or in the nauplii concentration, observed during the experiments can be attributed to the removal by *Alcyonium digitatum*.

Experiments in small enclosures

The chlorophyll *a* concentration decreased in experiments 1 to 4, and no evolution was observed in experiments 5 and 6. The rate of removal was then calculated in experiments 1 to 4 (Fig. 1): the mean rate of removal (± standard deviation) for these experiments was 3.52 ± 1.44 µg Chl*a* g^{-1} h^{-1}, that is a rate of removal of 0.16 ± 0.07 mg C_{org} g^{-1} h^{-1} (for a food availability of 2.20 mg C_{org} g^{-1}).

Table 3. Characteristics of the nutrition experiments of *Alcyonium digitatum* carried out in flume with nauplii of *Artemia sp.* (afdw = ash free dry weight).

Tableau 3. Caractéristiques des expériences de nutrition d'*Alcyonium digitatum* avec *Artemia sp.* en canal hydrodynamique (afdw = poids sec libre de cendres).

	Initial volume of water (l)	*A. digitatum* Biomass (g afdw)	Temperature (°C)	Current speed (cm s^{-1})	Nauplii Initial concentration (ind l^{-1})	(mg C l^{-1})
Experiments						
E12	190.0	21.36	18.6	9.9	45	0.68
E13	137.5	12.29	10.1	9.6	40	0.60
E14	181.3	20.19	13.7	11.2	40	0.60
Control						
C5	125.0	0	-	11.3	23	0.35

Table 4. Mean concentration (± standard deviation) in nutritional particles (*S. costatum* in µg Chl*a* l^{-1} and nauplii of *Artemia sp.* in ind l^{-1}) during control experiments.

Tableau 4. Concentration moyenne (± écart type) des particules nutritives dans les expériences témoins (*S. costatum* en µg Chl*a* l^{-1} et nauplii d'*Artemia sp.* en ind l^{-1})

Control	number of measurements	mean concentration in nutritional particles µgChl*a* l^{-1}	ind l^{-1}
C1	7	18.29 ± 0.49	
C2	7	20.07 ± 0.44	
C3	5		102 ± 23
C4	13		50 ± 18
C5	7		24 ± 3

The nauplii concentration decreased in experiments 7 to 9 and 11, and no evolution was observed in experiment 10. In experiment 7, the nauplii concentration was equal to zero after two hours. It was therefore impossible to calculate a linear trend based on these three values only ($n = 3$, $r = 0.936$, $p > 0.05$). A linear trend was observed in experiments 8, 9 and 11. The rate of removal was then calculated for these experiments (Fig. 2). The mean rate of removal was 53 ± 32 ind g^{-1} h^{-1}, that is a rate of removal of 0.79 ± 0.48 mg C_{org} g^{-1} h^{-1} (for an availability of 3.71 mg C_{org} g^{-1}).

Experiments in flume

The nauplii concentration decreased in the three experiments. A linear trend was observed in each experiment (Fig. 3) and the mean rate of removal was 42 ± 11 ind g^{-1} h^{-1}, that is a rate of removal of 0.64 ± 0.16 mg C_{org} g^{-1} h^{-1} (for an availability of 3.92 mg C_{org} g^{-1}).

In this case, the food availability could be expressed in terms of flow (i.e. nauplii concentration times current speed, in ind m^{-2} s^{-1}). The decrease of flow with time was similar for the three experiments (Fig. 4) conducted at the same initial flow (same current speed and same initial nauplii concentration).

Discussion

This set of experiments performed on the octocoral *Alcyonium digitatum* confirms previous observations with

