ISSN: 0001-5113 AADRAY	ACTA ADRIAT., 53(3): 375 - 387, 2012	

Ecology of gel-like marine snow event in the northern Adriatic Sea

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The development, aggregation, and senescence of amorphous marine snow aggregates in the northern Adriatic Sea off Rovinj, Croatia were investigated during an aggregation event from July to September, 1997. Aggregates and surrounding ambient water were sampled using SCUBA for bacterial and cyanobacterial abundance, dissolved oxygen, primary production, bacterial secondary production, dissolved organic carbon and dry weight measurements. Marine snow aggregates appear to be a rich protected environment that favors primary production and bacterial growth by making readily available marine organic moieties present in the gel's matrix. Aged aggregates form two separate zones: an outer well oxygenated almost transparent gel-like zone, and a dark almost-anoxic/anoxic central zone. The interstices of the aggregates contained high concentrations of dissolved organic carbon, especially in the central almost anoxic-anoxic zone, which can be correlated to microbial activity. When sinking below the pycnocline they efficiently bypass mid-water biota thus becoming an important component of the marine biological pump and a major mechanism for the movement of particulate and dissolved organic carbon towards the sea floor.

Key words: marine snow particles, gel-like aggregates, microbial habitat, ecological zonation, northern Adriatic Sea

INTRODUCTION

The notion of the microbial loop (POMEROY, 1974) still raises fundamental questions regarding source, fluxes, and mechanisms by which bacteria acquire nutrients. Bacteria are the most important entry point for the grazing food chain in seawater (NAGATA *et al.,* 2010), probably processing up to 50% of the primary production (CHO & AZAM, 1988; AZAM *et al.,* 1994). Early observations show that most bacteria in seawater appear in clumps or aggregates, emphasizing their association with particulate organic matter (SEKI, 1970). Results of experiments using size fractionation emphasize that colloidal rather than dissolved organic matter is probably the principal source of nutrients for heterotrophic microbial production in seawater (AMON & BENNER, 1996; SIMON *et al*., 2002). Observations of bacteria clustering on macrogels (DE LONG *et al.,* 1993) provide strong evidence that gels may comprise a rich source of microbial nutrients.

In the northern Adriatic Sea, the development of a pronounced pycnocline during the summer months can lead to an accumulation of large gel-like organic mega aggregates (HERNDL & PEDUZZI, 1988) that have been recognized for some time as playing a major role in the transfer of particulate organic carbon (POC) from the euphotic zone to the ocean floor (FOWLER & KNAUER, 1986; ALLDREDGE & SILVER, 1988). As the very largest aggregates of the macroscopic

mucus aggregate classification (STACHOWITSCH *et al.,* 1990), they have occurred as compact forms several meters in diameter intermittently for more than a century (MARCHETTI, 1990). Sticky organic matrixes of these huge aggregates have the potential to trap everything they encounter including organisms, particles, dissolved molecules, and trace metals from the ambient water (HEBEL *et al*., 1986; ALLDREDGE & SILVER, 1988). The mucopolysaccharide matrix (POSEDEL & FAGANELI, 1991) is greatly enriched with specific and highly active microbial associations (FOGG, 1995) and differs significantly from the surrounding environment in phytoplankton community composition (REVELANTE & GILMARTIN, 1991; KALTENBÖCK & HERNDL, 1992) with species in all stages of growth (NAJDEK, 1996). It was also reported that the actively living autotrophic fraction in marine snow of the northern Adriatic Sea mainly consisted of cyanobacteria (KALTENBÖCK & HERNDL, 1992).

The summer of 1997 in the northern Adriatic Sea was characterized by calm weather conditions providing a unique opportunity to closely monitor the development, aggregation, aging and senescence of marine snow from 31 July to 06 September in one single aggregation event. In this communication results from these measurements are presented to increase our understanding of the ecology of these very important particles in the cycling of matter in marine ecosystems.

