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Utilization of muddy detritus as organic matter source by the fan mussel Pinna nobilis

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Abstract

Knowledge of the feeding habits of marine species is fundamental for a better understanding of their relationship with the environment. Although phytoplankton has traditionally been reported as the main food source consumed by the Mediterranean fan mussel *Pinna nobilis*, recent studies have revealed that detritus represents an important food source for this species. We analysed the degree of acceptance of muddy detritus and the utilisation of its organic matter (OM) by *P. nobilis* on a group of 21 individuals [30.3-59.7 cm of total shell height (Ht)]. The specimens were collected between July and September 2012 in two areas (43°04´25" N; 5°46´7" E and 43°04´34" N; 5°47´32" E) of the Embiez archipelago, north-western Mediterranean (France). Our studies show that *P. nobilis* retains high quantities of OM from muddy detritus (47.50 ± 11.23% of filtered OM) irrespective of shell size. Smaller individuals, however, actively filter more detritus than large ones. The values of retained OM, together with previous studies on stomach contents, suggest that muddy detritus is a more important OM source than phytoplankton for this species.

Keywords: Mediterranean, bivalve, pinnidae, food acceptance, diet.

Introduction

The endemic Mediterranean fan mussel *Pinna nobilis* Linnaeus, 1758 is an emblematic large suspension-feeder that can measure more than one meter of total shell height (Ht) (Zavodnik *et al.,* 1991; Moreteau & Vicente, 1982; Butler *et al.,* 1993) and live at least 27 years (Garcia-March *et al.,* 2011). Unfortunately, their populations have significantly declined in the last decades (De Gaulejac & Vicente, 1990; Garcia-March, 2005) as a result of coastal development, fishing, and/or accidental harvesting by trawling and shell breakage by anchoring (Katsanevakis, 2005; Acarli *et al.,* 2011; Hendriks *et al.,* 2011). This is why it is under protection since 1992 when it was included in ANNEX IV of Council Directive 92/43/EEC (EC Habitats Directive) as an endangered species. The species was later (in 1999) included in ANNEX II to the Barcelona Convention. In nature, *P. nobilis* is exposed to complex mixtures of particles especially in nearshore habitats (Levinton *et al.,* 2002) where it achieves one of the fastest growths of all bivalves; young individuals can grow more than 10 cm year^{-1} in Ht (Moreteau & Vicente, 1982; Richardson *et al.,* 1999; Siletic & Peharda, 2003). A better description of the feeding ecology of marine bivalves provides a better understanding of the interrelations between their populations and marine ecosystems. Bivalves may modify eutrophic areas and consequently change the environment due to their activity (Newell, 2004) and environmental characteristics can determine the density of individuals or spatial distribution. Presently, there is a knowledge gap in the feeding ecology of *P. nobilis* (Garcia-March, 2005). Preliminary studies indicated that the species feeds on a combination of phytoplankton (Cardona *et al.,* 2007; Deudero *et al.,* 2009), organic matter (OM) from epiphytes of seagrass leaves (Kennedy *et al.,* 2001; Cabanellas-Reboredo *et al.,* 2010) and some zooplankton including other bivalve larvae (Davenport *et al.,* 2011). This constitutes evidence of the omnivore character of this species. However, the predominance of muddy detritus in the diet of *P. nobilis* has also been reported (Richardson *et al.,* 1997; Kennedy *et al.,* 2001). Likewise, Cabanellas-Reboredo *et al.* (2010), revealed that muddy detritus may represent 26.4% of the total diet. Furthermore, Davenport *et al.* (2011) reported a great domination of detritus, up to 95%, in the stomach content of 18 fan mussels collected in a coastal lagoon and Najdek *et al*. (2013) confirmed, using fatty acid profiling that, irrespective of size, *P. nobilis* predominantly ingest detritus. We actually do not know, however, the degree of utilisation per volume of this food source ingested by fan mussels, and some questions are still unanswered:

