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HAL Id: hal-00131181

https://hal.science/hal-00131181

Submitted on 6 Sep 2021

Comparative study of water-processing in two ciliary filter-feeding polychaetes (*Ditrupa arietina* and *Euchone papillosa*) from two different habitats

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ABSTRACT: A comparative study of feeding rates and structures was made with the 2 ciliary filter-feeding polychaetes *Ditrupa arietina* and *Euchone papillosa* from the Mediterranean Sea (Gulf of Lions, France) and the Gullmarsfjord (Sweden), respectively. The feeding rate (clearance) was measured as the volume of water cleared of 6 μm diameter flagellate cells (*Rhodomonas* sp.) per unit time. Most experiments were conducted at algal concentrations equivalent to about 0.4 to 3.8 μg chlorophyll a l^{-1}. The clearance rates of 'standard' 1.5 mg dry wt *E. papillosa* and 'standard' 3.0 mg dry wt *D. arietina* showed that the maximum weight-specific clearance rate was 114.7 ml h^{-1} mg^{-1} for *E. papillosa* and about 7 times lower, 15.7 ml h^{-1} mg^{-1}, for *D. arietina.* A relative large tentacle crown in *E. papillosa*, resulting in the higher specific clearance rate, may be the evolutionary result of 'minimal scaling' and adaptation to extremely low food concentrations. When the algal concentration was increased from 2000 to 10 000 cells ml^{-1} a 50 % decrease in the clearance rate was observed in *D. arietina*, presumably because the gut capacity was exceeded. A more pronounced tendency to become satiated was found for *E. papillosa*. No tendency to reduce the filter-feeding activity at even very low algal concentrations was noticed in the 2 polychaetes, and the filtering activity of both worms seems to be a basically continuous process. Video-microscope observations of *E. papillosa* showed that suspended algal cells approaching the pinnules suddenly accelerate and move through an arc of over 180° to be delivered on the frontal side of the pinnule. The transfer takes place at a maximum distance (radius) of about 25 μm from the pinnule. Scanning micrographs show the compound lateral cilia to be 20 to 25 μm long in both *D. arietina* and *E. papillosa* and to consist of 1 row of 4 cilia. The feeding current is generated by these compound cilia, which, during their power stroke, catch up with the particles.

KEY WORDS: Suspension-feeding · Filtration rates · Particle-retention mechanism · Adaptation to the environment · Feeding structures

INTRODUCTION

Ciliary filter-feeding occurs in many polychaetes (Fauchald & Jumars 1979, Nielsen 1987). Ciliated tentacle crowns functioning as downstream collecting systems, based on the 'catch-up principle', is characteristic of the families Sabellidae and Serpulidae. Their compound lateral cilia (cirri) generate a feeding current that enters the ciliary region where the same cilia, during their power stroke, catch up with suspended particles and transfer them to a frontal band of separate cilia on the downstream side; the frontal band transports the captured particles towards the mouth

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(Riisgård et al. 2000). Different aspects of filter-feeding in the sabellid polychaete *Sabella pavonina* have been studied during recent years. Jørgensen et al. (1984) determined the particle-retention efficiency; Riisgård & Ivarsson (1990) measured clearance rates; Mayer (1994) measured the particle velocity during the capture phase; and recently Mayer (2000) made a numerical simulation of flow fields and particle trajectories. The particle-capture mechanism and the feeding structures of the serpulid tentacle crown of *Spirorbis tridentatus* has recently been studied by Riisgård et al. (2000). It was found that *S. tridentatus* uses the same basic principle of ciliary 'catch-up' of particles as adopted by the entoproct *Loxosoma pectinaricola* and the cyclophore *Symbion pandora*.

The population density of ciliary filter-feeding polychaetes may be high in some marine areas. Over the last 25 yr the serpulid polychaete *Ditrupa arietina*, which lives in an unattached tusk-shaped, thick and calcareous tube (up to ~3.5 cm long), has become the dominant macrofaunal species on sandy bottoms in the Gulf of Lions (north-western Mediterranean Sea), with adult densities reaching more than 3000 ind. m^{-2} (Grémare et al. 1998b), resulting in a significant contribution of this polychaete to benthic secondary production and calcification (Medernach et al. 2000). The abundance is extremely high for the oligotrophic Mediterranean Sea, which typically has a low biomass but a high diversity of benthic macrofauna (Guille 1971). When the worm (body length ≈ 1 cm) is undisturbed and actively filter-feeding, the tentacle crown (length of tentacles ≈ 0.3 cm) is stretched out of the tube. When the highly sensitive worm becomes disturbed, it withdraws quickly into the tube, which is firmly closed by means of the flattish lens-shaped operculum. To further assess the ecological role of *D. arietina*, knowledge about water-processing and other aspects of the feeding biology is needed (Jordana et al. 2000).

The sabellid *Euchone papillosa* is found on muddy bottoms at depths between 15 and 100 m in the Gullmarsfjord on the Swedish west coast. The abundance varies from a few up to 200 ind. m^{-2}. The worm lives in a thin-walled tube (outer diameter ≈ 1 mm), built of mucoprotein with silt, which penetrates 3 to 8 cm into the sediment and stretches 5 to 7 cm up into the water column. When the worm (body length ≈ 1 cm) is undisturbed and actively filter-feeding the flat or somewhat funnel-shaped tentacle crown (length of tentacles ≈ 0.6 cm) is stretched out of the tube. *E. papillosa* is not amongst the dominant benthic species in the fjord, which is dominated by deposit-feeding animals at 75 m depth (Nilsson & Rosenberg 2000).

The adaptation of filter-feeders to ambient concentrations of suspended food particles is a subject of wide interest, and also current controversy. It is well known

that food availability may affect the pumping activity of many filter-feeding animals, possibly due to both the existence of a 'lower trigger level', below which the animals shut down, and an 'upper satiation concentration', above which the filtration activity is decreased (Riisgård & Larsen 1995, 2000). It is currently being debated whether the filter-pumps of benthic macroinvertebrates are in general adapted for continuous operation at a characteristic high and constant rate adapted to the prevailing ambient phytoplankton concentrations, which implies that the clearance capacity is exploited within a certain range of algal concentrations (Jørgensen 1990, 1996 Clausen & Riisgård 1996), or whether the animals are physiologically regulating their food intake by controlling the filtration rate according to quantity and food value of suspended particles in the water (Hawkins & Bayne 1992, Bayne 1998, but see Riisgård 2001). Seen in this perspective, it is of interest to make a comparative study of water-processing in 2 ciliary filter-feeding polychaetes, the serpulid *Ditrupa arietina* from the Mediterranean Sea and the sabellid *Euchone papillosa* from the Gullmarsfjord, Sweden.

The Gulf of Lions is oligotrophic with low phytoplankton concentrations in the water column (<1 µg chlorophyll *a* l^{-1}) except during a spring bloom of about 2 wk (Jacques 1970). The Liguro-Provençal current restricts the influence of the Rhône River to the continental shelf, resulting in high turbidity. During winter, this trend is amplified by easterly storms enhancing sediment resuspension (Grémare et al. 1997). In the Gulf of Lions, the phytoplankton supply to benthic filter-feeders is in general limited and mixed with inorganic material.

The water of the Gullmarsfjord is stratified, with a brackish surface layer above the halocline at about 15 m and oceanic water (34 psu; 6 to 12°C) below. A spring bloom usually occurs in March with phytoplankton concentrations between 15 and 25 µg chlorophyll *a* l^{-1}. In summer, the chlorophyll *a* (chl *a*) concentrations are around 4 µg l^{-1}, but may increase in the autumn to concentrations similar to that in spring (Lindahl & Hernroth 1988). In 1985 and 1986, the annual organic carbon sedimentation at 60 m depth in the Gullmarsfjord was estimated to be 160 g m^{-2}.