MATERIAL AND METHODS

Sampling

The study was conducted from July to September, 1997, in the Northern Adriatic Sea in the near vicinity of Rovinj, Croatia (Fig. 1, Table 1). In late July, stratification of the water column correlated with an accumulation of large aggregates at the pycnocline at about 10 to 15 m water depth (Fig 2a). Mass accumulation of huge more gel-like aggregates (Fig. 2b) occurred during early September. The predominantly elongated aggregates were between 1 m and 3-4 m in length. SCUBA divers using a 1 m rope determined the sizes of the aggregates. In order to show the development of distinct zonation within the interstices of the marine snow, aggregates of similar shape and with a minimum diameter of about 0.5 m were sampled in situ by SCUBA diving. Pre-cleaned 600 ml syringes with cut-off ends were used to take subsamples from the inner (center) and the outer (~ 3-5 cm

Table 1. Sampling depths, sampling course, positions of the sampled stations and dissolved oxygen (A - ambient water, B - aggregate outer zone, C - aggregate central zone) during July-September 1997, Northern Adriatic Sea

Station	Sampling depth (m)	Date year 1997	Position of the sampling stations	A ml O_2L^{-1}	B ml O_2L^{-1}	C ml O_2L^{-1}
1	12-14	31 Jul	45° 05’ 35” N, 13° 36’ 48” E	5.08	6.07±0.36	7.56±2.17
2	14-18	01 Aug	45° 05’ 24” N, 13° 37’ 16” E	5.22	5.15±0.19	4.05±0.45
3	18-24	02 Aug	45° 04’ 54” N, 13° 36’ 47” E	5.21	5.59±0.56	4.50±0.59
4	20-21	04 Aug	45° 05’ 29” N, 13° 36’ 57” E	5.22	5.97±0.05	5.47±1.53
5	16	01 Sep	45° 05’ 32” N, 13° 37’ 14” E	5.30	5.88±0.67	0.29±0.29
6	12-16	02 Sep	45° 05’ 34” N, 13° 37’ 28” E	5.19	5.63±0.42	0.06±0.06
7	12-16	03 Sep	45° 05’ 41” N, 13° 37’ 33” E	5.05	6.86±1.52	2.34±1.14
8	18	04 Sep	45° 04’ 52” N, 13° 37’ 00” E	5.35	3.16±2.11	0.00±0.00
9	20	05 Sep	45° 03’ 12” N, 13° 37’ 00” E	5.16	4.37±0.83	0.79±0.31
10	18	06 Sep	45° 03’ 25” N, 13° 36’ 48” E	5.09	3.25±1.15	0.99±0.99

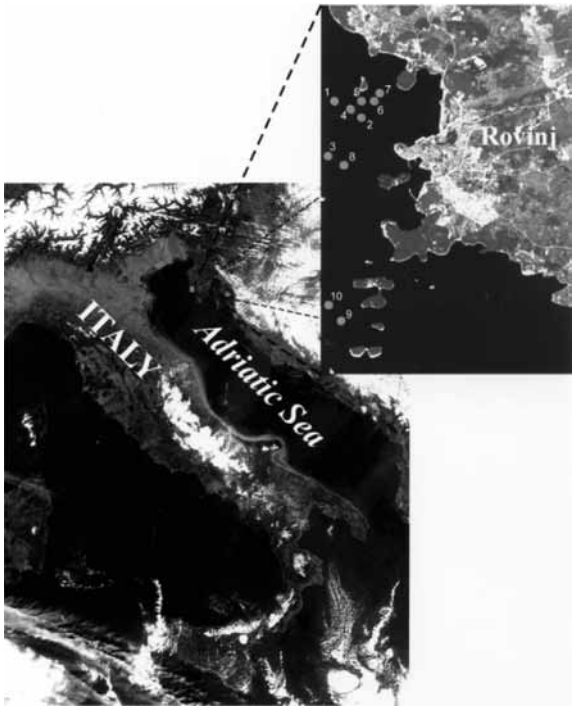

Fig. 1. Aggregate sampling stations (circles) and sampling course (numbers) in 1997 in the area of two nautical miles off Rovinj, Croatia. Sampling details are given in Table 1

Fig. 2.a) First appearance of large marine snow aggregates in summer 1997. Sampling station 1 at 12 m depth on 31 July 1997. Photo by Nadia-Valerie Queric

thick surface coating) zone of 20 aggregates (2 from each of 10 stations) and ambient water (samples were taken from a distance ~ 20 cm from the aggregate). As all sampled aggregates were large enough, SCUBA divers were able to avoid sucking surrounding seawater into the syringes. Immediately upon retrieval aboard, subsamples were separated for dissolved oxygen analysis. Ambient water and aggregate subsamples for bacterial counts were immediately fixed with buffered Formalin (2% final concentration) and stored in the dark at 4°C until analysis. The rest of the samples were stored in the dark at in situ temperature until further processing in the onshore laboratory.