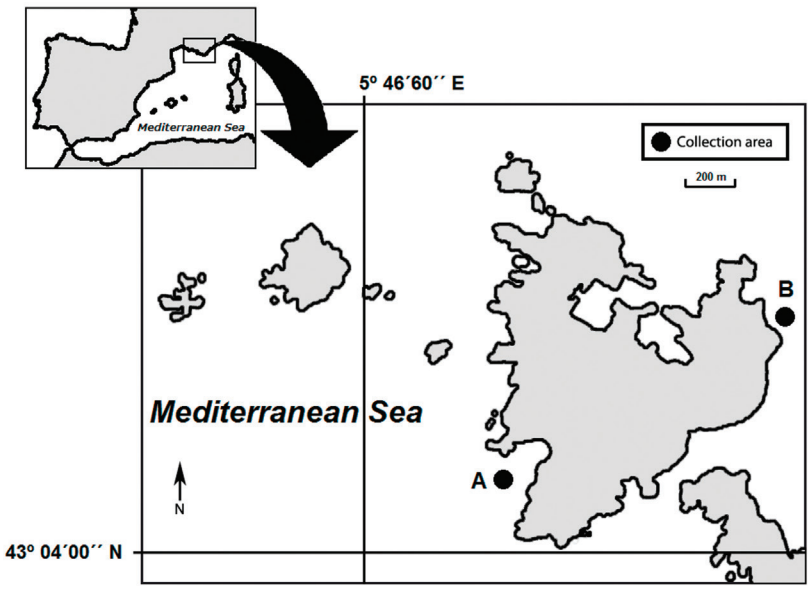

Fig. 1: Map of Embiez island (South-eastern France), showing the sites where individuals were collected for this study. a - open sea area. b - lagoon area.

to what degree is detritus utilized by *P. nobilis* as a source of organic matter (OM)? Is the intake of detritus an indirect consequence of habitat type or does *P. nobilis* use detritus as an important food source, without which survival could be compromised? The aim of the present work was to evaluate the quantity of OM that *P. nobilis* obtains from muddy detritus and its utilisation as an alternative food source. To this end, we tested the degree of acceptability of muddy detritus and also studied the balance of OM present in it before ingestion, and in faeces and pseudofaeces excreted by 21 individuals kept in laboratory facilities.

Materials and Methods

Study site and adult collection

Adult fan mussels, 21 in total, of a wide size range (30.3-59.7 cm of total shell height (Ht)) were collected during 4 surveys by SCUBA divers between July and September 2012, in the Embiez archipelago, north-western Mediterranean (France). A group of 13 specimens were taken from the open sea (43°04´25" N; 5°46´7" E), from 10 to 19 meters, living in *Posidonia oceanica* meadows, and another 8 individuals were collected from a sheltered shallow lagoon (Le Brusc), from 0.5 to 1.5 meters, protected from the open water by a *P. oceanica* barrier reef (43°04´34" N; 5°47´32" E) (Fig. 1). We decided to establish a wide size range instead of keeping a similar individual size in order to detect trends in food consumption related to the size of the animals. Three size categories were established (Fig. 2). Small individuals (30-39 cm of Ht); medium individuals (40-49 cm of Ht); large individuals (50-59 cm of Ht). Seven individuals were sampled for each size category. Special attention was given to extract the entire byssus without dislodging it from its attachment during the collection in order to reduce stress and facilitate re-settlement in the field after completing the experiments.

