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Efficiency of particle retention and clearance rate in the polychaete *Sabellaria alveolata* L.

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Abstract

The development of *Sabellaria alveolata*, a gregarious reef-building polychaete species, is maximal in Mont-Saint-Michel Bay (France), where trophic capacity is now threatened by increasing shellfish farming. As no data are available concerning the ecophysiological response of this species, the purpose of the present study was to obtain clearance rate and retention efficiency values to provide a first order of magnitude for the trophic role of this species. Data were obtained using a flow-through system with novel troughs suitable for 225 cm^2 reef blocks containing a mean number of 940 ± 102 (S.E.) individuals. The experimental diet used consisted of a mixture of two live microalgae, *Skeletonema costatum* (3800 cell ml^{-1}) and *Isochrysis galbana* (23 700 cell ml^{-1}), chosen to cover a broad size range (2 to 16 µm equivalent spherical diameter, ESD), as determined by a particle counter. On the basis of a mean clearance rate of 0.7 $l\,h^{-1}$ obtained with reef blocks, the mean rate for an individual was estimated at 7.5×10^{-4} $L\,h^{-1}$. Particles larger than 6 µm ESD were cleared with 100% efficiency, but *S. alveolata* was unable to retain particles smaller than 2 µm ESD. The results are compared with data obtained for other polychaete species, and clearance rate values are extrapolated to an entire reef. ***To cite this article: S. Dubois et al., C. R. Biologies 326 (2003).***

Résumé

Efficacité de rétention de particules et valeurs de filtration chez le polychète *Sabellaria alveolata* L. *Sabellaria alveolata* est un annélide polychète grégaire qui construit des formations récifales dont l'extension est maximale en baie du Mont-Saint-Michel (France) où la capacité trophique du milieu se pose aujourd'hui face au développement de la conchyliculture. A ce jour, aucune étude ne traite de l'écophysiologie de cette espèce. Le but de ce travail est d'obtenir les premières valeurs de filtration et d'efficacité de rétention chez cet organisme afin de fournir un premier ordre de grandeur de l'impact trophique de ces formations récifales. Les données ont été obtenues à partir d'un système en circuit ouvert contenant des enceintes expérimentales spécialement adaptées pour recevoir des portions de récif de 225 cm^2 contenant 940 ± 102 (S.E.) individus. Le régime alimentaire des organismes se composait de deux microalgues vivantes, *Skeletonema costatum* (3800 cellules ml^{-1}) et *Isochrysis galbana* (23 700 cellules ml^{-1}), choisies pour couvrir un large spectre de taille (de 2 à 16 µm, diamètre sphérique équivalent, DSE) déterminé par un compteur à particules. A partir d'une filtration moyenne de 0.7 $l\,h^{-1}$ obtenue sur une portion

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récifale, une filtration moyenne individuelle peut être calculée à 7.5×10^{-4} l h^{-1}. Les particules supérieures à 6 µm (DSE) sont retenues avec une efficacité de 100%, mais *S. alveolata* n'est pas capable de retenir celles inférieures à 2 µm (DSE). Les résultats sont comparés avec les données existant chez les polychètes et les valeurs de filtration extrapolée à l'ensemble d'un récif. ***Pour citer cet article : S. Dubois et al., C. R. Biologies 326 (2003).***

Keywords: Sabellaria alveolata; polychaete; clearance rate; retention efficiency; reef

Mots-clés : Sabellaria alveolata ; polychète ; filtration ; efficacité de rétention ; récif

1. Introduction

Polychaetes of the family *Sabellariidae* build structures, qualified as reefs, which can extend over several hectares. These reefs are known worldwide for their biodiversity. Their associated fauna has been studied on the coasts of India [1], South America [2], Spain and Portugal [3], and western America [4]. With respect to French coasts, Gruet [5–7] and more recently Dubois [8] have provided in-depth analysis of the associated fauna of *Sabellaria alveolata* reefs. This species is common along European coasts, occurring from Cornwall (Great Britain) [9,10] to the south of Morocco [11]. It builds structures of two major types: small sheet-like reefs adhering to rocks on the upper level of the intertidal zone and extensive formations of several hectares located on sand flats lower down in the intertidal zone. The latter, which are much less common, have developed most in two areas along the French coast: south of Noirmoutier Island (47°00N, 02°10W [6]) and in Mont-Saint-Michel Bay (48°40N, 01°40W [11]).