Besides possible adaptations of clearance rates to different environmental conditions, it was of interest to study the basic particle-capture mechanism and to reveal if common trends exist across taxonomic boundaries when relating performances to morphological characteristics such as volume of water being processed per unit of length of the ciliary bands.

The present work deals primarily with feeding rates and structures in *Ditrupa arietina* and *Euchone papillosa* in a comparative study, but video-microscope ob-

servations of the particle-capture process in the latter have also been made. Finally, comparison with other taxonomic groups of ciliary filter-feeding marine animals forms part of this work.

MATERIALS AND METHODS

Collection of polychaetes. Specimens of the sabellid polychaete *Euchone papillosa* (Sars) were collected on 6 March 2000 at 75 m depth in the Gullmarsfjord on the Swedish west coast (58° 22.7' N, 11° 36.3' E) by means of a USNEL spade-corer (700 kg) inside which transparent Plexiglas boxes (47 × 47 cm, height 39 cm) were installed before each deployment. The sediment core with almost intact fauna was brought to the nearby Kristineberg Marine Research Station and placed in an 8°C thermo-constant room, with running seawater (34 psu; 14°C), and kept until the start of the experiments. The number of *E. papillosa* in each box was between 20 and 50.

Specimens of the serpulid polychaete *Ditrupa arietina* (Müller) were dredged during early October 2000 from 20 m depth in the Bay of Banyuls-sur-Mer (Gulf of Lions, northwestern Mediterranean Sea, 38 psu; 17°C). The worms were kept in the laboratory for a couple of days before being packed in sealed plastic bags with seawater and air and taken to Kristineberg Marine Research Station, where all clearance measurements were performed during late October 2000. The worms were kept for several days in running deep ambient seawater (34 psu; 14°C) before being used in clearance experiments.

Clearance measurements. The clearance rate was measured as the volume of water cleared of 6 µm diameter flagellate cells (*Rhodomonas* sp.) per unit time. Algal cells from a fast-growing batch culture were added to a well-mixed aquarium (20 × 19.2 × 9.2 cm) with a known volume of water (*V*) and with a group of filter-feeding worms. Clearance measurements on *Euchone papillosa* were performed with a group of 16 worms placed individually in a glass-tube holder on the bottom of an aerated aquarium (8°C) with seawater and added algal cells. Clearance measurements on *Ditrupa arietina* were performed with a group of 100 worms placed individually in vertical position in holes drilled in a PVC block, which was placed on the bottom of a strongly aerated aquarium (14.5°C).

The reduction in the number of algal cells as a function of time was followed by taking samples (15 ml) every 10 to 15 min and measuring the algal concentration with an electronic particle counter (Elzone model 80 xy fitted with a 76 µm orifice tube). After measurement, the remaining water (about 13 ml) was immediately returned to the experimental aquarium to ensure only an insignificant reduction in the total volume of water. The clearance rate was determined from the exponential reduction in the algal cell concentration. The slope of the estimated regression line describing the natural logarithm (ln) of the algal concentration as a function of time (*t*), as well as the slope of the regression line in a control experiment without worms, were used for estimating the individual clearance rate as: *Cl* (ml h^{-1} ind.$^{-1}$) = (slope of regression line for aquarium with grazing worms – slope of regression line for control aquarium) × *V*(ml) × 60/*n*, where *n* = mean number of actively filter-feeding (tentacle crown extended) worms noted each time a sample was taken during the experiment.

After the experiments, the sizes of individual worms or groups of worms were expressed in several ways: body and crown length were measured within a capillary glass tube held under a stereomicroscope, wet weight (worms taken out of their tubes and adhering water sucked up on paper), dry weight (95°C in a oven, 48 h), and ash-free dry weight (AFDW: 4 h ashing of dry weight samples in a muffle furnace at 500°C). Sample weights were determined on a microbalance (in g to 4 decimal places).

Video observations. The particle-capture process in *Euchone papillosa* was recorded using a video camera (Kappa CF 11/1) attached to a microscope (Nikon with depth of focus of 60 µm at 40× magnification), and a 50 half-frames per second video recorder (Panasonic NV-FS200 HQ). An intact worm in its tube was fixed on the tip of a movable rod (rotational and translational) in a horizontal position about 1 cm from the bottom in a 10 × 10 cm Perspex observation chamber filled with seawater to a level of 2 cm. The chamber was placed on the microscope with the cross-table removed so that the microscope objective could be immersed into the water above the crown, which was illuminated through a thin glass window in the bottom of the chamber. The objective was far enough (6 to 7 mm) from the tentacles to not affect the rate and direction of flows. The seawater in the observation chamber contained 6 µm diameter flagellates (*Rhodomonas* sp.) at a concentration of about 3000 cells ml^{-1}. All observations were made at about 14°C during May 1999 at Kristineberg Marine Research Station. Captures of particles were traced from their position in successive video frames. The movements were followed by mounting a transparent plastic sheet onto the video screen so that the position of suspended particles could be marked with a pen directly on the sheet, frame by frame. Video pictures could also be copied by means of a video graphic printer (Sony UP-860 CE).

Electron microscopy. Specimens used for scanning electron microscopy (SEM) were narcotised with co-
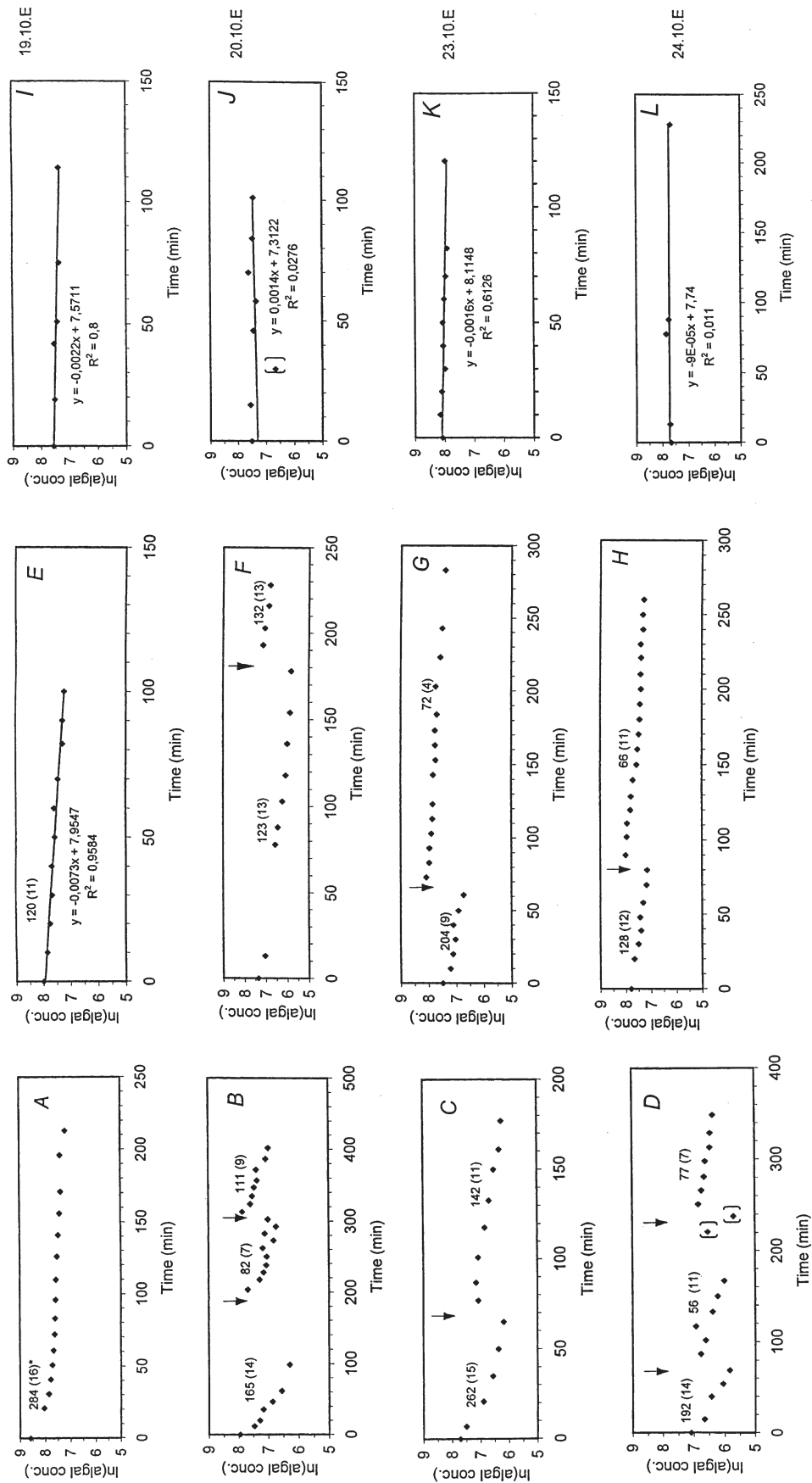
Fig. 1. *Euchone papillosa*. (A–H) Reduction in concentration of algal cells due to grazing by a group of 16 worms in an aerated aquarium. Individual clearance rates estimated on basis of linear slope in semi-log plots (Expts 18.10.E1 to 26.10.E1: see Table 1) are indicated together with number of actively filter-feeding worms (in parentheses). Arrows indicate new additions of algal suspension. The estimated regression line and its equation has been shown in one case (E). The clearance rate in (A) has been estimated on the basis of the 3 first points only. (I–L) Four examples of control experiments without worms

