

Ecology of amorphous aggregations (marine snow) in the Northern Adriatic Sea. III. Zooplankton interactions with marine snow

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ABSTRACT: The metazoan species composition in small stringer-shaped aggregates of marine snow from the Northern Adriatic Sea (<2 cm) was found to be distinctly different from the zooplankton community determined in ambient water. Larval stages dominated the marine snow associated community, with polychaete larvae being most important in terms of biomass. Occasionally polychaete larvae exceeded bacterial biomass and metabolism in marine snow. Together with juvenile turbellarians, they were found to be enriched in marine snow by factors >600 as compared to the surrounding water. Polychaete larvae utilize marine snow as a transport vehicle and as a food source as directly observed under the dissecting microscope. During summer, the only copepods found significantly enriched in marine snow were harpacticoids and *Temora stylifera*, whereas the dominant mesozooplankton species in ambient water were *Acartia clausi* and *Penilia avirostris*. Neither *A. clausi* nor *P. avirostris* were found associated with marine snow. Grazing experiments with *A. clausi*, which is the dominant calanoid copepod in the Northern Adriatic Sea, revealed that this copepod does not feed significantly on the marine snow associated phytoplankton biomass. Thus we conclude that the major fraction of the free-living filter-feeding herbivorous zooplankton is unable to utilize phytoplankton when embedded in the mucoid matrix.

INTRODUCTION

Sinking of large amorphous aggregates (marine snow) has recently been identified as one of the major mechanisms by which particulate organic matter is transported into the deep ocean (Fowler & Knauer 1986, Alldredge & Silver 1988). It is well documented that marine snow is frequently enriched in inorganic and organic nutrients (McCarthy & Goldman 1979, Shanks & Trent 1979, Herndl & Peduzzi 1988) as well as in various organisms, including phytoplankton (Knauer et al. 1982, Beers et al. 1986), bacteria (Alldredge et al. 1986), bacterivorous protozoa (Caron et al. 1982) and other microplankton (Silver et al. 1978). In terms of biomass, enrichment factors vary from 1.5 to 1000 depending on the source of the marine snow (Alldredge & Gotschalk 1990). It is therefore reasonable to assume that marine snow exhibits high metabolic activity as has been shown in a number of studies (Knauer et al. 1982, Herndl 1988). These nu-

trient-rich patches within the water column are a potential food source for planktonic metazoans.

Zooplankton contributes to particle flux through particle formation (Karl et al. 1988, Taylor 1989) via production of rapidly sinking fecal material and mucus feeding structures such as discarded appendicularian houses (Silver et al. 1984, Davoll & Silver 1986). The role of zooplankton in degrading marine snow, however, has received much less attention, although marine snow may be a food source for zooplankton organisms (Baylor & Sutcliffe 1963, Riley et al. 1964, Silver et al. 1978, Alldredge & Silver 1988). Alldredge (1972) presented direct evidence that cyclopoid copepods of the genus *Oncaea* feed on abandoned larvacean houses. Recently, Banse (1990) hypothesized that zooplankton grazing on marine snow might be a key to resolving the particle decomposition paradox (Karl et al. 1988). Another indication that zooplankton might utilize marine snow-mucus as a food source is the finding that the copepod *Acartia negligens* feeds on mucus secreted by scleractinian corals assimilating up to 50 % of the organic matter of the mucus (Richman et al. 1975). Another potential

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food source worth considering in marine snow are bacteria, which are too small to be filtered by copepods when freely in suspension. While single bacteria are too small to be effectively retained by the mesh of the maxillipeds (Nival & Nival 1976), they could be ingested along with the mucus of marine snow.

In the Northern Adriatic Sea, marine snow appears in the stratified water column as a decay product of algal blooms. Aggregates can reach several meters in length (Cori 1906, Stachowitsch et al. 1990). Herndl (1988) has shown that the microbial biomass in marine snow increases during prolonged periods of stratification, while at the same time the ambient water is depleted of planktonic organisms. The water column, therefore, represents a highly structured and patchy environment under such conditions.

The aims of this study were (1) to determine whether there is a zooplankton community associated with marine snow distinctly different from the zooplankton consortia of the ambient water, (2) to determine whether some zooplankters are specifically enriched in marine snow and (3) to determine the potential role of marine snow as a food source for zooplankton organisms.

MATERIAL AND METHODS

The main study location was 1.5 km off the Laboratorio di Biologia Marina at Aurisina in the Gulf of Trieste, Italy, (Northern Adriatic Sea) during 22 to 27 July, 22 to 26 August and 22 to 26 September 1990. Sampling was also performed off Piran, Slovenia, on 27 September 1989 and off Rovinj, Croatia, from 26 August to 4 September 1991. We selectively sampled marine snow with 60 ml disposable syringes by SCUBA diving. Metazoan plankton of ambient water was sampled using diver-operated 0.8 l hand-made plexiglass syringes since traditional net sampling was not possible due to the high abundance of marine snow in the water column. For each marine snow sample at least 10 times the volume was sampled without visible aggregates. Both marine snow and ambient water samples were brought back to the laboratory within 20 min for direct observations. We sorted living zooplankton organisms according to their taxonomic groups. The residual marine snow was used for dry weight and organic matter analysis.

The actual dry mass of marine snow was determined as described by Herndl (1988). Briefly, a 900 ml plexiglass cylinder (inner diameter 4 cm) was slowly moved through a selected depth layer and stoppered at both ends. For dry weight determination of marine snow, the contents of the plexiglass cylinders were filtered onto preweighed and precombusted Whatman GF/F glass

fiber filters (47 mm diameter), rinsed 3 times with distilled water and dried at 60°C to constant weight; a control cylinder in which no visible aggregates were enclosed was treated in the same way and subtracted from the dry mass of the marine snow cylinder. For chl *a* we followed the description in Parsons et al. (1984).