Concerning the ecological role of *Sabellaria* reefs, their function as a habitat has been most often studied (see the references cited above for associated fauna). The influence of these reefs on sedimentary processes has also been considered [12]. However, their trophic role within the ecosystem has never been quantified. Mont-Saint-Michel Bay possesses the largest *S. alveolata* reef in Europe [7], covering a surface area of ca 100 hectares, with polychaete densities of up to 60 000 worms m^{-2} [8]. No data are currently available concerning the ecophysiological responses of this species, which are of primary importance for assessment of food uptake in Mont-Saint-Michel Bay, where trophic capacity is threatened by increasing shellfish farming (oysters and mussels).

Studies of polychaete feeding are rare compared to those performed for molluscs, especially with regard to quantitative aspects of filter-feeding. Subsequent to the work of Jorgensen [13], Dales [14] provided some quantitative data on the filtering process in Sabellid and Serpulid worms. Since then, several studies have been carried out in polychaete families with suspension feeding activity, such as *Sabellidae* [15, 16], *Serpulidae* [17,18] and *Terebellidae* [19–21]. To our knowledge, the only study performed for *Sabellariidae* is that of Wells [22] concerning *Sabellaria kaiparaensis*, a species restricted to the New Zealand coast. Thus, basic data about feeding processes are still lacking, despite the fact that species of this family such as *S. vulgaris* on American coasts or *S. alveolata* on European coasts are very common.

The purpose of this study was to obtain clearance rate and retention efficiency values for *S. alveolata* in order to provide basic data concerning the trophic role of this gregarious species. The methodology to record ecophysiological responses was derived from flow-through systems used for suspension-feeding bivalves. This study is part of a larger project ('Programme national d'environnement côtier') designed to investigate the respective roles of the main primary consumers (cultivated species and wild biota) on phytoplankton and resuspended microphytobenthos in Mont-Saint-Michel Bay.

2. Materials and methods

2.1. *Sampling and conditioning of* Sabellaria alveolata

Samples were obtained from the Champeaux reef located in the eastern part of Mont-Saint-Michel Bay (Figs. 1, 2A and B). Blocks were extracted using

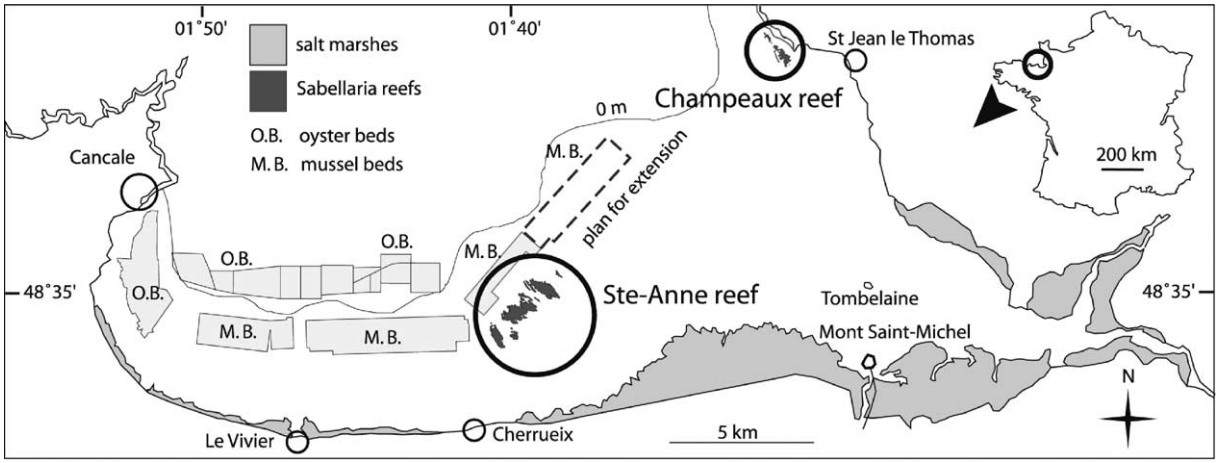

Fig. 1. Mont-Saint-Michel Bay and location of *S. alveolata* reefs.