caine or 7.5 % MgCl$_2$ in distilled water, fixed in 1 to 2 % OsO$_4$ in distilled water, dehydrated in an acetone series, and critical-point-dried (Nielsen 1987). Positions and length of the cilia were studied on the micrographs.

RESULTS

The reduction in algal concentration due to grazing by *Euchone papillosa* is shown in Figs. 1 & 2 together with examples of control experiments without worms. Individual clearance rates, estimated on the basis of slope of regression lines, are indicated together with number of active worms. Table 1 gives a summary of the experimental conditions and the measured clearance rates in all experiments performed with *E. papillosa*.

The reduction in algal concentration due to filter-feeding by a group of 100 *Ditrupa arietina*, and due to sedimentation in a control aquarium without worms, is shown in Fig. 3. The individual clearance rates are indicated together with number of actively filter-feeding worms. Table 2 summarises the experimental conditions and the measured clearance rate in all experiments with *D. arietina*, and indicates volume of water in the aquarium, initial and final algal concentration, slope of estimated regression lines, number of algal
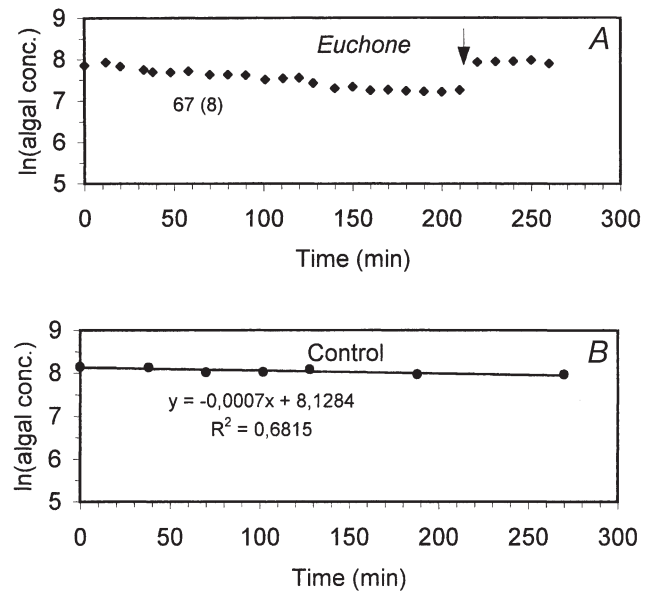

Fig. 2. *Euchone papillosa*. (A) Reduction in concentration of algal cells due to grazing by a group of 8 worms in an aerated aquarium. The individual clearance rate estimated on basis of linear slope in semi-log plot of first period after initial algal addition (Table 1: Expt 26.10.E2) is indicated together with number of actively filter-feeding worms (in parentheses). Arrow indicates new addition of algal suspension. (B) Control experiment without worms

Table 1. *Euchone papillosa*. Summary of clearance experiments with a group of 16 worms (8°C). Volume of water in aquarium, initial and final algal (*Rhodomonas* sp.) concentration, slope of regression line in plot of ln(algal conc.) as a function of time (cf. Figs. 1A–H & 2A), determination coefficient (r^2) and associated probability level (p), slope of regression line in control experiment without worms (cf. Fig. 1I–L), number of algal additions to aquarium during the experiment, number of actively filter-feeding worms (tentacle extended), and individual clearance rate are shown for all experiments; 95 % confidence intervals (CI) for clearance rates (computed on the basis of confidence limits of the slope of the semilogarithmic regression models linking algal concentration and time in each experiments) are indicated in parentheses; ns: slope not statistically different from zero (p >0.05)

| Expt (Fig.)	Vol. (ml)	Initial concentration (cells ml^{-1})	Final concentration (cells ml^{-1})	r^2	p	Slope of regression line	Slope control	Algal addition	Active worms	Clearance rate (95 % CI) (ml h^{-1} ind.$^{-1}$)
18.10.E1 (Fig. 1A)	3078	5410	1320	0.994	0.048	−0.0241[a]	No control	1	16	284 (13–555)
19.10.E1 (Fig. 1B)	2685	2810	545	0.928	<0.001	−0.0161	−0.00218	1	14	165 (104–226)
		2180	1100	0.598	0.009	−0.0061		2	7	82 (0–167)
		2595	1080	0.925	<0.001	−0.0087		3	9	111 (69–154)
20.10.E1 (Fig. 1C)	2685	2250	480	0.941	0.001	−0.0241	ns	1	15	262 (171–353)
		1180	520	0.959	<0.001	−0.0096		2	11	142 (113–171)
21.10.E1 (Fig. 1D)	2907	1210	345	0.971	0.002	−0.0173	−0.00165	1	14	192 (125–260)
		875	300	0.502	0.049	−0.0053		2	11	56 (0–136)
		930	580	0.971	<0.001	−0.0048		3	7	77 (54–100)
23.10.E1 (Fig. 1E)	3076	3010	1820	0.958	<0.001	−0.0073	−0.00162	1	11	93 (74–112)
24.19.E1 (Fig. 1F)	3076	1590	340	0.967	<0.001	−0.0089	ns	1	13	123 (101–145)
		1240	890	0.974	0.013	−0.0095		2	13	132 (48–216)
25.10.E1 (Fig. 1G)	3196	1810	840	0.878	0.002	−0.0103	−0.00115	1	9	204 (105–302)
		3230	1660	0.955	<0.001	−0.0028		2	4	72 (56–88)
26.10.E1 (Fig. 1H)	3197	2455	1280	0.965	<0.001	−0.0084	−0.00066	1	12	128 (102–154)
		3000	1450	0.904	<0.001	−0.0043		2	11	66 (53–80)
26.10.E2 (Fig. 2)	3320	2570	1430	0.948	<0.001	−0.0034	−0.00066	1	8	67 (58–76)