In order to obtain an estimate on the carbon content of polychaete larvae, which were found to dominate the zooplankton biomass in marine snow, 6 ampoules were filled with 20 polychaete larvae each and stored at –20°C in the dark. Prior to analyses, the samples were homogenized in a known volume of redistilled water and the organic carbon content was determined by a Beckmann TOC master 915-B after acidifying 2 ml of the suspension with 5 µl 10 % HCl to pH 2 and purging for 10 min with CO₂-free air. Glucose was used as a standard.

As polychaete larvae were found to dominate the metazoan community in marine snow, their sinking velocities were determined in order to compare sinking rates of the larvae with marine snow. Formalin-killed larvae (1 drop of concentrated formalin in 20 ml seawater) were carefully transferred into a 50 cm glass cylinder held at constant temperature. The body volume was estimated by measuring the length and width of the larvae and calculating the volume of a cylinder.

The palatability of marine snow associated phytoplankton was tested by measuring chl *a* and pheopigment concentration of the gut content of *Acartia clausi*, using the fluorometric technique described by Mackas & Bohrer (1976) as modified by Dagg & Wyman (1983). Between 30 and 50 individuals of *A. clausi* were placed in a 90 % acetone-water solution, homogenized with a glass tissue grinder and subsequently filtered through a Whatman GF/F filter (47 mm diameter). A high sensitivity SPF-500 RATIO spectrofluorometer (American Instruments Co.) was calibrated with pure chl *a* (Sigma Chemicals) as a standard.

To determine the saturation threshold of food for adult *Acartia clausi* (males and females combined), 60 to 100 individuals of *A. clausi* were subjected to different concentrations of *Nitzschia closterium* (pennate diatom) in 1 l plexiglass rolling tanks in dim light for 4 h. The algal concentration was determined by measuring chl *a* at the beginning and end of each experiment. After each experiment, 30 to 50 copepods were collected onto a 300 µm Nitex screen and immediately transferred into a 90 % acetone-water solution using fine forceps. Sampling was performed in duplicate.

In order to compare our results on the feeding pattern obtained in the laboratory with the diel feeding pattern under natural conditions we measured the total pigment content of *Acartia clausi* over a diel cycle in the natural environment. On 12–13 April 1990, 50 specimens of *A. clausi* were collected by net tows in 5 m

depth over a 24 h period at 2 h sampling intervals using a 300 μm plankton net. Specimens of *A. clausi* were preserved in 90 % acetone within 10 min.

Two experimental systems were set up to investigate the ability of *Acartia clausi* to prey on marine snow: (1) aggregates consisting of the diatom *Nitzschia closterium* only and (2) aggregates which were produced from natural seawater collected in the Gulf of Trieste by rolling tank incubations (Shanks & Edmondson 1989). For the first approach, dense *N. closterium* cultures in a stationary phase were incubated in Whatman GF/F filtered seawater in 10 l plexiglass rolling tanks until a sufficient number of aggregates appeared (usually within 3 d). Prior to exposing the aggregates to copepods, they were separated from suspended single cells by differential settlement. A 100 ml glass cylinder was filled with Whatman GF/F filtered seawater and kept at 4°C. Aggregates were transferred from the rolling tanks (18°C) into the surface layer of the glass cylinder with a wide-mouthed pipette. Due to the higher density of the (4°C) cold water only larger aggregates settled to the bottom. In less than 5 min, aggregates larger than 3 mm in diameter settled to the bottom while single cells remained in the upper part of the cylinder. Subsequently, the sedimented aggregates were collected again and the treatment described above was repeated twice. After 3 'rinses' no single cells were detectable at the bottom of the cylinder. The aggregates were then transferred to a rolling tank filled with GF/F filtered seawater. In order to compare the potential of *A. clausi* to feed on food items of different stages of aggregation, we performed additional control experiments using *N. closterium* cultures which were filtered through a 65 μm net and diluted to a density lower than 5 $\mu\text{g chl a l}^{-1}$ ('single cells'). Filtered seawater served as control for the background fluorescence of copepods with empty guts. Sixty to 100 copepods (starved for 12 h) with empty guts were introduced into 1 l rolling tanks and incubated for 4 h in dim light at 18°C. The chl *a* and pheopigment content of the *N. closterium* single-cell suspension was measured before and after the experiment. To determine the amount of cells which came off the aggregates during the incubation, we measured also the chl *a* content of the aggregates and the ambient water after the experiment. After each experiment the copepods were collected and their gut pigment content determined as described above.

In the second experiment, aggregates were generated by rolling natural seawater as described by Shanks & Edmondson (1989). The 10 l rolling tanks were kept at 18°C and an illumination of 60 $\mu\text{E m}^{-2} \text{s}^{-1}$ until aggregates appeared after 4 d. Particles generated in this way were very similar to marine snow collected in summer 1990. Therefore, we subsequently

refer to these aggregates as 'marine snow'. These aggregates were collected by a wide-mouthed pipette and washed in the same way as *Nitzschia closterium* aggregates. As control we used ambient water containing no visible particles; 0.2 μm filtered seawater served as control for background fluorescence. Ambient water was filtered through a 65 μm Nitex screen to eliminate or destroy all aggregates >65 μm in diameter. For each treatment, 50 to 100 copepods were put into 1 l rolling tanks and incubated in dim light for 4 h. After the experiment the fluorescence of the gut content of the copepods was measured as described before. The chl *a* and pheopigment concentrations of the water and the aggregates were measured as in the experiment with *N. closterium*.