a 225-cm^2 metal corer 15 × 15-cm wide (Fig. 2C). The core depth chosen represents the thickness of the living part of the reef. Gruet [6] has shown that this part is about 15-cm wide, equivalent to the distance between the aperture of the tube occupied by the worm when filtering or building and the layer to which it can withdraw during low tide or periods of stress. Thus, the reef is dead below the first 15 first centimetres, consisting of mud-filled tubes used by the worms as a support. If core depth had been less than 15 cm, too many individuals would have been injured. Five samples were extracted in the same area to maintain a similar hydrodynamic environment, and from the same reef stages (platforms), according to the definitions provided by Gruet [5,7].

Samples were carefully washed in seawater and placed in an aquarium containing natural seawater with a flow-through system at a constant temperature (15 °C). Individuals were acclimated for two weeks and fed live algal cultures of *Skeletonema costatum* and *Isochrysis galbana* three days before the start of the experiment. These microalgae were chosen to cover a broad size range (2 to 16 µm, Equivalent Spherical Diameter, ESD) as determined by a particle counter. During the acclimation period, dead individuals were easily detected and carefully removed. In the course of experiment, no mortality had been noticed.

Platform stages generally have a very low abundance of other species associated with *S. alveolata* [8]. However, to avoid disturbances, some rare juveniles of the mollusc *Venerupis saxatilis* within micro-crevices and individuals of nemertean *Lineus* sp. or polychaetes such as *Perinereis cultrifera* and *Eulalia ornata* were extracted from the reef blocks.

2.2. Experimental equipment

Ten-litre troughs based on those used in studies of *Crassostrea gigas* [23] and *Lanice conchilega* [21] were constructed and adapted to *S. alveolata*. Their size needed to be large enough to receive a perforated removable box (Figs. 2D, 3) containing the 15 × 15 × 15-cm^3 reef core. Once the removable box was inserted into the trough, a 2-l volume flow chamber existed along the upper surface of the reef, with two baffles ensuring laminar flow. The volume of this flow chamber was adjusted to detect significant filtration. Below this flow chamber, the rest of the cored reef remained immersed in seawater and without connection with the upper circulating water (Fig. 3).

This experimental set-up functioned like the flow-through system described by Palmer and Williams [24] for suspension-feeding bivalves. It consisted of five troughs connected in parallel and containing living individuals plus a control consisting of a reef block without polychaetes or associated fauna. The control was obtained by drying a reef core at 60 °C for 3 days and then leaving it at ambient temperature for a week, with regular washing with seawater. The six troughs received seawater filtered onto 0.45-µm Millipore R.A. filters and mixed in a 200-l tank with an experimental diet composed of *I. galbana* and *S. costatum*. These