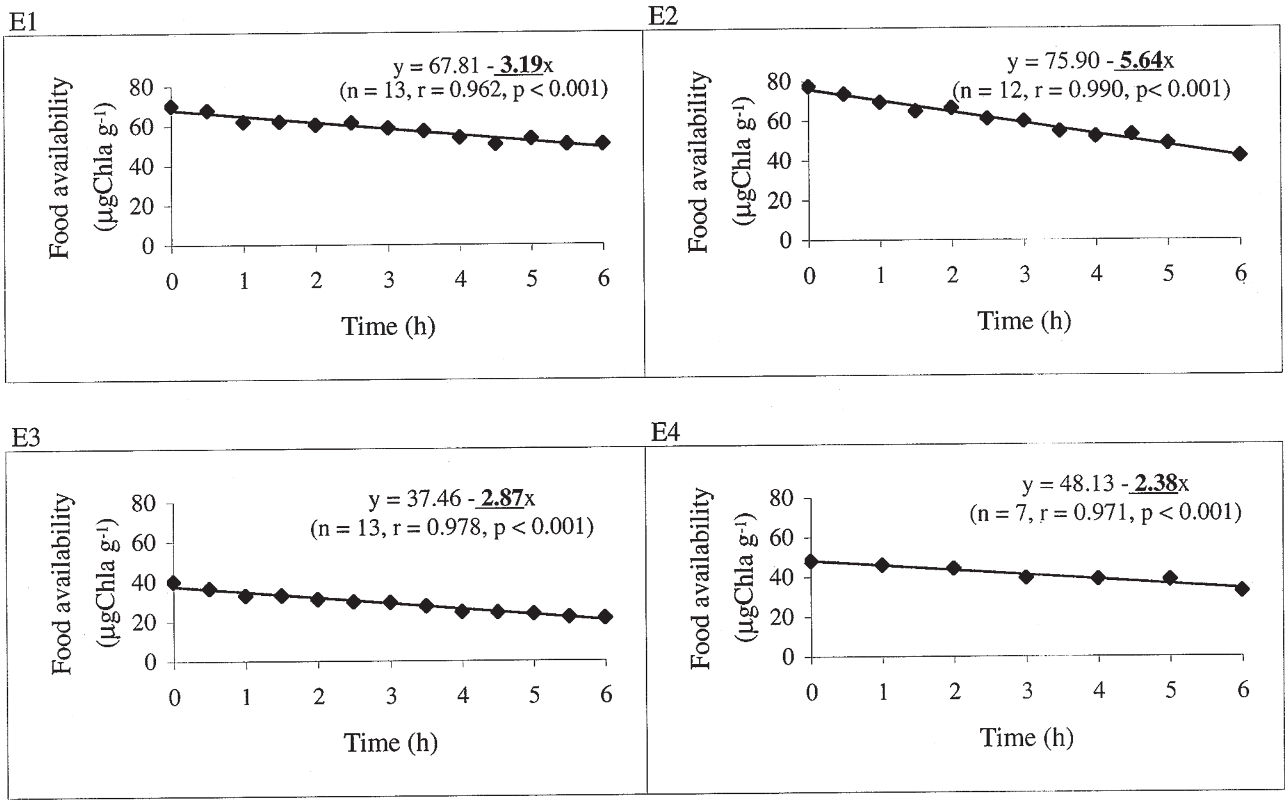

Figure 1. Trends in food availability in nutrition experiments of *Alcyonium digitatum* carried out in small enclosures with *Skeletonema costatum* and calculation of the removal rate for E1 to E4: 3.19, 5.64, 2.87 and 2.38 µg Chl*a* g^{-1} h^{-1}.

Figure 1. Evolution de la disponibilité en nourriture au cours des expériences de nutrition d'*Alcyonium digitatum* en petit volume avec *Skeletonema costatum* et calcul du taux de prélèvement pour les expériences E1 à E4 : 3,19 ; 5,64 ; 2,87 et 2,38 µg Chl*a* g^{-1} h^{-1}.