As polychaete larvae were found to occur in high densities in marine snow and have been observed under the microscope to feed on marine snow, respiration measurements were performed to obtain an estimate on their energy demand. Although the determination of pigment concentrations in the gut is a powerful tool to examine the ingestion of algal-enriched food, it allows only limited predictions of the actual assimilation efficiency of ingested food. By measuring respiration it is possible to compare the ecological significance of the metazoan community with other living compartments in marine snow such as bacteria. *Prionospio* sp. larvae (Spionidae) were collected from marine snow samples. The larvae were incubated in 0.2 μm filtered seawater (polycarbonate filter) for defecation for 1 h and subsequently rinsed twice in 0.2 μm filtered seawater to remove the major fraction of bacteria prior to transfer into the incubation vessels (cartesian divers). For measuring the oxygen consumption, the cartesian diver method described in Zeuthen (1950) and Klekowski (1971) and as more recently described by Schiemer et al. (1990) was used. The 'background' respiration of the remaining bacteria was tested in empty divers and was below the detection limit of this method over a 3 h period. Antibiotics such as penicillin and chloramphenicol were not added since there is evidence that both affect respiration of eucaryotes (Taylor & Pace 1987). A single larva was introduced into the chamber. An air bubble with a known volume ranging from 2.47 to 3.32 μl was placed next to the chamber. Once brought into the flotation vessel, the system was allowed to adapt to the respective temperature for at least 45 min before starting the measurement. The increase in specific gravity of the diver due to oxygen consumption was measured in 30 min intervals by applying negative pressure to the flotation vessel. Five readings were performed for each larva (total incubation period: 2.5 h per larva). The temperature was kept constant during the experimental procedure (20.1°C). The read-

ings in mm Brodie solution were converted into oxygen consumption by the formula:

$$dVO_2 = (V_q dP 273) (P_0 T)^{-1} \quad (1)$$

where dVO_2 = rate of oxygen consumption ($\mu\text{l h}^{-1}$); V_q = volume of the gas phase (μl); dP = pressure change (mm Brodie); P_0 = normal pressure for the system (mm Brodie); and T = temperature of the system ($^{\circ}\text{K}$). dP in time was tested for linearity and averaged as $dP \text{ h}^{-1}$ before it was used for calculation.

RESULTS

Overall characteristics of marine snow

The abundance of marine snow probably of phytoplankton origin deviated only in a narrow range among the sampling dates. Dry weight of marine snow ranged from 6.3 g dry wt m^{-3} of seawater in July 1990, to 7.8 g dry wt m^{-3} of seawater and 8.7 g dry wt m^{-3} of seawater in September 1990. The values are depth integrated from 10 m depth to the surface. In September

1989 and summer 1990, marine snow appeared in the forms of globules and stringers with a maximum length of 2 cm (for terminology of marine snow consult Stachowitsch et al. 1990). Bacterial density in marine snow did not change significantly during July and August (1.4×10^6 cells ml^{-1}) and decreased in September 1990 (4×10^5 cells ml^{-1}). Larger and denser aggregates (clouds) reaching several meters in length only appeared in summer 1991 and remained in the water column until September.

The zooplankton community of marine snow

Only the major groups of zooplankton inhabiting marine snow (such as polychaete larvae) or dominant species (like *Convoluta* aff. *convoluta*) were enumerated (Table 1). These groups or single species accounted for more than 90 % of all living zooplankton organisms in marine snow. In September 1989 and July and September 1990, polychaete larvae were the most abundant organisms found in marine snow (Table 1a), attached in a manner as shown in Fig. 1. In

Table 1. (a) Mean abundances of metazoans in 1 l stringer-shaped marine snow during 1989 and 1990. Clouds were not present during this period. In order to compare abundances in marine snow and ambient water, enrichment factors (EF) are calculated on the basis of numbers per volume. ∞ indicates that no metazoan was found in the ambient water samples. As metazoan plankton abundances were similar in September 1989 and September 1990, the data were combined. (b) Comparison of the zooplankton composition between stringer shaped marine snow (< 2 cm) and clouds (> 1 m) during September 1991

(a)	July 1990 (n = 6)			August 1990 (n = 8)			September 1989/1990 (n = 13)		
	Mean	Range	EF	Mean	Range	EF	Mean	Range	EF
Polychaete larvae ^a	278	50–883	344	217	50–617	436	608	33–3633	765
Juvenile turbellarians	25	0–50	62	123	17–217	∞	192	17–1208	670
Nauplii ^a	58	0–100	145	406	50–783	163	165	17–1233	3.7
Harpacticoids	39	0–100	6	160	66–250	3.5	96	0–242	10
<i>Temora stylifera</i> ^a	19	0–67	∞	25	0–83	∞	75	0–120	200
Others	19	0–50	3.7	31	0–50	2.2	41.7	0–83	1.2
(b) Type of aggregate:									
	Stringers (< 2 cm) (n = 12)			Clouds (> 1 m) (n = 10)					
	Mean	Range		Mean	Range				
Polychaete larvae	153	10–367		0	0				
Juvenile turbellarians	22	30–67		0	0				
Nauplii	263	48–583		70	13–233				
Other larvae	0	0		157	73–375				
Harpacticoids	110	71–133		161	118–291				
<i>Penilia avirostris</i>	31.6	0–190		95	0–267				
<i>Evadne</i> sp.	3.6	0–20		32	0–75				
<i>Podon</i> sp.	1.9	0–19		0	0				
<i>Acartia clausi</i>	0	0		35	0–192				
Others	9.6	–		47	–				
Dead animals or exuviae	732	108–2136		1765	483–4367				

^a Grazing on marine snow observed under dissecting microscope

August 1990, nauplii exceeded the polychaetes in terms of numbers but not in biomass, since nauplii were at least 10 times smaller according to their body length. During September 1991, samples were more heterogeneous than during all other sampling periods. Polychaete larvae appeared only in small stringers and at lower densities than in 1989 and 1990 (Table 1). As compared to small stringers, large and dense clouds showed a remarkably different composition of the zooplankton community. These aggregates contained many exuviae and dead or presumably trapped

animals which might be an indication of their age (Table 1b). In general, the abundance of living zooplankton in these clouds was about half the abundance found in stringers.