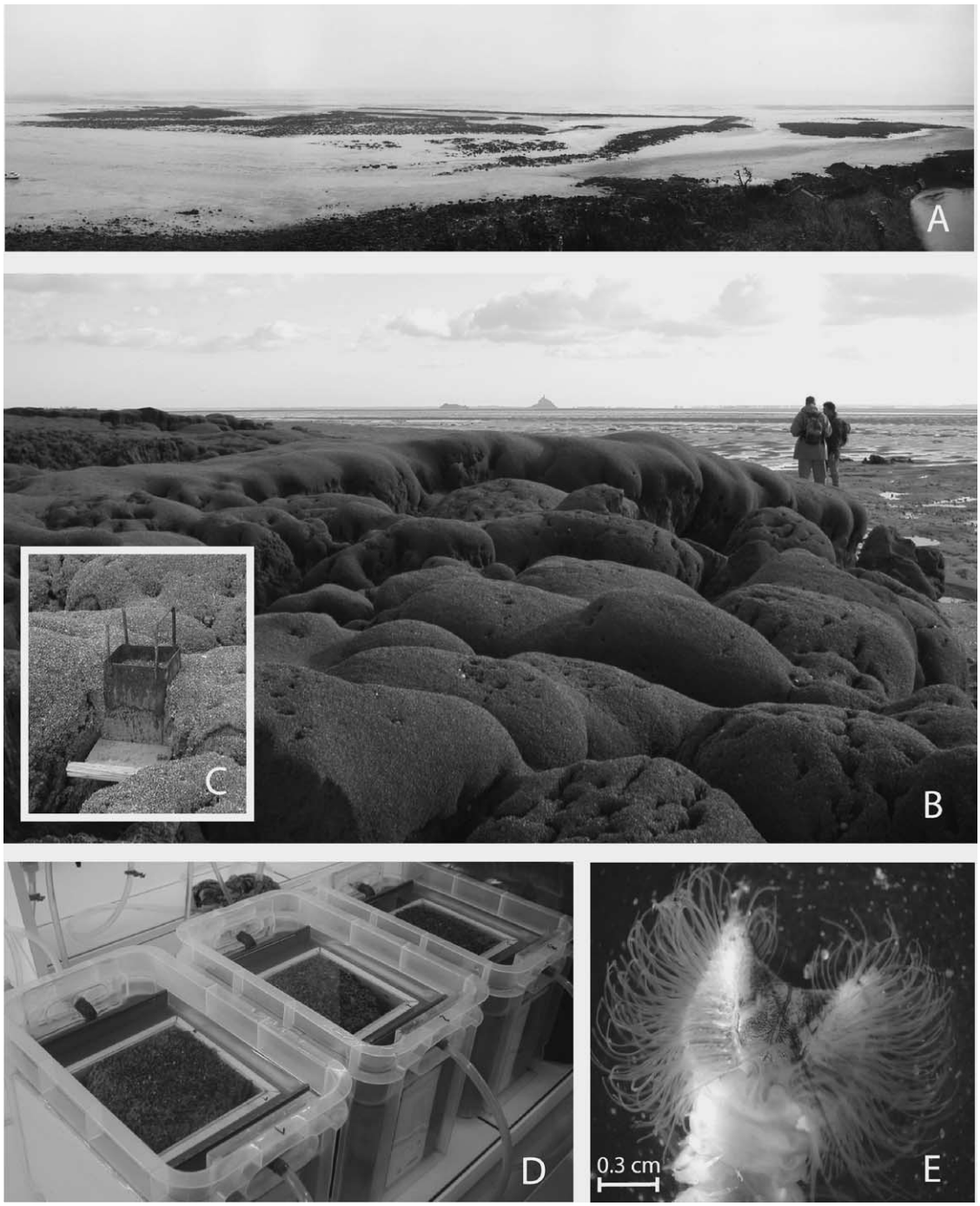

Fig. 2. (**A**) General view of the reef formation at Champeaux (Normandy, France). (**B**) Part of the reef showing coalescent ball-shaped structures and platform stages. (**C**) Corer in the reef. (**D**) Troughs containing reef blocks. (**E**) Ventral view of the cephalic part of *Sabellaria alveolata*, with tentacular filaments in extension.

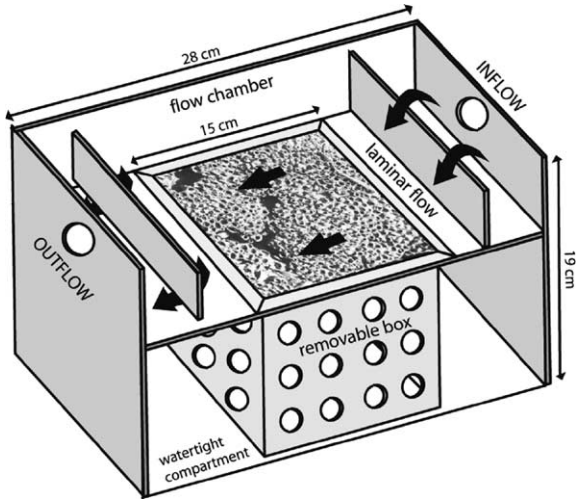

Fig. 3. Details of the experimental troughs containing *Sabellaria* reef blocks. Laminar water flow is shown by black arrows.