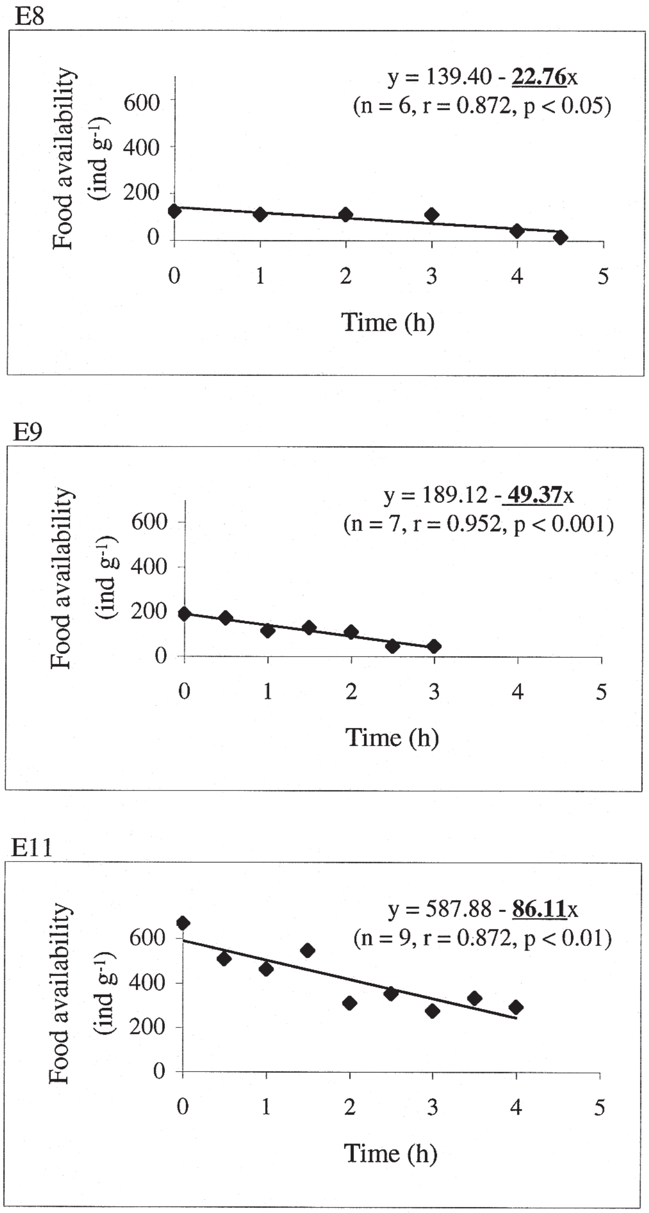

Figure 2. Trends in food availability in nutrition experiments of *Alcyonium digitatum* carried out in small enclosures with nauplii of *Artemia sp.* and calculation of the removal rate for E8, E9 and E11: 23, 49 and 86 ind g^{-1} h^{-1}.

Figure 2. Evolution de la disponibilité en nourriture au cours des expériences de nutrition d'*Alcyonium digitatum* en petit volume avec des nauplii d'*Artemia sp.* et calcul du taux de prélèvement pour les expériences E8, E9 et E11 : 23, 49 et 86 ind g^{-1} h^{-1}.