The body volume of the polychaete larvae ranged from 0.0016 to 0.41 mm³ per larvae with a mean (\pm SD) of 0.036 ± 0.08 mm³ ($n = 34$) in July 1990, 0.02 ± 0.005 mm³ ($n = 31$) in September 1990 and 0.012 ± 0.0046 mm³ ($n = 8$) in September 1991. The total organic carbon (TOC) content of polychaete larvae amounted to $6.4 \times 10^{-4} \pm 3 \times 10^{-4}$ mg C ind.⁻¹ ($n = 6$). The mean sinking

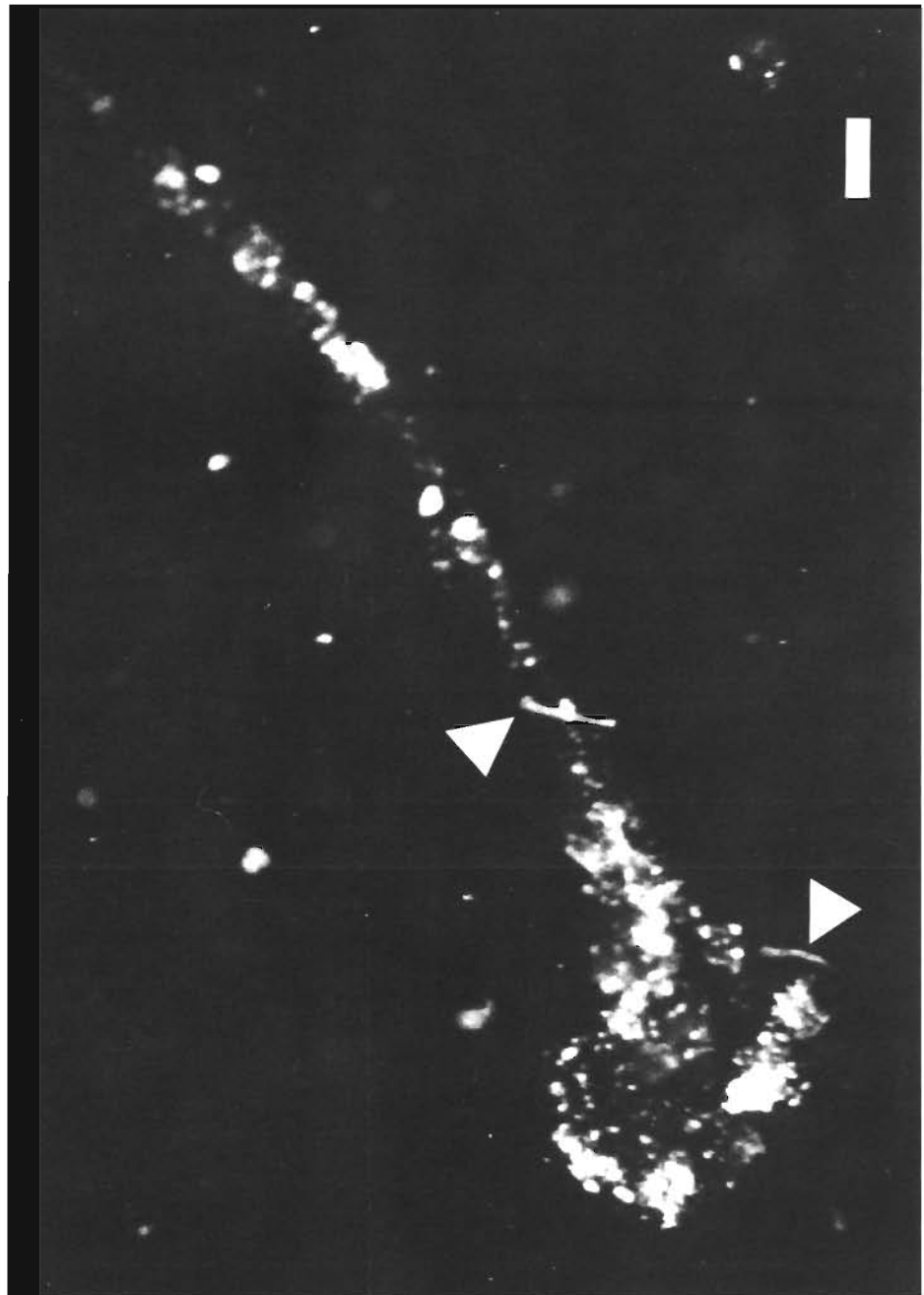


Fig. 1. *In situ* photograph of 2 polychaete larvae (arrows) attached to a marine snow-stringer. Scale bar = 1 mm