Experimental settings

The individuals were labelled and accommodated in 2,600 L open circuit tanks one week prior to the start of the experiments. Each individual was fixed vertically to the bottom of the tank with the anterior part introduced in a plastic basket without sediment. Maximum shell width and height (W and Ht respectively) were measured in every fan mussel to the nearest millimetre with a device specifically designed for this species (García-March *et al.*, 2002). Each tank held between 6-8 fan mussels. The visual inspections confirmed that all the specimens quickly responded well to the new accommodation parameters, which were similar to those in Le Brusc lagoon. In the lagoon, temperature ranges between 20-28˚C during summer (Riva & Vicente, 1976; Francour & Sartoretto, 1991). Then water was filtered and tempered to 20˚C before arriving in the tanks. All animals were cleaned by removing the epibionts from their valves. In contrast, the effect of symbiont species such as *Pontonia pinnophylax* and *Nepinnotheres pinnotheres*, which commonly feed on the same food sources as *P. nobilis* (Cabanellas-Reboredo *et al.,* 2010) was dismissed in this study. Taking into account the quantity of detritus added (20 g), we considered the alteration of results as almost negligible due to the action of these symbionts.

To carry out the detritus feeding tests, fan mussels were individually placed in 60L tanks with filtered water. In order to reduce stress, the specimens were placed in the tanks one hour before the experiments started. Water temperature was kept constant during the process (20˚C).

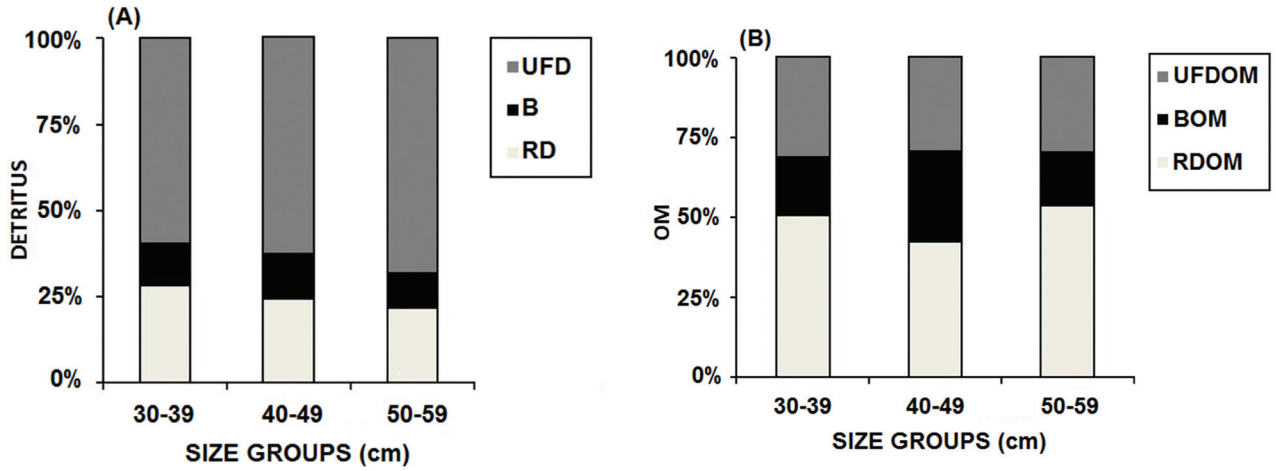

Fig. 2: Fate of total detritus and organic matter (OM) fractions observed in detritus feeding experiments. a detritus percentages. Note that filtered detritus (FD) is the sum of B + RD. b OM percentages. Note that filtered OM (FOM) is the sum of BOM + RDOM. (B) biodeposits (faeces and pseudofaeces). (BOM) biodeposits OM. (RD) retained detritus after 8 hours. (RDOM) retained detritus OM. (UFD) unfiltered detritus. (UFDOM) unfiltered detritus OM.

Gentle and constant aeration (120 L/h) was used to keep detritus particles in suspension. Fan mussels were not fed on the day before the experiments to ensure that their guts were mostly empty. We checked that no food rejection occurred at the beginning of the experiments from previous meals, thus confirming our previous observations that the specimens eliminate most of the digested food in less than 24 h. Therefore, despite the fact that typical duration of similar closed-circuit experiments for other bivalves usually last 5 hours (Griffiths, 1980; Berry & Schleyer, 1983; Vincendeau & Robert, 1987), the duration of our experiments was set to 8 hours. Only after this time could we are confident that most excretion had occurred. A variation in the digestion time may occur due to several parameters such as water temperature, food source, the bivalve species or the size of the animals among others (Deslous-Paoli, 1987). Thus, we adjusted the period of the experiment for *P. nobilis* to the length of time when rejection of biodeposits had clearly stopped. On the other hand, given the large water volume of the tanks (60L) and previous personal observations, we were confident that the 8 h experiment would not cause excessive stress to the animals. Experiments were replicated 3 times per individual with a week interval between them.