[a]First 3 points in Fig. 1A
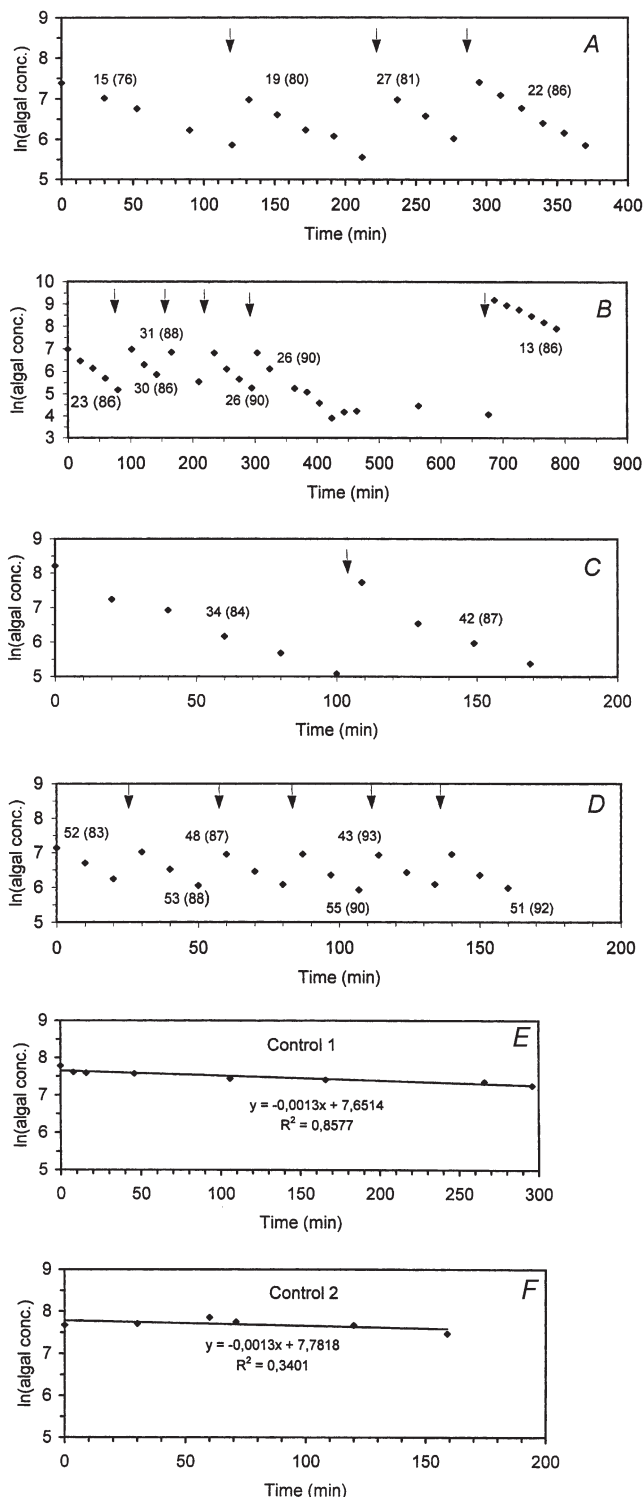
Fig. 3. *Ditrupa arietina*. (A–D) Reduction in concentration of algal cells due to grazing by a group of 100 worms in an aerated aquarium. Individual clearance rates estimated on basis of linear slope in semi-log plots (Expts 20.10.D to 24.10.D: see Table 2) are indicated together with number of actively (crown tentacle extended) filter-feeding worms (in parentheses). Arrows indicate new additions of algal suspension. (E,F) Examples of control experiments without worms

additions, and mean number of actively filter-feeding worms during each experiment.

Table 3 compares the tentacle crown parameters described in Fig. 4 and the clearance rates of *Euchone papillosa* and *Ditrupa arietina*. The clearance rate of a 'standard' 1.5 mg dry wt *E. papillosa* is shown both as the mean of all measurements after the first algal addition, and (in parentheses in Table 3) as the mean of all measurements after the second and third algal additions (Table 1); this was done because of a trend to lower rates during an experiment, possibly due to increasing satiation. The clearance rate of a 'standard' 3.0 mg dry wt *D. arietina* is shown both as the mean of all measurements (except for Expt 21.10.D5, in which the high algal concentration obviously satiated the worms) and (in parentheses) as the mean of all rates measured in the last 2 series (23.10.D and 24.10.D: Table 2); this was done because of a trend to higher rates with increasing acclimation time in the laboratory. It is seen that the clearance rate per centimetre of ciliary band was 0.2 to 0.4 ml h^{-1} cm^{-1} for *E. papillosa* and slightly higher (0.4 to 0.6 ml h^{-1}) cm^{-1} for *D. arietina*. The maximum weight-specific clearance rate was 114.7 ml h^{-1} mg^{-1} for *E. papillosa* and about 7 times lower (15.7 ml h^{-1} mg^{-1}) for *D. arietina*. The body mass and length of the 2 worms are shown in Table 4.

Examples of particle capture by *Euchone papillosa* are shown in Fig. 5. Particles approaching the pinnules with the upstream water suddenly accelerate and move through an arc of over 180° to be delivered on the frontal side of the pinnule and then transported toward the mouth. The velocity component of particle motion in the plane recorded ranged from upstream values of about 0.5 mm s^{-1} (i.e. the particle moved about 10 µm between 2 video frames separated by 1/50 s) to maximum values of 0.8 to 0.9 mm s^{-1} during transfer, to about 0.2 mm s^{-1} during transport on the frontal side of the pinnule. At locations of maximum velocity, particle images were blurred to the extent of about 2 particle diameters. During transfer, particles have a velocity component normal to the plane recorded and, assuming a path forming an angle of 45° with the normal, actual maximum velocities may be 2 times those observed. Fig. 5c shows that transfer takes place at a maximum distance (radius) of about 25 µm from the pinnule. The examples given in Fig. 5 show how particles approaching a pinnule with the upstream water (particles with broken outlines in Fig. 5) come into focus in the microscope, whereupon the particles are caught up by the lateral cilia and transferred to the frontal side of the tentacle.

The scanning micrographs show the compound lateral cilia to be 20 to 25 µm long in both *Ditrupa arietina* and *Euchone papillosa* and to consist of 1 row of 4 cilia (Fig. 6). In *E. papillosa* a series of compound, possibly sensory, cilia were observed just abfrontal to the lateral ciliary band.

Table 2. *Ditrupa arietina*. Summary of clearance experiments with 100 worms (14.5°C). For different series of experiments are indicated volume of water in the aquarium, initial and final algal (*Rhodomonas* sp.) concentration, slope of regression line in plot of ln(algal conc.) as a function of time (cf. Fig. 3A–D), determination coefficient (r^2) and associated probability level (p), regression slope of regression line in control experiments without worms (cf. Fig. 3E,F), number of algal additions made during the experiment, number of actively filter-feeding worms (tentacle crown extended), and individual clearance rate are shown for all experiments. 95% confidence intervals (CI) on clearance rates are indicated in parentheses

Exp. (Fig.)	Volume (ml)	Initial conc. (cells ml^{-1})	Final conc. (cells ml^{-1})	Slope of regression line	r^2	p	Slope control	Algal addition	Active worms	Clearance rate (95% CI) (ml h^{-1} ind.$^{-1}$)
20.10.D (Fig. 3A)	1620	1620	350	−0.0128	0.992	<0.001	−0.0012	1	76	15 (14–16)
		1070	260	−0.0168	0.999	<0.001		2	80	19 (14–24)
		1070	415	−0.0238	0.999	0.012		3	81	27 (0–63)
		1640	350	−0.0206	0.998	<0.001		4	86	22 (20–23)
21.10.D (Fig. 3B)	1630	640	180	−0.0219	0.995	<0.001	−0.0016	1	86	23 (20–26)
		1080	350	−0.0281	0.984	0.080		2	86	30 (0–81)
		950	255	−0.0298	0.978			3	88	31
		910	190	−0.0255	0.978	0.011		4	90	26 (13–39)
		920	190	−0.0257	0.981	0.087		5	90	26 (0–75)
		9885	2740	−0.0128	0.996	<0.001		6	86	13 (12–14)
23.10.D (Fig. 3C)	1630	3700	160	−0.0301	0.987	<0.001	−0.0009	1	84	34 (31–43)
		2290	220	−0.0382	0.962	0.019		2	87	42 (18–73)
24.10.D (Fig. 3D)	1760	1260	515	−0.0448	0.999	0.009	−0.0012	1	83	52 (42–61)
		1125	420	−0.0488	0.999	0.015		2	88	53 (36–70)
		1050	440	−0.0436	0.999	0.049		3	87	48 (0–96)
		1960	375	−0.0520	0.990	0.064		4	90	55 (0–128)
		1030	440	−0.0424	0.988	0.069		5	93	43 (0–105)
		1050	400	−0.0488	0.981	0.088		6	92	51 (0–142)