species, maintained in the culture collection of the Marine Biology Laboratory of the College of Sciences in Nantes, were grown in a culture room (temperature: 14 °C; photoperiod: L14/D10; light intensity: 100 $\mu\varepsilon\,m^{-2}\,s^{-1}$ with $\mu\varepsilon$ = microEinstein). The diet in the 200-l tank was adjusted to 23 700 cells ml^{-1} (s.d. = 2600; $n = 6$) for *I. galbana* and 3800 cells·ml^{-1} (s.d. = 130; $n = 6$) for *S. costatum* in order to obtain a distinct bimodal size distribution over the 2–16 µm range (ESD). Mean particulate volume per litre of seawater in the 200-l tank was 2.8×10^6 $mm^3\,l^{-1}$ (s.d. = 1×10^6; $n = 6$). Flow speed was adjusted with Gilmont© flow-meters to 2.5 $L\,h^{-1}$ (according to an abacus under 1 atm and 20 °C) to maintain inflow particle concentration 30% higher than at outflow, thereby avoiding recirculation artefacts [25] and abnormal feeding conditions [26].

2.3. Measurements

Polychaetes were placed in troughs one hour prior to any measurements. Five measurements, with an interval of one or two hours, were made during the experiment. Each measurement (at 10 h, 12 h, 13 h, 15 h and 16 h) consisted in water samples collected simultaneously from the six troughs (5 + 1 control). Duration of sampling was about 30 s. Mean values have been calculated using all five troughs. Particle-size distributions were determined with a Multisizer particle counter fitted with a 100-µm aperture. Particle counts were made with coefficients of coincidence < 5%. All particle sizes are expressed as equivalent spherical diameter (ESD). Particle concentrations were estimated for a size range of 2 to 16 µm. Retention efficiencies were computed for this entire size range as: $E_r(\%) = 100 \times [(\text{Inflow} - \text{Outflow})/\text{Inflow}]$, where 'Inflow' represents particle concentration in the control and 'Outflow' particle concentration in the troughs containing the animals. Details about retention efficiency calculations are given in Barillé et al. [23]. Retention efficiency data were then used to avoid underestimation of clearance rate calculations due to small particles cleared from the suspension by polychaetes, but not retained on tentacular filaments (Fig. 2E), and therefore released into troughs. To determine this potential underestimation, three retention ratios (Inflow – Outflow/Inflow) were calculated from particle counter data as the sum of particle concentrations in 2–16 µm, 3–16 µm, 6–16 µm size ranges. The clearance rate was subsequently calculated only for particles above a threshold ensuring that all were cleared with 100% efficiency. Given the mean flow in an individual trough, the clearance rate ($l\,h^{-1}$) was calculated as: [Inflow − Outflow/Inflow] × flow rate.

After experiments, all individuals were killed in 4.5% formaldehyde solution. Tubes were then disintegrated in seawater, and all *S. alveolata* individuals were collected and counted, and their dry meat weight was estimated after 48 h at 65 °C.

2.4. Statistical analysis

One-way ANOVA was used to test for differences in clearance rates. Data were checked for normality and homogeneity of variance. A significant level of $p < 0.05$ was used in all tests.

3. Results

Size spectra obtained with the particle counter and expressed in ESD (Fig. 4A) showed two modes at the inflow of the experimental troughs. The first, at around 4 µm ESD, was due to *I. galbana* (linear length of cells = 5–6 µm), while the second, more dispersed and centred around 10 µm ESD, was due to *S. costatum* (chain length of five cells = 50 µm). In some cases,