We fed the animals with muddy detritus <200 µm collected from Le Brusc Lagoon. The detritus was dried at 60˚C for 48 h for weighing the dose and then rehydrated using filtered sea water for better distribution in the tanks. Previous tests performed before experiments allowed us to set the best dose in terms of acceptance and mucus production. Therefore, the final ration established for each experiment was 20 g dry weight. In other species, such as *Mytilus edulis*, Davenport *et al*. (2000) reported a particle range in the guts from 100 µm to 1000 µm. However, Newell *et al.* (1989) and Dupuy *et al*. (1999) reported particle ranges <110 µm in *M. edulis* and between 5 µm and 100 µm in *Crassostrea gigas*, respectively. Furthermore, most of the largest particles present in the guts of *Pinna nobilis* have a size ≤200 µm with the exception of a few copepods and macroalgae fragments larger than 500 µm (fig. 5 in Davenport *et al*., 2011). Therefore, we adopted the threshold of 200 µm as the maximum limit for our experiments, in order to minimize particle rejection due to excessive size.

In order to establish the OM content of the detritus fed to the specimens, two subsamples of 20 g were prepared from a sample of 40 g. One subsample was added to the tank at the beginning of the experiment while the other one was used as control and calcined using the method by Conover (1966) to determine its OM. A preliminary experiment was made to ensure that the mean percentage of OM present in both subsamples was the same. Three sets of 40 g of muddy detritus were dried at 60˚C for 48 h, sieved through a 200-µm mesh, divided in 2 identical subsamples of 20 g using the technique of quartering (Krumbein & Pettijohn, 1938) and then ashed at 550˚C for 2 h (Conover, 1966). The assay concluded that all subsamples had an identical percentage of OM, thus confirming that we could establish the OM content of the detritus given to the animals (DOM) from the control subsamples.

From the detritus supplied to the fan mussels, we considered as filtered detritus (FD) the quantity of material that was captured by fan mussels. Biodeposits (B) (faeces and pseudofaeces), the fraction of FD excreted after digestion or discarded after being filtered. The material that a specimen may hold inside its body after the duration of the experiment was considered as retained detritus (RD). The unfiltered detritus (UFD) was material that had not reached the gills and therefore was not filtered by the animals. Consequently, to calculate the proportions of filtered and retained detritus OM (FOM and RDOM respectively) we subtracted from total OM the weight

of OM in the UFD fraction (UFDOM). We understand that RDOM is ingested OM either subjected to longer digestion or metabolised (Brillant & MacDonald, 2000). After the 8-hour experiment, B and UFD were identified. Most of the B were collected with a micropipette before they had reached the bottom of the tanks. Those recovered from the bottom were clearly distinguishable from the UFD due to the difference in shape and consistency. Both B and UFD were collected taking special care to avoid mixing them, and filtered through a 35-µm mesh. Samples were dried (60˚C / 48 h) and calcined (550˚C / 2 h) to determine their amount of OM (both from BOM and UFDOM). The bulk of water was filtered through a 35 µm mesh once experiments were finished, in order to collect any mucus or remaining suspended material, which presumably would be the origin of dissolved OM. However, the OM detected after calcining using Conover's (1966) method with a measurement precision of 10^{-4} g was negligible. The quantity of RD remaining in the gut of the pinnids and of RDOM after 8 hours was determined by default. Considering the protection level and status of *P. nobilis* in the Mediterranean Sea, no subject was sacrificed to study gut content and dry weight. Individuals were reintroduced in their original collection places once the experiments were completed.