DISCUSSION

Video observations

The paths and velocities of particles indicate that particle velocity accelerates with the water that enters the region swept by the compound lateral cilia, and the particles are then caught up by 1 or possibly more of the compound cilia (Fig. 6) during their power stroke (Fig. 5). This accelerates a particle and rapidly moves it in a curved path to the midline at the frontal side of the pinnule. At this stage of the power stroke, the particle is pushed out of the main water current which moves past the pinnule, and as the compound lateral cilia come to rest so does the particle. Downstream-collecting has been observed in larvae of gastropods, bivalves, polychaetes, and entoprocts and in adult sabellid and serpulid polychaetes, entoprocts, and some rotifers (for reviews see Nielsen 1987 and Riisgård et al. 2000).

Clearance experiments

Some differences and similarities between the 2 ciliary filter-feeding polychaetes *Euchone papillosa* and *Ditrupa arietina* are apparent. The ciliary length-specific clearance rates are very similar, about 0.4 to 0.6 ml h^{-1} cm^{-1} (Table 3).

Table 3. *Euchone papillosa* and *Ditrupa arietina*. Comparison of tentacle crown variables (Fig. 4) and water-processing. Clearance rate of a 'standard' *E. papillosa* is shown both as the mean (± SD) of all measurements after first algal addition, and (in parentheses) as the mean of all measurements after a second and third algal addition (Table 1). Clearance rate of a 'standard' *D. arietina* is shown both as the mean of all measurements (except for Expt 21.10.D5) and (in parentheses) as the mean of all rates measured in the last 2 series, 23.10.D and 24.10.D (Table 2)

| Variable	*Euchone papillosa*	*Ditrupa arietina*
Number of tentacles	18	25
Length of tentacles (mm)	6.9	2.0
Number of pinnules per tentacle	80	68
Length of pinnules (mm)	1.53	0.25
Total length of lateral ciliary band (*L*, cm)	441	85
Temperature (°C)	8	14
Clearance rate of 'standard' worm (*F*, ml h^{-1})	172 ± 71 (92 ± 32)	47 ± 7 (35 ± 13)
Dry weight of 'standard' worm (*W*, mg)	1.5	3.0
Ciliary length-specific clearance rate (*F/L*, ml h^{-1} cm^{-1})	0.4 (0.2)	0.6 (0.4)
Weight-specific clearance rate (*F/W*, ml h^{-1} mg^{-1})	114.7 (61.3)	15.7 (11.7)
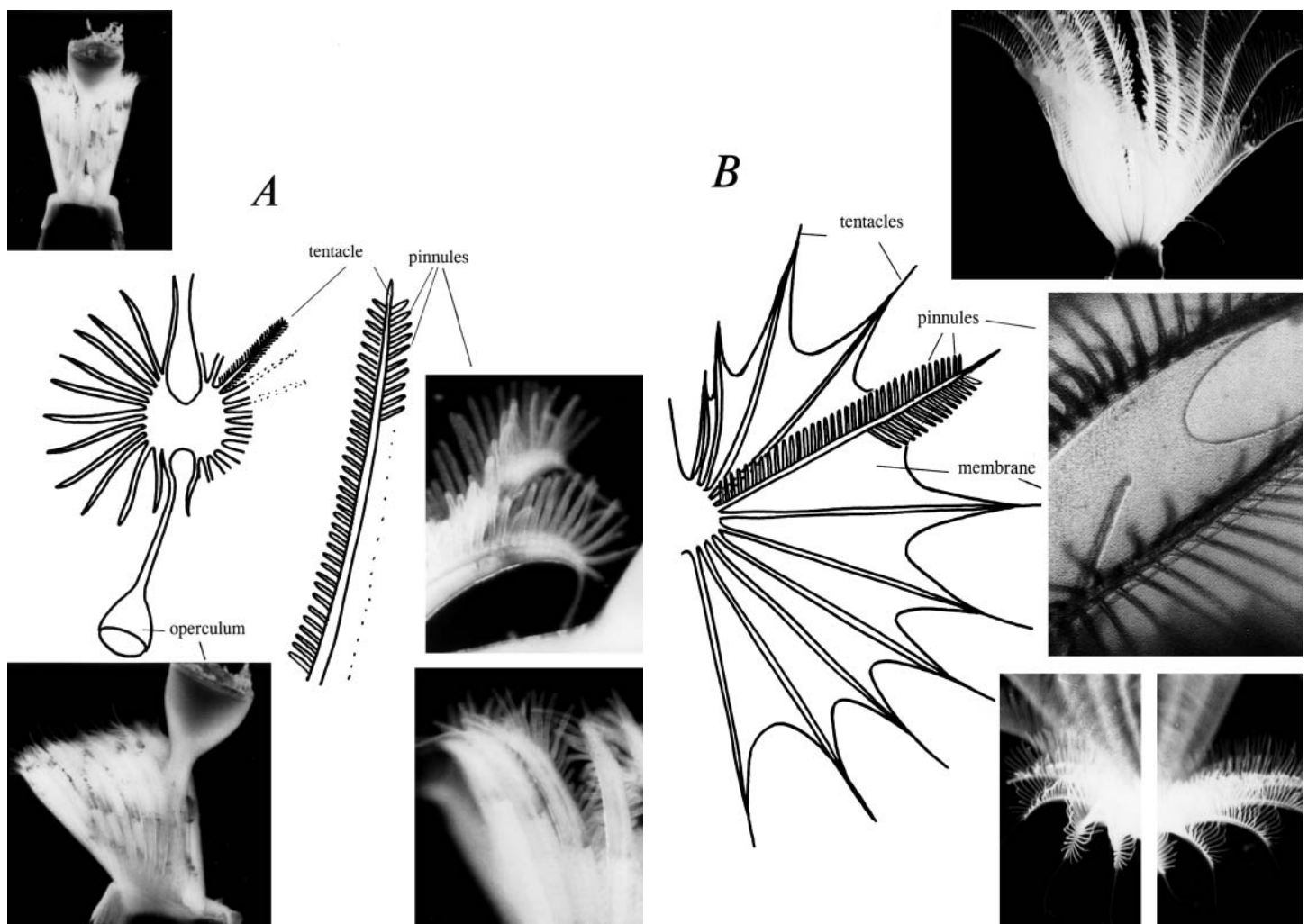
Fig. 4. (A) *Ditrupa arietina*. Video-graph pictures and sketch of serpulid tentacle crown and individual filament with 2 rows of pinnules; mean number of tentacles (length = 2 mm) is 25 (varies between 22 to 28); mean number of pinnules (diameter = 0.025 mm, length = 0.25 mm) on the bi-pinnate tentacles is 68; total length of the ciliary band on each lateral side of the pinnules is estimated at $25 \times 68 \times 0.25 \times 2 = 850$ mm (Table 3). (B) *Euchone papillosa*. Video-graph pictures and sketch of sabellid crown with tentacles and pinnules; the crown, which is webbed with a thin membrane for 2-thirds of its length, consists of 22 filaments, namely 18 bi-pinnate (diameter = 0.637 mm, length = 6.9 mm) with tapered tips, and 4 apinnate; a pinnate filament has 2 rows, each with 40 pinnules; each pinnule (diameter = 26 µm, length = 1.53 mm) has 2 rows of ciliary bands; total length of the water pumping ciliary band is estimated at $18 \times 80 \times 1.53 \times 2 = 4406$ mm (Table 3)

Because cilia are cell organelles that may be expected to have some basic characteristics in common across taxonomic boundaries, a comparison of the existing knowledge seems appropriate (Table 5). The volume of water cleared by a ciliary filter-feeder is determined by the beat frequency, the width, the length of the cilia, and the distance between neighbouring cilia. It is interesting to note that the lateral cilia, which pump water through some kind of a filter (e.g. mucus net in ascidians and lancelets, ciliary sieve in bryozoans, cirri trap in mussels: Larsen & Riisgård 1995, 2000, Riisgård et al. 2000), have comparable water-processing performances, usually in the range of 0.3 to 0.6 ml h^{-1} cm^{-1} of ciliary band. Echinoderms (in which the method of sus-

pension-feeding by ciliated bands is not yet fully understood: Hart 1991) and veliger larvae and polychaetes (both with water-pumping and particle-capturing compound cilia) also fall within this range of performance. The significance of this remarkable uniformity remains to be explained in deeper detail.