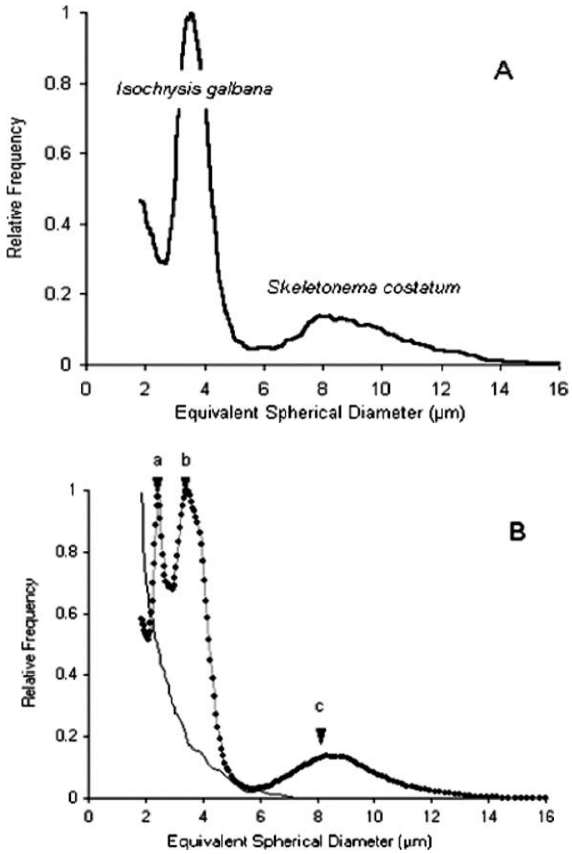

Fig. 4. (**A**) Particle size spectra of the diet. (**B**) Dotted line: size spectra at the outflow of the experimental troughs, showing peaks for *I. galbana* and *S. costatum* (respectively b and c) and a third peak (a) corresponding to an emission of spermatozoa. Full line: size spectra for inorganic particles expelled by individuals during the experiment.

a third peak at 2.5–3 µm ESD appeared for size distributions at the outflow of the experimental troughs (Fig. 4B). Microscopy studies revealed that these particles corresponded to spermatozoa. However, these size distributions could no be used to compute retention efficiencies. A similar phenomenon of even smaller particles at the outflow was recorded in several troughs. Observations of worm activity inside the troughs showed that some individuals expelled particles from the tubes. Size analysis of these particles directly pipetted near the tubes revealed that most were under 4 µm ESD (Fig. 4B), while microscopy studies indicated that they were not a gamete emission. Despite the two-week acclimation period in filtered sea-

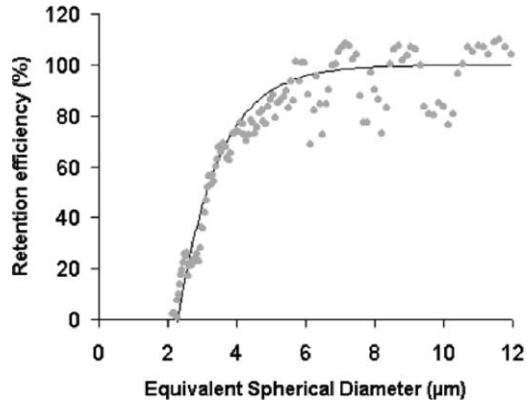

Fig. 5. Retention efficiency of *S. alveolata* for the tested diet.

Table 1
Mean retention ratios of *Sabellaria alveolata* reef blocks based on the sum of all particles counted for three size ranges at five time intervals

	2–16 µm	3–16 µm	6–16 µm
10 h	0.15 (0.06)	0.25 (0.07)	0.34 (0.07)
12 h	−0.10 (0.18)	−0.03 (0.17)	0.30 (0.06)
13 h	−0.04 (0.08)	0.04 (0.07)	0.26 (0.05)
15 h	−0.31 (0.18)	−0.18 (0.15)	0.26 (0.04)
16 h	−0.35 (0.17)	−0.27 (0.18)	0.24 (0.02)

Standards errors are given between parentheses ($n = 5$).

water, it seems likely that worms collected in a turbid area retained small inorganic particles released during the experiment. Each size distribution at the outflow of the troughs was therefore carefully examined prior to retention efficiency calculations.