Statistical analysis

The data were analyzed using the SPSS® program. The normality and homocedasticity of variables were confirmed by the Kolmogorov-Smirnov (K-S) test, P-P / Q-Q plots and Levene´s test respectively. To estimate the hypothesis of the possible relationship between muddy detritus and size of animals the Pearson correlation coefficient was computed comparing size category with B, BOM, FD, FOM and RDOM.

Results

Detritus consumption

Muddy detritus was quickly ingested by the specimens. A 60L tank with one *P. nobilis* could be cleaned of suspended detritus in less than an hour. On average (average ± SE, N = 21) B rejected after 8 hours weighed 2.51 ± 0.66 g, *i.e.* 12.57 ± 3.31% of the total. The UFD weighed 12.73 ± 0.85 g, i.e. 63.49 ± 4.26% of the total. The gross retained material from the total added was 4.76 ± 0.91 g, *i.e.* 22.58 ± 4.54% . In relation to the FD, the B formation was relatively small (34.57 ± 8.65% of total detritus minus UFD) indicating a good acceptability of this food source. The mean values of detritus ingested and the OM content of each component for the 21 individuals are shown in Table 1. The 20 g given to the animals contained, on average, 0.95 ± 0.23 g of OM (4.70 ± 1.15% of total detritus added). The UFD contained an average of 0.27 ± 0.13 g of OM (29.38 ± 12.39% of total OM). This UFDOM was unfiltered and therefore unavailable to the fan mussels. It is important to note that if the weight of the UFD and the OM were directly proportional, the UFD should have contained 63.65% of total OM added. The reduced UFDOM content most probably indicates early decantation of the densest OM deprived fraction of detritus. The BOM was 0.20 ± 0.08 g (32.66 ± 14.95% of total OM supplied minus UFDOM), indicating that fan mussels retained 0.47 ± 0.25 g of FOM (47.50 ± 11.23% of total OM supplied minus UFDOM). The Pearson correlation does not show sufficient significance between the size of the fan mussel and RDOM ($F_{(1,19)} = 0.184$, $P > 0.05$); therefore, retention of OM was independent of shell size. However, it seems that the largest individuals tend to show higher RDOM values than smaller ones (Fig. 2b). There was a significant negative correlation between fan mussel size and FD (i.e. B + RD) ($F_{(1,19)} = -0.686$, $P < 0.05$) (Fig. 2a) following the ratios: small > medium > large. There was no significant correlation between animal size and B production ($F_{(1,19)} = -0.443$, $P > 0.05$), between animal size and BOM ($F_{(1,19)} = -0.300$, $P > 0.05$) and between the quantity of FOM (i.e. BOM + RDOM) and size of individual ($F_{(1,19)} = 0.101$, $P > 0.05$).

Discussion

This study reveals that muddy detritus is quickly accepted and easily ingested by *P. nobilis* and that nearly half of the ingested OM contained in the detritus is retained or metabolised by the bivalve. In agreement with the observations of Davenport *et al.* (2011) and Najdek *et al.* (2013), we also found a significant decrease in FD with increasing shell size following the ratios: small > medium > large. Najdek *et al*. (2013) also indicated that smaller individuals were clearly associated with a detrital food chain, probably as a consequence of the closer distance to the substrate, and that animals changed progressively to a more selective diet with increasing size and distance from the bottom. In our study, fan mussels were kept out of the substrate and exposed to identical conditions of suspended detritus, thus confirming the positive preference for detritus by smaller individuals but irrespective of their distance from the substrate. This supports the hypothesis of a lower specificity in the selection of food source by small *P. nobilis* vs. large ones, which has already been suggested by Davenport *et al.* (2011).