velocity of killed larvae was $71.6 \pm 23.8 \text{ m d}^{-1}$ ($n = 24$). The majority of the polychaetes belonged to the Nectochaeta stage with long embryonal setigers tightly kept along the body surface during gliding through the organic matrix of marine snow. Taxonomically, the nectochaetes found in our samples belonged to 4 species of 3 families: the Spionidae, Nereidae and Disomidae. Most abundant was the genus *Prionospio* (Spionidae) with about 73% of the total number of nectochaetes, other spionids represented 8%, Nereidae 14% and *Poecilochaetus serpens* about 5%. In July, we found a few individuals of the Metatrochophora of *Chaetopterus variopedatus* in the marine snow samples. The turbellarians found in the samples were all juvenile acoetes. Although there were considerable uncertainties as to which species they actually belonged, they all carried endosymbiotic algae and fit well into the descriptions of adult *Convoluta* aff. *convoluta* which is a very common Acoela in the Northern Adriatic Sea living mainly in the phytal. Although their number did not exceed the number of polychaetes, nauplii, or harpacticoid copepods, the enrichment factor calculated for *C.* aff. *convoluta* was higher than in all other groups except for polychaetes. In both marine snow and ambient water nauplii significantly contributed to the microzooplankton. The harpacticoid copepods were abundant; compared to the other groups, however, they were only weakly enriched in the aggregates (Table 1). *Temora stylifera* was the only calanoid copepod found enriched in marine snow during 1989 and 1990. We observed very few individuals of the cladoceran dominated zooplankton community which adhered to the stringers. In September 1991 many more specimens – mainly of the species *Penilia avirostris* – became entangled in large clouds. The remaining zooplankton (Metazoa) are summarized in Table 1 as 'others' and consisted of cyclopoid copepods, cladocerans, copepodite stages, appendicularians, plutei and veliger larvae, but accounted for less than 10% of the zooplankton in marine snow in terms of numbers. As revealed by direct observations and video analyses of polychaete larvae in petri dishes under the dissecting microscope the polychaete larvae exhibited 2 different feeding patterns: The nectochaetes and the Metatrochophora of *C. variopedatus* both were capable of swallowing the mucus matrix of marine snow directly. Alternatively they fed on ciliates and other small particles using their ciliated girdle. The fecal pellets produced were highly variable in length (from 0.05 to 1.3 mm), not very compact and remained in the matrix of marine snow. Additionally to polychaete larvae, larger nauplii and *T. stylifera* have been observed feeding on marine snow under the dissecting microscope (as indicated by the superscript 'a' in Table 1).

Grazing experiments with *Acartia clausi*

When grazing on single cells of *Nitzschia closterium*, the total gut pigment content of *Acartia clausi* was linearly correlated with the chl *a* concentrations of the algal suspension and reached a maximum gut content of $2.2 \text{ ng chl } a \text{ ind.}^{-1}$ at an algal concentration of $5 \mu\text{g chl } a \text{ l}^{-1}$. At chl *a* concentrations ranging from 5 to $24 \mu\text{g chl } a \text{ l}^{-1}$, there was no further increase in the gut pigment content. In laboratory feeding experiments with *N. closterium*, the gut fluorescence values were significantly higher (Mann-Whitney 2-sample test, $p < 0.01$) in the single cell treatment than in experiments where aggregates of *N. closterium* were offered (Table 2, Fig. 2). In the second experiment using marine snow as aggregated food source, *A. clausi* ingested significantly more plant pigments in natural seawater with no visible aggregates than during marine snow exposure (Mann-Whitney 2-sample test, $p < 0.01$; Table 2, Fig. 2). The gut fluorescence of *A. clausi* measured in the Gulf of Trieste was much lower than in the feeding experiments with *N. closterium*. Over the diel cycle, the pigment content varied between 0.05 ng per copepod at 8:00 h and 0.23 ng per copepod at 2:00 h (Fig. 3). The algal concentration during the sampling period was $0.8 \mu\text{g chl } a \text{ l}^{-1}$ at 3 m,

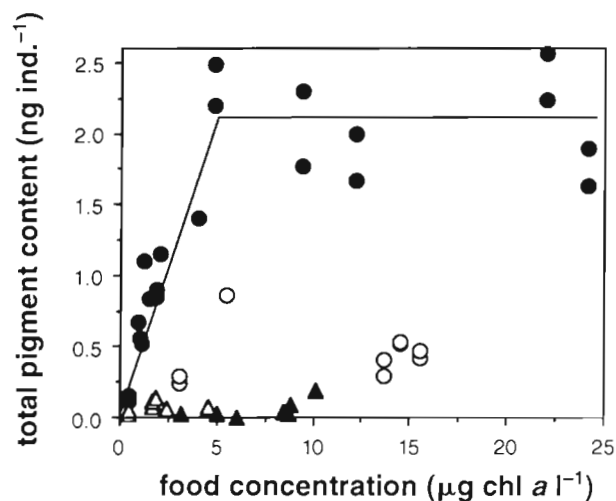


Fig. 2. *Acartia clausi*. Pigment concentration in the gut as dependent on food source: *Nitzschia closterium* aggregates (\blacktriangle), single cells of *N. closterium* (\bullet), marine snow (\triangle) and natural aggregate-free seawater (\circ). Each point represents the mean of 30 to 50 copepods. Triangles indicate chl *a* concentration in aggregates normalized to 1 l bottle volume; thus chl *a* was highly concentrated in the aggregates. Line indicates the relation of *A. clausi* gut pigment content to concentration of *N. closterium* single cells (measured as chl *a*) after 4 h of incubation. Up to a chl *a* concentration of $5 \mu\text{g l}^{-1}$, the relation to gut content is directly proportional: $y = 0.14 + 0.43x$ ($r^2 = 0.893$, $n = 14$, $p < 0.001$). At chl *a* concentrations of more than $5 \mu\text{g l}^{-1}$, gut content reaches saturation