The retention efficiency curve obtained for the experimental conditions used shows an inflection at around 4 µm ESD (Fig. 5). Below this size, retention efficiencies decrease rapidly, and worms are unable to retain particles smaller than 2 µm ESD. Eighty percent of 4-µm-ESD particles were retained by *S. alveolata*, and all particles larger than 6 µm ESD were cleared with 100% efficiency. The clearance rate calculation was therefore based on particles above 6 µm ESD, as determined by the particle counter, which corresponded to the microalga *S. costatum*. This choice was also supported by calculations of the retention ratios for the three size ranges at the five time intervals (Table 1), which showed that most determinations for the 2–16-µm and 3–16-µm ranges provided negative values related to generation of the particles identified

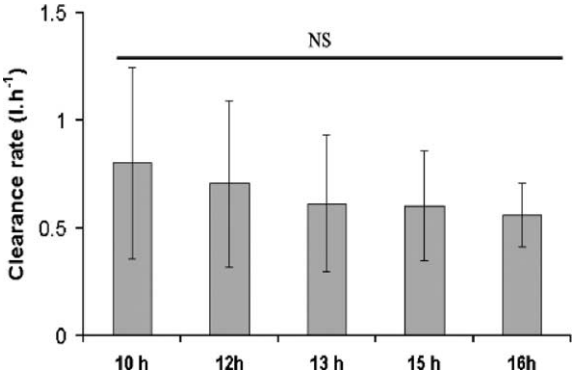

Fig. 6. Mean clearance rates of *S. alveolata* calculated at five time intervals ($n = 5$; 95% confidence intervals are shown).

above. In all cases, mean retention ratios increased from the widest to the narrowest range (6 to 16 µm), while variability decreased.

Comparison of the mean clearance rate (CR) calculated for the five experiments did not reveal any significant statistical differences (Fig. 6, ANOVA, $P < 0.05$), although a regular decrease of variability was observed from 10 to 16 h. A mean clearance rate of 0.7 $\mathrm{l\,h^{-1}}$ (with a 95% confidence interval of 0.41 to 0.72 $\mathrm{l\,h^{-1}}$) was calculated for all data. Since the 225 $\mathrm{cm^2}$ reef blocks used for the experiment contained a mean number of 940 ± 102 (S.E.) individuals (2.74 ± 0.45 $\mathrm{g\,dmw^{-1}}$), the mean clearance rate of an individual was estimated at 0.00075 $\mathrm{l\,h^{-1}}$ (assuming that all the worms were equally filtering).

4. Discussion

This work reports the first retention efficiency and clearance rate data for the polychaete *Sabellaria alveolata*, a gregarious species widely distributed along European coasts. In some shellfish ecosystems, the reef formations built up by this polychaete reach several hectares (e.g., Bourgneuf Bay or Mont-Saint-Michel Bay), but its role in the trophic web has been largely disregarded. Clearance rate data are needed for *S. alveolata* in order to assess the role of this species as a potential trophic competitor with farmed bivalves, especially in Mont-Saint-Michel Bay, where the largest reef formations in Europe are found.