Part of the biodeposits corresponded to material that had been processed by the animal and followed a quick digestion. The formation of pseudofaeces implies that fan mussels sort and discard some of the captured particles before ingestion. This undesired material is expelled through the rejection channels, unique to Pinnidae (Czihak & Dierl, 1961). After 8 hours of experiment some detritus was retained and either metabolized or subjected to longer digestion (4.76 ± 0.91 g, e.g. 65.42 ± 8.65% of

Table 1. Individual balance of material administered in the detritus feeding experiments. The different fractions observed in the process and their respective organic matter (OM) content are expresed in grams (g) and percentage (%) with respect to the total added. (B) biodeposits (faeces and pseudofaeces). (FD) filtered detritus is the sum of biodeposits + retained detritus (B + RD). (RD) retained detritus after 8 hours. (D) detritus added. (UFD) unfiltered detritus.

	INPUTS					OUTPUTS										RETAINED			
	D	DOM		FD		FOM	B	BOM		UFD	UFDOM		RD			RDOM			
Individual	**(g)**	**(g)**	**(%)**	**(g)**	**(%)**	**(g)**	**(%)**	**(g)**	**(%)a**	**(g)**	**(%)**	**a**	**(g)**		**(%)**	**(g)**	**(%)**	**(g)**	**(%)a**
12/000	20.00	0.81	4.05	6.64	33.20	0.68	83.95	2.38	35.84	0.24	35.29	13.36	66.80	0.13	16.05	4.26	64.16	0.44	54.32
12/001	20.00	0.79	3.95	6.50	32.50	0.55	69.62	1.95	30.00	0.17	30.91	13.51	67.50	0.24	30.38	4.55	70.00	0.38	48.10
12/002	20.00	0.92	4.60	5.60	28.00	0.55	59.78	2.10	37.50	0.12	21.82	14.41	72.00	0.37	40.65	3.50	62.50	0.43	46.74
12/003	20.00	1.66	8.30	6.10	30.50	1.35	81.33	2.34	38.36	0.14	10.37	13.93	69.50	0.30	18.67	3.76	61.64	1.21	72.89
12/004	20.00	1.26	6.30	6.20	31.00	1.12	88.89	2.02	32.58	0.11	9.82	13.85	69.00	0.14	11.11	4.18	67.42	1.01	80.16
12/005	20.00	0.95	4.75	7.00	35.00	0.77	81.05	2.42	34.57	0.27	35.06	13.05	65.00	0.18	18.95	4.58	65.43	0.5	52.63
12/006	20.00	0.78	3.90	7.10	35.50	0.43	55.13	2.01	28.31	0.16	37.21	12.93	64.50	0.35	44.87	5.09	71.69	0.27	34.62
12/007	20.00	1.18	5.90	8.00	40.00	0.79	66.95	2.42	30.25	0.11	13.92	12.05	60.00	0.39	33.05	5.58	69.75	0.68	57.63
12/008	20.00	1.00	5.00	8.60	43.00	0.58	58.00	2.43	28.26	0.07	12.07	11.45	57.00	0.42	42.00	6.17	71.74	0.51	51.00
12/009	20.00	1.20	6.00	6.40	32.00	0.55	45.83	1.68	26.25	0.15	27.27	13.62	68.00	0.65	54.17	4.72	73.75	0.4	33.33
12/010	20.00	0.90	4.50	7.70	38.50	0.5	55.56	3.17	41.17	0.17	34.00	12.32	61.50	0.40	44.44	4.53	58.83	0.33	36.67
12/011	20.00	0.85	4.25	7.60	38.00	0.44	51.76	2.33	30.66	0.14	31.82	12.43	62.00	0.41	48.24	5.27	69.34	0.3	35.29
12/013	20.00	1.05	5.25	7.90	39.50	0.79	75.24	2.23	28.23	0.24	30.38	12.13	60.50	0.26	24.76	5.67	71.77	0.55	52.38
12/014	20.00	0.95	4.75	8.80	44.00	0.72	75.79	3.13	35.57	0.24	33.33	11.24	56.00	0.23	24.21	5.67	64.43	0.48	50.53
12/015	20.00	0.80	4.00	7.20	36.00	0.59	73.75	3.75	52.08	0.28	47.46	12.84	64.00	0.21	26.25	3.45	47.92	0.31	38.75
12/016	20.00	0.74	3.70	8.40	42.00	0.53	71.62	1.99	23.69	0.18	33.96	11.60	58.00	0.21	28.38	6.41	76.31	0.35	47.30
12/025	20.00	0.61	3.05	7.10	35.50	0.42	68.85	3.58	50.42	0.31	73.81	12.92	64.50	0.19	31.15	3.52	49.58	0.11	18.03
12/026	20.00	0.76	3.80	7.50	37.50	0.54	71.05	1.24	16.53	0.25	46.30	12.54	62.50	0.22	28.95	6.26	83.47	0.29	38.16
12/027	20.00	0.85	4.25	8.00	40.00	0.65	76.47	3.15	39.38	0.31	47.69	12.01	60.00	0.20	23.53	4.85	60.63	0.34	40.00
12/028	20.00	0.98	4.90	7.40	37.00	0.83	84.69	3.04	41.08	0.24	28.92	12.65	63.00	0.15	15.31	4.36	58.92	0.59	60.20
12/029	20.00	0.84	4.20	7.60	38.00	0.74	88.10	3.44	45.26	0.33	44.59	12.43	62.00	0.10	11.90	4.16	54.74	0.41	48.81
Average	20.00	0.95	4.70	7.30	35.36	0.67	70.63	2.51	34.57	0.20	32.66	12.73	63.49	0.27	29.38	4.76	65.42	0.47	47.50
(±SD)	±0.00	±0.23	±1.15	±0.85	±4.3	±0.23	±12.38	0.66	±8.65	±0.08	±14.95	±0.85	±4.26	±0.13	±12.39	±0.91	±8.65	±0.25	±11.23