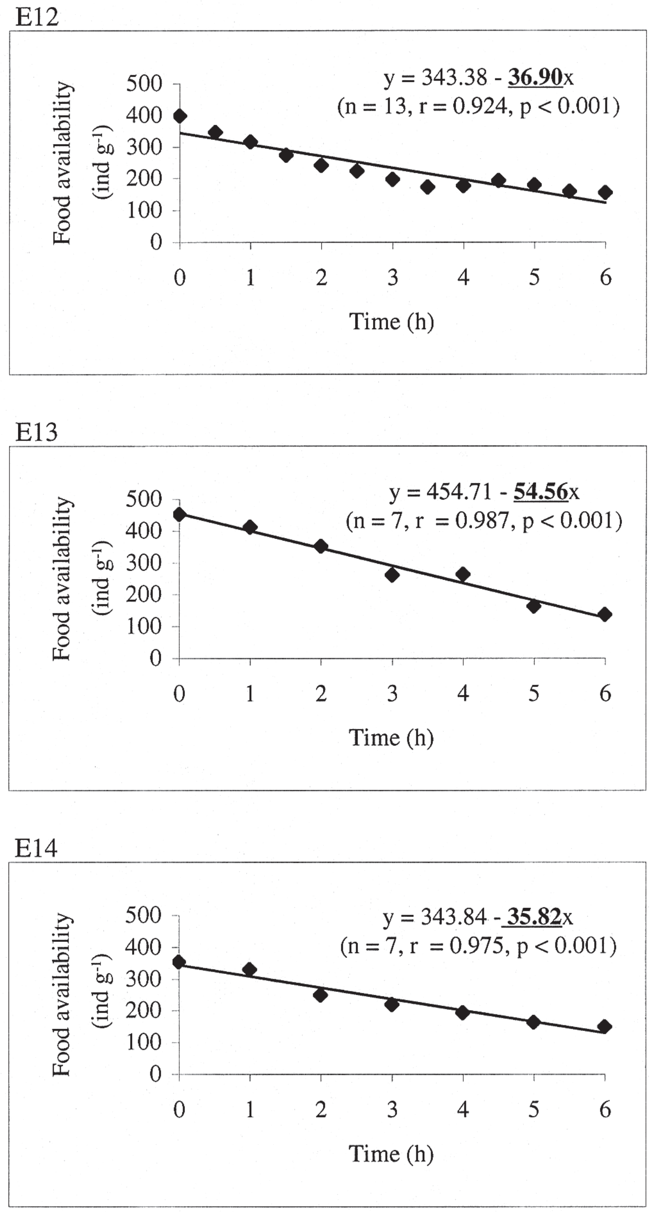

Figure 3. Trends in food availability in nutrition experiments of *Alcyonium digitatum* carried out in the flume with nauplii of *Artemia sp.* and calculation of the removal rate for E12 to E14: 37, 55 and 36 ind g^{-1} h^{-1}.

Figure 3. Evolution de la disponibilité en nourriture au cours des expériences de nutrition d'*Alcyonium digitatum* en canal hydrodynamique avec des nauplii d'*Artemia sp.* et calcul du taux de prélèvement pour les expériences E12 à E14: 37, 55 et 36 ind g^{-1} h^{-1}.

different approaches that some soft corals may not be fully depending on animal diet. Roushdy & Hansen (1961) demonstrated the ability of *A. digitatum* to filter and digest phytoplankton by the transfer of *Skeletonema costatum* labelled with ^{14}C to different tissues of the colonial animal. Using also the ^{14}C method, Sorokin (1991) showed the ability of some common reef octocoral (*Mopsella aurantia*) to feed on algae. Elyakova et al. (1981) reported the occurrence of the plant-digesting enzymes amylase and laminarinase in three soft corals of the genus *Alcyonium*

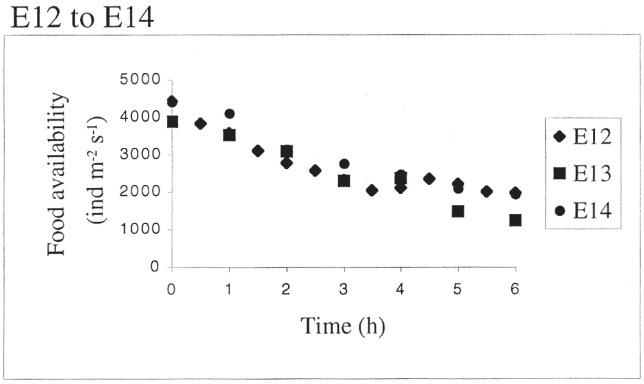

Figure 4. Trends in flow of food in nutrition experiments of *Alcyonium digitatum* (E12 to E14) carried out in the flume with nauplii of *Artemia sp.*

Figure 4. Evolution du flux de nourriture au cours des expériences de nutrition d'*Alcyonium digitatum* en canal hydrodynamique avec des nauplii d'*Artemia sp.*

possessing zooxanthellae. Sebens & Koehl (1984) found in the coelenteron content of *Alcyonium siderium* a mixed diet consisting predominantly of suspended matter, which included both animal (small zooplankton) and vegetal remains (algal fragments, plant hairs and diatoms). Fabricius et al. (1995a) demonstrated the ability of the soft coral *Dendronephthya hemprichi* to filter phytoplankton, by fluorometrically following the gradual accumulation of phytoplankton in starved colonies, after their reintroduction in natural sea water.

Fabricius et al. (1996) estimated the feeding rate of *D. hemprichi* by in situ measurements of chlorophyll removal from natural sea water. The metabolism of *D. hemprichi* seemed to be slightly higher than that of *Alcyonium digitatum* since Fabricius et al. (1995b) estimated a respiratory carbon demand of 0.27 mg g^{-1} h^{-1} for *D. hemprichi* while we measured, in a previous study, a respiratory carbon demand of 0.16 mg g^{-1} h^{-1} for fed colonies of *A. digitatum* (Migné & Davoult, 1997b). A slightly lower nutritional gain might then be expected for *A. digitatum*. The high removal rate measured with *D. hemprichi* lead Fabricius et al. (1996) to the conclusion that suspension feeding on phytoplankton was the main nutrition mode of this species. This assumption is in contradiction with the general agreement that the ability of some octocorals to filter fine particulate matter is not likely to allow for a significant amount of food accumulation (Lewis, 1982). This removal rate, equivalent to an uptake of phytoplankton carbon of 0.68 mg g^{-1} h^{-1}, is closer to the rate determined here for *A. digitatum* in experiments performed with zooplankton (0.71 mg g^{-1} h^{-1}), than to the rate determined in experiments performed with phytoplankton (0.16 mg g^{-1} h^{-1}).