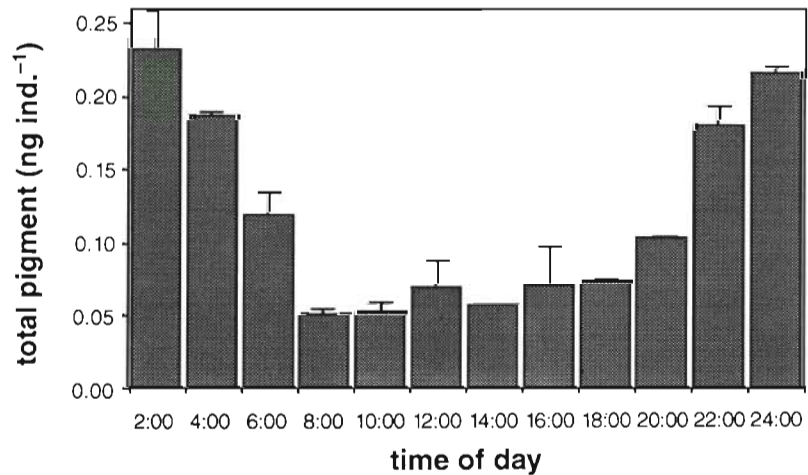


Fig. 3. *Acartia clausi*. Diel variation in total pigment content (chl *a* and pheopigments) in the Gulf of Trieste (Northern Adriatic Sea) in April 1990. Bars indicate range of 2 subsamples

1.2 $\mu\text{g chl } a \text{ l}^{-1}$ at 5 m and 1.3 $\mu\text{g chl } a \text{ l}^{-1}$ at 10 m depth.

Oxygen consumption of *Prionospio* sp. larvae

The average oxygen consumption (\pm SD) of *Prionospio* sp. larvae was $5.19 \pm 1.55 \text{ nl O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ ($n = 11$). Fig. 4 demonstrates the dependence of the oxygen consumption on the body volume. The relation of the body volume and the respiration of an organism is best described by the equation $R = a V^b$, where R = respiration; V = volume of an organism; a and b are constants calculated by the linear regression of the log-transformed R and V values. Using the respiration data of the polychaete larvae in $\text{nl O}_2 \text{ h}^{-1}$ and their body volume in mm^3 , $a = 275.7$ and $b = 0.90$.

DISCUSSION

Feeding activity in *Acartia clausi* exhibited a distinct diel cycle (Fig. 3). These field data are of the same order of magnitude as data obtained from *A. clausi* fed on natural aggregate-free seawater in our experiments (Fig. 2) much lower, however, than the values obtained in grazing experiments with a single cell suspension of *Nitzschia closterium* (Fig. 2). This indicates that food with little or no chl *a* comprises a major fraction of the diet of this copepod in the Northern Adriatic Sea. Omnivory is also described for other copepod species (Gaudy 1974, Lonsdale et al. 1979, Sheldon et al. 1986, Gifford & Dagg 1988, Wiadnyana & Rassoulzadegan 1989, Stoecker & Capuzzo 1990).

The mechanism of selection seems to be triggered by the motion of the prey, whereas chemoreception is

Table 2. Experiments performed with *Nitzschia closterium* aggregates (a) and marine snow produced in rolling tanks using natural seawater (b). Chl *a* content of the algae exposed to the copepods and total pigment content of the copepods after the incubation are given as mean values and ranges of all replicates. Surrounding water: filtered seawater containing cells which became detached from the aggregates during the experimental procedure; (–) not determined

Treatment	n	Food concentration chl <i>a</i> $\mu\text{g l}^{-1}$		Gut content (ng copepod ⁻¹)	
		Average	Range	Average	Range
(a) <i>Nitzschia closterium</i>					
GF/F filtered seawater	7	0.025	0.006–0.08	0.024	0.006–0.042
Single cells	7	1.63	0.87–1.73	1.0	0.53–1.57
Aggregates	7	7.18	3.2–10.09	0.055	0.01–0.08
Surrounding water	7	0.073	0.028–0.092		
(b) Marine snow					
GF/F filtered seawater	8	–	–	0.025	0.01–0.038
Aggregate-free water (63 μm filtered)	9	10.39	3.05–15.45	0.46	0.28–0.86
Aggregates	9	2.22	0.55–4.60	0.074	0.028–0.14

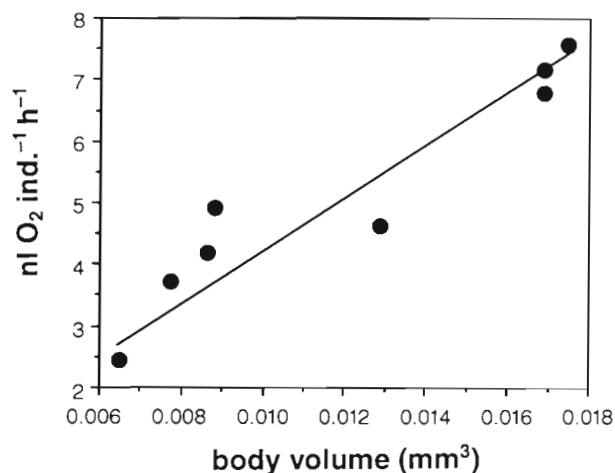


Fig. 4. *Prionospio* sp. Dependence of respiration rates on biomass. The curve represents the respiration rates derived from the formula $R = 275.7 V^{0.9}$, where R = respiration ($\text{nl O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) and V = body volume (mm^3)