(a) Values are calculated with respect to filtered detritus (FD).

FD). This observation indicates that there is a complex process of particle selection and digestion in *P. nobilis* and that total excretion could need more than 8 h. Brillant & MacDonald (2000) observed that part of the ingested material in *Placopecten magellanicus* could be subjected to a long intracellular digestion. Bayne *et al*. (1989) described a variation of gut passage time and filtration rates in *Mytilus edulis* as a strategy to achieve constant absorption efficiencies under different food concentrations. In this species, the finest particles of ingested food are stored in stomach diverticular folds for further digestion (Widdows *et al.,* 1979). Accordingly, Decho & Luoma (1991) suggested that different digestion processes with different absorption capabilities may be considered as a strategy to obtain better absorption efficiencies. A similar mechanism of digestion could be occurring in *P. nobilis*, thus retaining part of the filtered detritus more than 8 h to improve absorption efficiencies of OM. Future experiments with this species could include animals unfed for several days before adding the detritus doses and the collection of material excreted for several days after food input.

There is evidence that muddy detritus represents the major OM source for *P. nobilis* whereas phyto- and zooplankton would provide the necessary complements for a healthy diet. As postulated by Davenport *et al.* (2011) and subsequently confirmed by Nadjek *et al.* (2013), *P. nobilis* ingests and assimilates predominantly detritus in its diet, although the species also ingests much higher quality items such as phyto- and zooplankton. These provide the necessary mono- and polyunsaturated fatty acids (MUFA and PUFA, respectively) (Nadjek *et al.*, 2013). Our results confirm high utilisation of OM from muddy detritus by *P. nobilis*; not only was the detritus quickly ingested, but also 47.50 ± 11.23% of FOM was retained. The variation of food production in natural environments during the year (Souchu *et al.,* 2001) may also affect the ingestion of one specific source. Thus, *P. nobilis* could feed almost exclusively on OM from muddy detritus during some seasons typically poor in phytoplankton in the Mediterranean Sea (e.g. during winter). In any case, the capability to obtain most OM from muddy detritus could be the explanation of *P. nobilis* achieving one of the fastest growths in all bivalves. Sediments and detritus have been found to play an important role in the diet of other bivalves. River fine sediment supplemented to the diet of juveniles of freshwater bivalves *Villosa iris* and *Pyganodon grandis* increased their growth two-fold in 45 days, compared to those fed only on a microalgae diet (Gatenby *et al.*, 1996). Muddy detritus, on the other hand, is a supplement or alternative food source for the tropical bivalve *Anadara* spp. to support its metabolic requirements in mangrove-coral associated ecosystems (Buhadi *et al.,* 2013).