The results of the present set of experiments tend to show that *Alcyonium digitatum* feeds more efficiently on zooplankton (nauplii of *Artemia sp.*) than on phytoplankton (*S. costatum*). This observation is in agreement with the results of Sorokin (1991) who compared the assimilation rates (A expressed in µg C g^{-1} dry colony weight d^{-1}) of different heterotrophic sources of feeding (*Artemia* nauplii, or rotifers, or microalgae, labelled with ^{-14}C) for thirteen alcyonarians. Only one species (*Paralemnalia clavata*) showed a slightly higher assimilation rate for algae (A of algae : A of rotifers ratio = 1.3), while the most active predator was the asymbiotic *Dendronephthya gigantea* (A of nauplii : A of algae ratio = 120). Two symbiotic species of the genus *Alcyonium* included in Sorokin's study had a higher assimilation rate for animal food (A of rotifers : A of algae ratio = 13.3 for *Alcyonium sp.* and A of nauplii : A of algae ratio = 17.9 for *Alcyonium molle*). As we have no idea on the phyto- and zoo-plankton assimilation efficiency of *A. digitatum*, we can only compare the removal rates. In our experiments the zooplankton removal rate was only 4.4 time higher than the phytoplankton removal rate. Thus, feeding on phytoplankton for *A. digitatum* seems consistent enough not to be neglected, and the ability of the species to use different sources of feeding can be an advantage in periods of zooplankton depletion. The sampling of coelenteron content of *Alcyonium siderium* by Sebens and Koehl (1984) also demonstrated the ability of this species to use different sources of feeding: over a diurnal cycle the percentage of vegetal food in total prey weight could range from low (9 %) to slightly dominant (60 %). For this species, the vegetal food consisted essentially of algal fragments and plant hair, phytoplankton (diatoms) always accounting for less than 1 % of the total coelenteron content weight.

As passive suspension feeders, octocorals depend on the ambient currents for the transport of food particles through their filter structures. Experiments on the nutrition of passive suspension feeder thus must be performed under current conditions. The three experiments performed here under average conditions for food availability and current speed showed the feasibility of this kind of experiment on *Alcyonium digitatum*. Further experiments (with other food concentration and other current speed) are necessary to test the influence of flow on food intake rates. The rates of particle uptake are commonly related to the water flow in a nonlinear trend, the physical constraints (low probability of encountering a particle in a low flow, and difficulty in capturing particles passing through the filter at higher speeds) limiting the linear trend observed under average conditions. Fabricius et al. (1995b) measured, in situ as in flow tanks, different intake rates of phytoplankton by a soft coral for different flow speed. They also observed that contraction of colonies occurs predominantly at very low or very high flow. They suggest that the reduced feeding efficiency of the species under these flow conditions may be related to polyp retraction and colony contraction. In our experiments, the expansion of colonies was not controlled and the activity of polyps was neither increased by the flow (as observed by Fabricius et al., 1995b) nor by the presence of food particles (as observed by Lewis, 1982). Contraction reduces colony height, which effectively reduces the coral filtration area and thus its rate of food encounter (Shimeta & Jumars, 1991). Moreover, contracted polyps are unlikely to be able to capture food particles. Thus, the rates of removal calculated here were not the maximum rates, but they included different conditions of contraction or expansion of the colonies and polyps. They also integrated different conditions of temperature, a factor that likely influence feeding rates, like many other biological activities (Kooijman, 2000). Nevertheless, the experiments were performed in the range of temperature encountered by *A. digitatum* during most of the year. Within this range the influence of temperature was supposed to be reduced, as it was demonstrated for a suspension feeder snail (Brendelberger and Jürgens, 1993). The rates indicated in our study were obtained in laboratory and under saturating conditions and so they are not likely to allow estimates of in situ removal rates.

Conclusion

This study tends to prove that *Alcyonium digitatum* preferentially feeds on zooplankton, a conclusion which justifies its description as a carnivorous animal. In addition, the study also confirms the ability of the species to feed on phytoplankton, showing its trophic opportunism in relation to sources of feeding. The contribution of phytoplankton must then not be neglected in the nutrition of this species and in the study of transfer of matter from the water column to the benthic population.

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