It is striking that the maximum weight-specific clearance rate is about 7 times higher in *Euchone papillosa* than in *Ditrupa arietina* (Table 3). The hypothesis of 'minimal scaling' implies that energy for functions other than pump work can only be justified when that part of the organism responsible for the pumping action is dimensioned for continous feeding (Jørgensen 1975, Clausen & Riisgård 1996, Riisgård &

Goldson 1997, Riisgård & Larsen 2000). Therefore, the relatively large tentacle crown in *E. papillosa*, resulting in a 7 times higher specific clearance rate, may be the evolutionary result of 'minimal scaling' and adaptation to extremely low food concentrations. The general trend for *E. papillosa* (Table 1), but not *D. arietina* (Table 2), to become satiated after a second algal addition to the experimental aquarium supports this interpretation. Use of high particle concentrations in earlier clearance experiments may explain the generally low values found for filter-feeding polychaetes by other workers (Dales 1957, 1961, Buhr 1976, Klöckner 1978, Shumway et al. 1988, Davies et al. 1989). For example, in a study of *Lanice conchilega*, Buhr (1976) used a *Dunaliella marina* algal concentration of 40 000 cells ml⁻¹, which is more than 10 times above the 'satiation' concentration found for *Sabella pavonina* (Riisgård & Ivarsson 1990) and for *E. papillosa* and *D. arietina* in the present work. Likewise, in a clearance study of the sabellid polychaete *Myxicola infundibulum*, Shumway et al. (1988) used 17 000 to 35 000 algal cells ml⁻¹.

In many marine filter-feeders there is a 'lower threshold' for phytoplankton concentration below which the animals reduce the filtration rate, e.g. mussels close their valves at concentrations below about 0.5 µg chl a l⁻¹ (Riisgård & Randløv 1981, Dolmer 2000a,b); ascidians reduce the water-pumping ciliary activity in the openings of the branchial sac when the phytoplankton concentration is low (Petersen & Riisgård 1992, Petersen et al. 1999), bryozoans shut down (Barnes & Clarke 1994, Riisgård & Goldson 1997), and the facultative filter-feeding *Nereis diversicolor* may switch to surface deposit feeding if the concentration of suspended food particles falls below a certain 'trigger level', (Vedel et al. 1994, Riisgård & Kamermans 2001). No conspicuous tendency to reduce filter-feeding activity at even very low algal concentrations was noticed in the 2 polychaetes studied in the present work - apart from a tendency in *Ditrupa arietina* for an increase in the number of active individuals and in their individual clearance rate during the experimental period (Table 2), a phenomenon which may be ascribed to increasing adaptation to the laboratory conditions. The initial and final algal concentrations used in the clearance experiments appear in Tables 1 & 2. The relationship between chl a concentration (µg chl a l⁻¹) and concentration of *Rhodomonas* sp. (C, ×10³ cells ml⁻¹) was determined by Clausen & Riisgård (1996) as: chl a = 1.25 × C. Most experiments

Table 4. *Euchone papillosa* and *Ditrupa arietina*. Body wet weight, dry weight, ash free dry weight (AFDW), and length of crown tentacles and body (± SD)

	Wet wt (mg)	Dry wt (mg)	AFDW (mg)	Length of tentacles (mm)	Length of body (mm)
Euchone papillosa					
Expt 1 (n = 15)	5.6 ± 3.6	1.7 ± 1.0		6.6 ± 1.1	11.3 ± 3.2
Expt 2 (n = 17)	4.2 ± 3.7	1.5 ± 0.7		5.9 ± 1.3	10.8 ± 2.4
Group (n = 10)	6.4	1.3	1.1		
Group (n = 13)	7.1	1.4	1.2		
Mean ± SD	5.8 ± 1.3	1.5 ± 0.2	1.15	6.3	11.1
Ditrupa arietina					
Group (n = 5)	14.0	3.4	2.1	2.7 ± 0.2	10.7 ± 0.8
Group (n = 15)	13.7	2.5	1.5		
Mean	13.9	3.0	1.8		

in the present work were conducted at algal concentrations equivalent to about 0.4 to 3.8 µg chl a l⁻¹. These concentrations are comparable to phytoplankton biomass in natural waters. Thus, the median value for Danish fjords and coastal waters is 5.1 µg chl a l⁻¹ corresponding to 4000 *Rhodomonas* sp. cells ml⁻¹ (Sand-Jensen et al. 1994). The algal concentrations used in the present work appear to be relatively low compared to those in most coastal temperate waters, but the natural concentrations at the living sites of the 2 polychaetes are more appropriate references.

In the Bay of Banyuls-sur-Mer, chl a concentrations are minimal during summer (i.e. between 0.2 and 0.4 µg l⁻¹) and maximal during the late winter/early spring bloom, when for shorts periods of time they can reach up to 5 µg l⁻¹ (Jacques 1970, Jordana 2000). Chl a concentrations close to the sea bed in the immediate vicinity of field populations of *Ditrupa arietina* are usually <1 µg l⁻¹ (Jordana 2000), corresponding to <800 *Rhodomonas* sp. cells ml⁻¹. Concentrations used in the present study may thus have been slightly higher than generally experienced by the worms during most of the year. This may explain the absence of a lower trigger level in *D. arietina*.

The chl a concentrations in surface water of the Gullmarsfjord are about 4 µg l⁻¹ during summer, which is considerably higher than in the Bay of Banyuls-sur-Mer. The sedimentation rate of particulate organic material (POM) during the winter and spring is about 0.5 g dry wt m⁻² d⁻¹, and during summer and early autumn the sedimentation rate varies between about 0.6 and 1.4 g dry wt m⁻² d⁻¹. The annual sedimentation of particulate organic carbon (POC) which may reach the deeper bottoms below the halocline is approximately 160 g m⁻² (Lindahl 1988). The size and the ability of *Euchone papillosa* to utilise these particles is not known, but the following considerations may be useful as a first approach. Presuming that 1 ml O₂ ≈ 0.5 mg POC ≈ 1 mg

Table 5. Volume of water cleared of particles per cm ciliary band in various marine filter-feeders. lc: lateral cilia; pcc: prototroch compound cilia; clc: compound lateral cilia; cb: ciliated band