probably of minor importance for prey detection (Jonsen & Tiselius 1990). Potential grazing on large motionless particles, however, requires a very different behavior including the ability to rupture aggregates much larger than the usual prey. In our experiments the pigment concentration in the gut of *Acartia clausi* exposed to aggregates of *Nitzschia closterium* did not correlate with the chl *a* concentrations in the aggregates and were much lower compared to the values derived from the single cell treatment (Fig. 2). In incubations with marine snow the copepods displayed significantly lower gut-content values than those fed on natural seawater (Table 2b). If *A. clausi* can take advantage of the patchy distribution of food by ingesting attached phytoplankton along with marine snow, much higher total pigment contents would have been detected in the guts. However, only insignificantly higher pigment contents were detected after incubations with marine snow compared to copepods kept in filtered seawater. This slight increase can be explained by algae coming off the aggregates during the feeding experiment since it was not possible to keep all algae attached to the aggregates during 4 h incubation, as demonstrated in experiments with *N. closterium* monospecific aggregates (Table 2a). In our feeding experiments we assume that the chl *a*:carbon ratio is the same in marine snow and ambient water; this, however, might not necessarily be true although we sampled marine snow and ambient water from the same tank. The grazing experiments with *N. closterium* indicate that the low pigment concentrations in the guts in the marine snow treatment is not caused by the different

chl *a*:carbon ratio but by the inability of *A. clausi* to prey on aggregates (and especially their associated phytoplankton). Concerning feeding on algae in different shapes, Schnack (1983) reported a very similar behavior of *Temora stylifera*, *Calanus helgolandicus*, *Centropages chierchiae* and *Calanus carinatus*. In her study, *Thalassiosira partheneia* was offered as prey in 2 different forms: as single cells and whole colonies. It appeared that the copepods are not able to feed on whole colonies of this algae, but ingested single cells after disintegration. Schnack (1983) further hypothesized that even raptorially feeding species are discouraged by colony formation and the mucoid halo of the algae.

Temora stylifera was the only calanoid copepod enriched in the aggregates and has been observed grazing on marine snow during this study. This species is known to be strongly predatory. Gaudy (1974) compared *Acartia clausi* and *T. stylifera* and found a preference for algal diet for *A. clausi*; *T. stylifera*, however, can be considered as both herbi- and carnivore with a remarkable ability to prey even on large *Artemia salina* nauplii. Searching for a morphological manifestation of the different behavior of *Acartia clausi* and *T. stylifera* concerning grazing on marine snow, we found differences in their feeding appendages. *T. stylifera* has massive mandibular cutting edges, whereas the cutting edges of *A. clausi* are more fragile. We measured the teeth on the mandibular edges and calculated the edge index according to the formula given by Itho (1970; cited in Omori & Ikeda 1984). Both copepods belong to omnivore types; *A. clausi* tends towards herbivory and *T. stylifera* towards carnivory. Also the long setae of the first maxilliped of *A. clausi* which cover a large area indicate a preference for filtering small particles. The large mandibles and the reduced length of the maxilliped setae of *T. stylifera*, on the contrary, seem to be more suitable for grabbing larger particles including marine snow. Nevertheless the importance of marine snow contributing to the metabolic demand of *T. stylifera* remains unknown.

The cladoceran *Penilia avirostris* is the most dominant species in the mesozooplankton community of the Northern Adriatic Sea during summer (Fonda Umani 1985). *P. avirostris* feeds on smaller cells than *Acartia clausi* (Fonda Umani & Cocchietto 1988) and prefers nanoflagellates (2 to 5 μm in diameter) over small diatoms (4 to 12 μm in diameter) (Turner et al. 1988). Therefore it is likely that *P. avirostris* is not able to feed on marine snow either. Moreover, the morphology of its carapace, which encloses even the limbs, most probably prevents this animal from grazing on larger particles (presumably gathering small particles only by filtration). *A. clausi* and *P. avirostris* together comprise 30 to

90 % of the total mesozooplankton biomass during the summer months. Thus we may conclude that algae embedded in the mucoid matrix remain ungrazed by most of the zooplankters present in ambient water.

The metazoans embedded in the aggregates were dominated by polychaete larvae, juvenile acoele turbellarians, nauplii and harpacticoid copepods. The species composition was very similar during 1989, 1990 and in the small stringers of 1991. This is surprising because one might expect fluctuations of organisms due to pulses of larval dispersal. These organisms exhibited enrichment factors ranging from 3.5 to 765. In terms of biomass, polychaete larvae dominate the metazoan microzooplankton community in marine snow. Spionidae are known to spawn in summer (Riedl 1985) and subsequently comprise a significant portion of the microzooplankton community. For July 1990, the biomass of the polychaete larvae in terms of carbon represented $178 \mu\text{g C l}^{-1}$ while the bacterial biomass amounted only to $26.4 \mu\text{g C l}^{-1}$ (conversion factor: $20 \text{ fg C cell}^{-1}$) in marine snow (Karner & Herndl 1992). These exceptionally high biomass concentrations for pelagic polychaete larvae can only be explained by the attachment to a substrate providing both food and a transport vehicle (discussed later). While the biomass ratio in terms of carbon of polychaete larvae:bacteria in July 1990 is 6.7 in marine snow, this ratio for the ambient water is only 0.064. Our respiration data provide information on the carbon demand for catabolism of the polychaete larvae. To convert the O_2 -consumption rates into carbon equivalents we used the formula:

$$C = R \text{ RQ } (12/22.4),$$

where C = carbon equivalent ($\mu\text{g C animal}^{-1} \text{ h}^{-1}$), R = respiration rate ($\mu\text{l O}_2 \text{ animal}^{-1} \text{ h}^{-1}$) and $12/22.4$ = the weight (12 g) of carbon in 1 mol (22.4 l) of carbon dioxide. RQ, the respiratory quotient, changes as a function of the excretory product and is 0.97 for ammonia (Gnaiger 1983). Since marine zooplankton is primarily ammonotelic (Omori & Ikeda 1984) we used 0.97 for the RQ. R is calculated for an average body volume of 0.012 mm^3 using the equation $R = 275.7 V^{0.9}$. The mean O_2 consumption rate is therefore $0.124 \mu\text{l O}_2 \text{ ind.}^{-1} \text{ d}^{-1}$, or in terms of carbon $0.064 \mu\text{g C ind.}^{-1} \text{ d}^{-1}$. Since no data are available on the net growth efficiency of polychaete larvae, we took an average net growth efficiency of 30 to 70 % as has been given for crustacean zooplankton by Conover (1968; cited in Raymont 1983); therefore we estimated the actual carbon demand for the polychaete larvae as 0.09 to $0.22 \mu\text{g C ind.}^{-1} \text{ d}^{-1}$; multiplying this value with the average number of polychaete larvae present in marine snow in July 1990, we arrive at an organic carbon demand for the polychaete larval community in marine snow of 25 to $60 \mu\text{g C l}^{-1} \text{ d}^{-1}$, which is in the same order of