Ecophysiological responses were obtained by applying a methodology derived from a flow-through system used to study suspension feeding in bivalves. The choice of a reef block instead of a single individual was related to technical and biological considerations. Although some adjustments were necessary for the troughs used, the equipment (pump, flowmeter) designed to measure bivalve physiological responses [27] was appropriate to detect response in a reef block. Moreover, responses obtained with a mean number of 940 individuals per block integrated inter-individual behaviours such as proximity or constraint effects (see for example [28,29]). Behavioural responses in gregarious species generally differ for isolated individuals and groups of individuals of the same species, e.g. for mussel beds [30,31] or bryozoans [32]. Thus, it was considered more realistic to obtain clearance rate data for a reef block rather than a single individual, as these data could be used in the context of an ecological study, i.e. in an ecosystem. If it is considered that 0.0225 $\mathrm{m^2}$ of reef (the surface area sampled in this study) has a mean clearance of 0.7 $\mathrm{l\,h^{-1}}$, this value can be extrapolated to filtration for the entire Sainte-Anne reef (Fig. 1). This reef, regarded as the largest *S. alveolata* formation in Europe, is gradually being surrounded by mussel farms. Aerial photographs indicate that this reef area covers 98 ha (Dubois, unpublished data), so that the reef clearance rate should be 30 500 $\mathrm{m^3\,h^{-1}}$. Due to its position on the shore, the mean daily immersion period is about 13 h. During this period, the Sainte-Anne reef filters 396 500 $\mathrm{m^3}$ of seawater. Given a value of around 0.4 $\mathrm{m^3}$ water per square metre per day. The Sainte-Anne reef population clearance rate appears to be well below the rates of ca 100 $\mathrm{m^3\,m^{-2}\,day^{-1}}$ found in dense mussel beds [33]. In the project designed to evaluate the trophic capacity of Mont-Saint-Michel Bay, this simple calculation should be used as an order of magnitude. To assess the impact of *Sabellarian* reefs, comparisons need to be made with the filtration pressure exerted by cultivated species (mussels and oysters), whose stock estimations are currently in progress. And vice versa, it is also possible that the reefs could be endangered by a lack of food for the worms. Obviously, this scale-up calculation must rely on complementary experimental work, particularly studies of the influence of the main environmental factors (temperature, turbidity, food concentration, hydrodynamic) on the ecophysiological responses of these worms.

The mean individual clearance rate of *S. alveolata* determined in this study (0.00075 $L\,h^{-1}$) can be compared with the only results reported for the genus *Sabellaria*, i.e. a rate of 0.018 $L\,h^{-1}$ (25 times higher) found by Wells [22] for the species *S. kaiparaensis*. This author assessed the clearance rate by means of variations in optical density in a closed circulation system using graphite suspension, according to the method proposed by Dales [14]. However, no details are given concerning particle size, temperature or cell concentration. A comparison with Sabellids and Serpulids [14] indicates that the *S. alveolata* clearance rate is much lower than that of larger species such as *Sabella pavonina* (0.073 $l\,h^{-1}$) or *Myxicola infundibulum* (0.28 $l\,h^{-1}$) as well as smaller species such as *Pomatoceros lamarcki* (0.027 $l\,h^{-1}$) or *Hydroides norvegica* (0.011 $l\,h^{-1}$), but close to that of *Spirorbis borealis* (0.00023 $l\,h^{-1}$) or *Salmacina dysteri* (0.00029 $l\,h^{-1}$). Nevertheless, the value determined here for *S. alveolata* is probably underestimated, because of the assumption that all worms were equally active. A recent study of the filtering activity of *Ditrupa arietina* [17] indicates that this Serpulid could spend less than 25% of its time feeding. Therefore, further investigations are needed to assess the number of filtering worms, together with determinations of particle size and concentration analysis.

Ropert and Goulletquer [21], who studied the trophic competition between *Lanice conchilega* (Polychaeta: Terebellidae) and cultivated oysters, obtained worm clearance rates ranging from 0.073 to 0.108 $l\,h^{-1}\,ind^{-1}$ and retention efficiencies starting above 4 µm. Jørgensen et al. [34] found an optimum particle size retention of 3 µm in *Sabella penicillus*, a species characterised by a downstream collecting process [35]. The results obtained in the present study suggest that *S. alveolata* is less efficient than the above-mentioned Sabellid polychaete in retaining small particles. Examination of the structure and ciliation of the feeding organs of *S. alveolata* should help in interpreting these differences (Dubois et al., in preparation). However, *S. alveolata* has a retention efficiency comparable to that of the cultivated oyster *C. gigas* [21,23], which indicates that both species exploit a similar particle-size range. Wild oysters have recently colonised the degraded part of the Sainte-Anne reef, where *S. alveolata* is no longer abundant. In addition to spatial competition, the trophic impact of bivalves on the recolonisation of the reef by *S. alveolata* is a critical development.

Further experiments are needed to elucidate the role of the sabellarian reef in the functioning of Mont-St-Michel Bay in the context of divergent views regarding the worms as competitors for cultivated species or as artisans of historical bioconstructions that are part of national or world heritage.

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