Taxonomic group/species	Type of ciliary band	Total length of ciliary band in an individual (cm)	Temp. (°C)	Clearance rate (ml h^{-1} ind.$^{-1}$)	Vol. water cleared per cm ciliary band (ml h^{-1})
Lancelets: adults					
Branchiostoma lanceolatum	lc		15		0.56[a]
Ascidians: adults					
Ciona intestinalis	lc	2431	15	1993	0.82[b]
Styela clava		7150	15	2736	0.38[c]
Bivalves: adults					
Mytilus edulis	lc	6145	13	7450	1.2[d]
Mya arenaria	lc	22900	11	4510	0.2[e]
Geukensia demissa	lc	6247	28.5	6150	0.98[f]
Bivalves: larvae					
Mercenaria mercenaria	pcc	0.025	28.5	0.012	0.48[g]
Mytilus edulis	pcc	0.047	12	0.011	0.23[h]
	pcc	0.047	15	0.031	0.66[i]
Polychaetes: adults					
Euchone papillosa	clc	441	8	172	0.4[j]
Ditrupa arietina	clc	85	14	47	0.6[j]
Sabella pavonina	clc	3931	14	7080	1.8[k]
Echinoderms: larvae					
Pisaster ochraceus	cb		10–15		0.35[l]
Stylasterias forreri	cb		10–15		0.70[l]
Orthasterias koehleri	cb		10–15		0.60[l]
Dermasterias imbricata	cb		10–15		0.64[l]
Ophiopholis aculeata	cb		10–15		0.22[l]
Parastichopus californicus	cb		10–15		0.54[l]
Strongylocentroutus purpuratus	cb		10–15		0.30[l]
S. droebachiensis	cb		10–15		0.42[l]
Dendraster excentricus	cb		10–15		0.29[l]
Mean ± SD					0.45 ± 0.1
Bryozoans: adults					
Celleporella hyalina	lc	0.68	10	0.12	0.18[m]
			15	0.16	0.24[m]
			20	0.17	0.25[m]
Electra pilosa	lc	1.04	18	0.28	0.26[n]
			15	0.23	0.22[o]
Electra bellula	lc	0.55	22	0.08	0.15[p]

[a]Value from Riisgård & Svane (1999). [b]Pharynx area of a 155 mg dry wt *Ciona intestinalis* was determined in present work as 8.5 cm^2, and total band-length of the lateral cilia as 286 cm cm^{-2}; clearance rate (F) was estimated from: F(ml h^{-1}) = 118 W (g total dry wt)$^{0.68}$ given by Petersen & Riisgård (1992) as 1993 ml h^{-1}; volume of water cleared per cm lateral ciliary band was estimated as 1993/(8.5 × 286) = 0.82 ml h^{-1} cm^{-1}. [c]Pumping rate of individual *Styela clava* with pharynx area of 25 cm^2 measured by Riisgård (1988a) at 2736 ml h^{-1}, presuming total band-length of lateral cilia to be 286 cm cm^{-2} (as for *C. intestinalis*, see [b]), volume pumped per cm lateral cilia band would be 2736/(25 × 286) = 0.38 ml h^{-1} cm^{-1}. [d]Clemmesen & Jørgensen (1987) measured total band-length of lateral cilia in *Mytilus edulis* as 250 cm cm^{-2} gill area. Møhlenberg & Riisgård (1979) measured both pumping rate and gill area of *M. edulis*; for a 1 g dry weight mussel with a pumping rate of 7450 ml h^{-1} and a gill area of 24.58 cm^2, volume of water pumped (cleared) per cm lateral ciliary band is estimated at 7450/(24.58 × 250) = 1.2 ml h^{-1} cm^{-1}. [e]*Mya arenaria* (Dorthe Fischer Seerup pers. comm.). [f]Riisgård (1988b) measured filtration rate cm^{-2} gill area for 1 g dry weight mussel at 6150/24.99* = 246 ml h^{-1} cm^2 (*a*-value for gill area in Table 1 of Riisgård [1988b] is here corrected to 24.99); presuming that the ~ 40 µm-broad gill filaments are separated by 40 µm-wide interfilament gaps, the volume of water cleared per cm lateral ciliary band would be 246/(1/0.004) = 0.98 ml h^{-1} cm^{-1}. [g]Riisgård (1988c) measured maximum clearance rate of 3 d old hard clam larvae, *Mercenaria mercenaria*, at ~0.012 ml h^{-1}; circumference of velum of 2 d old hard clam larvae (Gallager 1988, his Fig. 2) is calculated at about 0.025 cm; volume of water cleared by larval prototroch ciliary band is estimated at 0.012/0.025 = 0.48 ml h^{-1} cm^{-1}. [h]Circumfence of velum (L) of a *M. edulis* veliger larva (shell height = 150 µm) is about L = π × shell height = π × 0.015 = 0.047 cm; clearance (F) was measured by Riisgård et al. (1980) at 0.011 ml h^{-1} (F/L = 0.23 ml h^{-1} cm^{-1}). [i]Clearance rate of *M. edulis* determined as in [h], but with F = 0.031 ml h^{-1} (Riisgård et al. 1981), so that F/L = 0.66 ml h^{-1} cm^{-1}. [j]Details, in present Table 3. [k]All data on *Sabella pavonina* from Riisgård & Ivarsson (1990); 'standard' worm (65 mg dry wt) tentacle has crown of 39 tentacles, and mean number of pinnules (length = 0.12 cm) on bi-pinnate tentacles = 420; total length of ciliary band estimated as L = 39 × 420 × 0.12 × 2 = 3931 cm; clearance rate (F, ml h^{-1}) of 'standard' worm at 8 and 14°C estimated from equation: F (ml min^{-1}) = 90 + 2t (°C) at 6360 and 7080 ml h^{-1}, respectively; ciliary length-specific clearance rate = F/L estimated at 1.6 and 1.8 ml h^{-1} cm^{-1}, respectively. [l]Data from Hart (1996, his Table 2). [m]Total length of ciliary band is 2 × the total length of all tentacles: 2 × 0.34 = 0.68 cm; clearance rate of 6 µm particles = 0.16 ml h^{-1} zooid^{-1} (Riisgård & Manríquez 1997, their Table 4); volume of water cleared is therefore 0.16/0.68 = 0.24 ml h^{-1} cm^{-1}. [n]Maximum individual zooidal clearance rate of 0.28 ml h^{-1} measured by Riisgård & Goldson (1997); total length of all tentacles measured at 0.52 cm by Riisgård & Manríquez (1997); because each tentacle has 2 lateral ciliary bands, volume of water cleared is estimated at 0.28/(2 × 0.52) = 0.27 ml h^{-1} cm^{-1}. [o]Determined as in [m], but clearance rate of 0.23 ml h^{-1} zooid^{-1} was obtained by Menon (1974). [p]Lisbjerg & Petersen (2000) measured clearance rate of 0.8 ml h^{-1} zooid^{-1}; number of tentacles (length = 0.025 cm) varies between 10 and 12; based on 11 tentacles, volume cleared per cm lateral ciliary band would be 0.08/(11 × 0.025 × 2) = 0.15 ml h^{-1}
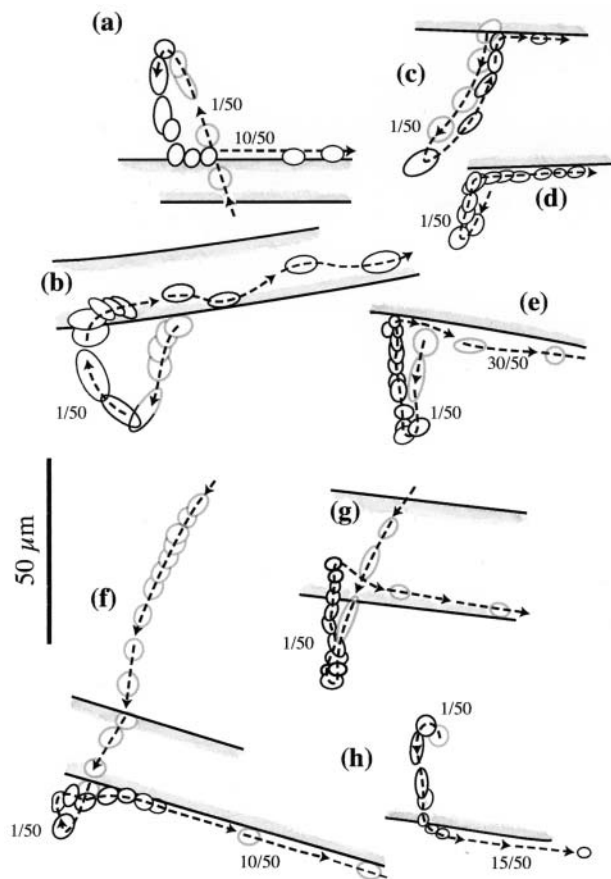
Fig. 5. *Euchone papillosa*. Examples of particle capture. Time interval between successive video frames are indicated (1 frame = 1/50 s; 10 frames = 10/50 s). Particles approaching the pinnules accelerate and move through an arc of 180° to the frontal side of the pinnule and are transported toward the mouth. Transfer takes place at a maximum distance of about 35 μm from the pinnule (C). Particles approaching a pinnule have broken outlines because they are out of microscope focus. At locations of maximum velocity, particle images were blurred to a length of about 2 particle diameters (about 12 μm)