The fraction of detritus that *P. nobilis* filtrated had proportionally more OM per weight of detritus than total detritus: FOM contained 0.67 ± 0.23 g, N = 21 of OM (70.63 ± 12.38% of total OM minus UFDOM). As a consequence, OM in UFD was diluted. It should have been 63.65% of total OM supplied with detritus. However, UFDOM was 29.38 ± 12.39%, N = 21 of total OM. The UFD was mostly formed by the largest and densest fraction of detritus, which precipitated earlier than the rest. Fine particles were suspended in the water column for a longer time thus facilitating filtration by *P. nobilis*. These particles tend to contain more OM than larger and denser ones (Karickhoff *et al.,* 1979; Decho & Luoma, 1991). Therefore, the low OM content of UFD (0.27 ± 0.13 g of total OM) could be explained by the relation between particle size and OM concentration. In laboratory conditions, this selection process by gravity could be used to concentrate OM from detritus without the necessity of filtering an excess of material smaller than 200 µm. Almost one half of the FOM was retained by *P. nobilis* when a single dose was provided. If more feedings are given during the day, the OM input could also be increased for more energetic diets. Considering that the FOM and the BOM are independent of shell size, the increase of OM in the diet with muddy detritus could be regulated according to the production of B and similar doses could be given irrespective of shell size. This could constitute an advantage by avoiding the necessity to prepare different diets according to individual size. However, experiments with more individuals grouped by size categories should be made to better understand the utilization of muddy detritus and its OM at each size. Additionally, costs derived from phytoplankton production could be reduced in *P. nobilis* hatcheries using detritus supplements. On the other hand, this would better emulate the common food sources of fan mussels in coastal regions (Butler *et al.,* 1993; Kennedy *et al.,* 2001; Davenport *et al.,* 2011; Najdek *et al.,* 2013).

Considering the environmental implications of detritus feeding in natural conditions, a dense population of *P. nobilis* could contribute to maintaining clear waters and recycle OM of resuspended detritus. This would constitute an additional value for the relationship between *P. nobilis* and *Posidonia oceanica* meadows, where the bivalve usually inhabits (Garcia-March, 2003). In this regard, it has been estimated that some populations of bivalves may filter up to 100% of the water column in a single day (Strayer *et al.*, 1999) and oysters able to reach rates of filtration of $22 \cdot 10^5$ $L \cdot h^{-1}$ in populations with a density of 157.6 individuals/m^2 (zu Ermgassen *et al.*, 2013). These high filtering rates allow bivalves to graze on most of the phytoplankton production in coastal and estuarine ecosystems (Greene *et al.*, 2011; Petersen *et al.*, 2012). Similarly, *P. nobilis* populations could contribute to maintain healthy environments by reducing the quantity of suspended particulate matter and OM content of sediments.

We are carrying out complementary studies in order to understand the specific parameters determining the fan mussel energy balance, and study the biochemical composition of the rations provided and material excreted. These experiments will increase knowledge about the

nutritional needs of *P. nobilis* and thereby could be used for the establishment of hatcheries of this endangered species. Moreover, in terms of commercial production, this information could be useful and thus be extended to the management of other filter feeders in order to reduce phytoplankton production costs. The costs of food supply may be considerably reduced if part of the microalgae diet is substituted by muddy detritus with high OM richness.

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