magnitude as the calculated bacterial carbon demand of $30 \mu\text{g C l}^{-1} \text{ d}^{-1}$ in July 1990 (recalculated from Karner & Herndl 1992). This indicates that the turnover of carbon due to the activity of polychaete larvae can even exceed bacterial carbon turnover; it demonstrates also the potential importance of metazoans in energy and material transfer in particles. When large amorphous aggregates appeared in the water column in August and September 1991, the zooplankton species composition obviously changed with the age of marine snow and the living zooplankton biomass was comparatively low in large aggregates. Only in stringers of a few mm to cm length did we find polychaete larvae in a density similar to those found in summer 1990 (Table 1).

Shanks & Edmondson (1990) studied marine snow sedimentation in the Atlantic off North Carolina (USA) and stressed the contribution of meiobenthic species like nematodes to the metazoan community on marine snow. Interestingly, we could not find any nematodes enriched in marine snow, even though the water column at our sampling station did not exceed 15 m in depth. Besides polychaete larvae, we found large amounts of turbellarians. Adult *Convoluta* aff. *convoluta* is usually abundant in the phytal (Apelt 1969). Occasionally, however, they also emerge into pelagic regions where they might become entrapped in marine snow. Hagerman & Rieger (1981) found large numbers of juvenile acoeles and other soft-bodied meiofauna in sediment trap samples off North Carolina, which indicates the occurrence of meiofauna in the water column due to resuspension. We do not know how many of the harpacticoid copepods we found in marine snow are actually of meiobenthic origin, as we did not distinguish among holoplanktonic, hypoplanktonic and benthic types.

The zooplankton community in marine snow takes advantage of this specific habitat within the pelagic environment. Some organisms we found utilize marine snow as a food source, as direct observations of polychaete larvae, nauplii and *Temora stylifera* have revealed. *Convoluta* aff. *convoluta* relies to a large extent on its endosymbiotic diatoms (Ax & Apelt 1965) and therefore the juvenile acoeles may benefit from high inorganic nutrient concentration found in marine snow (Kaltenböck & Herndl 1992). The main fraction of the zooplankton community in marine snow consists of larvae and juveniles (Table 1), which can take advantage of the buoyancy of marine snow for their dispersal. Using inverted sediment traps in addition to conventionally deployed traps, Herndl (in press) showed that marine snow exhibits a bidirectional flux which is obviously influenced by the metabolic activity of marine snow attached microorganisms. The average net flux for marine snow depends on the depth and on the time

of day. The upward flux can even exceed the downward flux in 4 m depth during daytime (Herndl in press). The settling velocities of the larval polychaetes not associated with marine snow vary between 22.9 and 108.7 m d⁻¹, which lies in the range (8.64 to 259.2 m d⁻¹) given by Butman (1986). The water column in the Northern Adriatic Sea does not exceed 35 m and therefore they would rapidly settle to the bottom. Thus by locating in marine snow, larvae can reduce sedimentation velocity and save energy which is normally expended in active swimming motion and consequently enhance their dispersal.

In oligotrophic marine systems phytoplankton biomass is controlled by zooplankton; consequently, particle flux to the deep ocean is largely mediated in the form of fecal pellets (Knauer et al. 1979, Karl et al. 1988). In eutrophic environments, however, zooplankton cannot cope with the development of phytoplankton; the consequence of this is that phytoplankton becomes senescent as they are inefficiently grazed, leading to massive sinking of decaying cells to the ocean's interior (Smetacek 1985). Particle flux into the aphotic zone or to the bottom occurs therefore not only via fecal pellets but – to a large extent – via ungrazed, decaying phytoplankton cells. In the Northern Adriatic Sea, the formation of large buoyant mucous sheets might be interpreted as a manifestation of a large ungrazed fraction of phytoplankton, especially the part that is embedded in marine snow. The rather insignificant grazing of *Acartia clausi* on marine snow – as shown in this study – implies that primary production of phytoplankton associated with marine snow does not enter directly the plant-herbivore food web like in the ambient water but is utilized by the heterotrophic microbial consortia. Only a few associated species might act as a metazoan link between primary production and higher trophic levels. The high biomass of heterotrophic organisms which utilize marine snow (bacteria, protozoa and larval stages of metazoa) would lead to a rapid disappearance of aggregates if phytoplankton were not able to take advantage of the liberated nutrients and continually produce mucus (along with other microbes) leading to a remarkable constant marine snow mass throughout the summer.

In summary we have demonstrated that *Acartia clausi*, which is the dominant copepod in the Northern Adriatic Sea, is not able to feed significantly on the autotrophic compartment in marine snow and that living herbivorous zooplankton is only weakly enriched in small marine snow particles. On the other hand, larval stages of metazoans exhibited high enrichment factors in marine snow and might be, at least occasionally, the dominant consumers (over bacteria) of organic carbon in marine snow, not only in terms of biomass, but also in their carbon demand. We conclude, therefore, that in

nearshore marine snow more attention should be paid to these small metazoans as their role in the carbon flux through marine snow might not be trivial.

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