POM ≈ 20 J (e.g. Gnaiger 1983, Smaal & Widdows 1994), a sedimentation rate of 160 g POC m^{-2} yr^{-1} would transfer [$160 \times 20\,000 = 3200$ kJ m^{-2} yr^{-1} = 8767 J m^{-2} d^{-1} =] 0.877 J cm^{-2} d^{-1} down to the zoobenthos in the Gullmarsfjord. A rough estimate of the respiration rate (R, ml O_2 h^{-1}) of a 'standard' (Table 4) 1.5 mg dry wt *E. papillosa* obtained by from the equation $R = 0.13\,W$ (g dry wt)$^{0.66}$ (applied to *Sabella pavonina* by Riisgård & Ivarsson 1990) would be [0.0018 ml O_2 h^{-1} = 0.036 J h^{-1} =] 0.864 J d^{-1}, and by using $R = 0.141\,W^{0.668}$ (applied to the sabellid *Myxicola infundibulum* by Shumway et al. 1988) would be 0.879 J d^{-1}. The area of the (usually horizontally placed) tentacle crown of an undisturbed 'standard' *E. papillosa* is [$\pi \times 0.63^2$ =] 1.25 cm^2. The amount of POC falling down directly onto the tentacle crown is equivalent to [1.25×0.877=] 1.1 J d^{-1}, which is sufficient to cover the energy need of the worm if the assimilation efficiency of the ingested POC is about 80%. However, it is unknown whether the POC is in a form available to the worms, with the particles of a suitable size to be captured and ingested, and the organic carbon digestible. If the food is mainly fresh phytoplankton the following considerations may be relevant: The energy content of a *Rhodomonas* sp. cell is 1.75 μJ (Kiørboe et al. 1985), which implies that the ingestion rate (I) must be equivalent to $0.036/(1.75 \times 10^{-6})$ = 20 570 cells h^{-1}, which is possible if the mean algal concentration = $I/(Cl)$ [= 20 570/172] = 120 cells ml^{-1} (or 0.15 μg chl *a* l^{-1}). A similar estimate for *Ditrupa arietina* results in a minimum algal concentration of 680 *Rhodomonas* sp. cells ml^{-1} (or 0.85 μg chl *a* l^{-1}).

Clearance studies by Riisgård & Ivarsson (1990) on the ciliary filter-feeding polychaete *Sabella pavonina* showed that the clearance rate was high and constant for algal (*Dunalilella marina* and *Rhodomonas* sp.) concentrations ranging between about 2000 and 4000 cells ml^{-1}. At concentrations > 4000 cells ml^{-1} the clearance
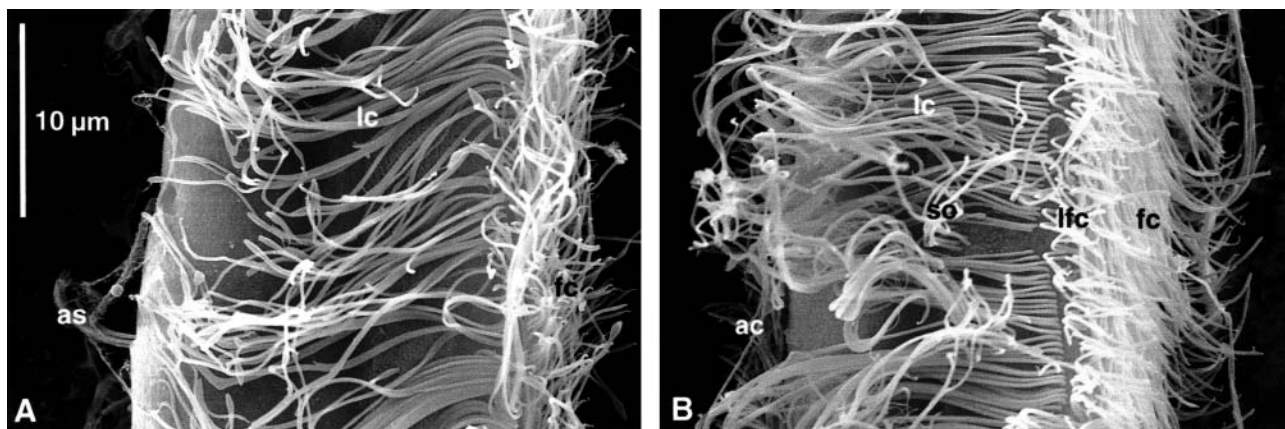

Fig. 6. *Ditrupa arietina* (A) and *Euchone papillosa* (B). Lateral views of pinnules, SEM. ac: abfrontal cilia; as: abfrontal sensory organ; fc: frontal cilia; lc: lateral (compound) cilia; lfc: laterofrontal cilia; so: sense organ

rate was reduced, presumably because the gut capacity was exceeded. A similar phenomenon was found for *Ditrupa arietina* in the present work when the algal concentration was increased from about 2000 to nearly 10 000 cells ml^{-1}, which resulted in a 50% decrease in the clearance rate (from 26 to 13 ml h^{-1} ind.$^{-1}$, see Table 2: Expt 21.10.D). The Bay of Banyuls-sur-Mer is characterised by strong water movements, which can lead to transitory drastic increases in suspended particle concentration through sediment resuspension (Grémare et al. 1997, 1998a). The relatively high concentrations associated with the onset of satiation in *D. arietina* may be an adaptation to such a changing environment. As previously mentioned, there was a tendency for reduced clearance in *Euchone papillosa* after more than 1 algal addiditon. This indicates that the concentrations used in the experiments may have been higher than generally experienced by *E. papillosa* at its natural site. This once more emphasises the general need for more knowledge about actual algal concentrations in the immediate vicinity of filter-feeding zoobenthos (Vedel 1998, Dolmer 2000a,b, Riisgård & Larsen 2000).

A realistic area-specific population-filtration capacity of *Euchone papillosa* and *Ditrupa arietina* may be estimated at [200 ind. m^{-2} × 172 ml h^{-1} ind.$^{-1}$] = 0.8 and [1000 ind. m^{-2} × 47 ml h^{-1} ind.$^{-1}$] = 1.1 m^3 water m^{-2}d^{-1} respectively. In comparison, the population filtration rates in coastal waters where population filtration capacities are typically higher, between 1 and 10 m^3 water m^{-2}d^{-1} (Lemmens et al. 1996, Riisgård & Larsen 2000). Realisation of these estimated capacities is highly dependent on the filtering activity. Both worms are extremely sensitive to experimental conditions, and even the slightest disturbances cause them to immediately withdraw into their tubes. To judge from the present work, the filtering activity of both worms seems to be a basically continuous process. This is consistent with the previous observation of a positive correlation linking duration of individual filtration events and total time spent filtering in *D. papillosa* (Jordana et al. 2000), although it should be stressed that filtering activity may show seasonal changes related to the reproductive cycle and age structure of the population (Jordana et al. 2000), and that repetition of short filtration events may be associated with low filtering activity of the worms.

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