Fig. 2. b) Diver behind one large marine snow aggregate on sampling station 9 at 20 m depth on 5 September 1997. Photo by Nadia-Valerie Queric

Dry weight

For dry weight determination of marine snow 2 ml of aggregate subsamples were filtered onto preweighed and precombusted (500ºC) Whatman GF/F glass fiber filters (47 mm diameter), rinsed 3 times with distilled water and dried at 60ºC to constant weight.

Dissolved oxygen

Both ambient water and marine snow subsamples were introduced in a gentle stream into Winkler flasks (V ~ 50 ml) until the flasks overflowed. Analysis was performed avoiding any bubbles during sampling. One half ml of reagent 1 (40 g $MnCl_2$ tetrahydrate in 100 ml of redistilled water) and 0.5 ml reagent 2 (30 g KOH plus 60 g KI in 100 ml of redistilled water) was added to the flasks to achieve precipitation of $Mn(OH)_3$. The sample flasks were then shaken vigorously to mix the contents and to disperse the precipitate finely throughout. After

the precipitate has settled at least halfway down the flask, the flask was shaken again vigorously to disperse the precipitate. Samples were then stored in dark container at constant temperature until titration in the onshore laboratory. Analyses were carried out immediately upon arrival at the onshore laboratory using an automatic burette according to Carpenter (CARPENTER, 1965).

Bacterial counts

Five ml of ambient water, and 2 ml formalin-fixed samples (2 % final conc.) of the inner and outer zone of each aggregate were used for the enumeration of bacterial cells. For more accurate microscopic enumeration of bacterial cells from the aggregate matrix, 2 ml of each aggregate subsample were diluted 1:50 in artificial (autoclaved and 0.2 µm filtered) seawater and mixed 5 times for 10 s. One half ml of this dilution was further diluted in 3 ml 0.1 M PPi (Tetrasodium Pyrophosphate) in order to disintegrate the polysaccharide matrix and mixed with a vortex mixer for 1 min prior to and after staining with DAPI (4',6-diamidino-2-phenylindole; 1 µg ml^{-1} final concentration) for 15 min. Without exceeding 200 mbar, samples were then filtered onto a 0.2 µm pore-size black polycarbonate filter (Millipore, Ø 25 mm), backed by a supporting filter (Millipore HA, Ø 25 mm, 0.45 µm pore-size). Filters were mounted with low-fluorescent mounting oil (Nikon) and examined by epifluorescence microscopy (Leitz Laborlux) under UV excitation (Ploemopak fluorescence unit). The number of microscopic fields was adjusted to maintain an enumeration standard error of < 5 %.

Cyanobacterial abundance

For the purpose of this study a published cyanobacteria data set (Table 1. in MÜLLER *et al*., 1998) was used since both studies used the exact same aggregates.

Primary production measurements

Immediately upon arrival at the onshore laboratory 5 ml subsamples of each unpreserved aggregate and ambient water sample were placed in each of 3 transparent (light) and two black (dark) 20 ml glass scintillation vials and incubated in a water bath incubator at the irradiance of 120 µE m^{-2} s^{-1} and at in situ temperature for 15 min before the addition of 7.4 MBq (in 100 µl water) of $NaH^{14}CO_3$ (2.07 GBq/mmol, 2.0 mCi/ml, Amersham) to each vial. After incubation for 15 min, samples were acidified with 6 N HCl to pH <2 in order to remove the radioactivity not incorporated into organic compounds and left open in a fume hood for 24 h (PUŠKARIĆ & MORTAIN-BERTRAND, 2003). The samples were not filtered to include both particulate (intracellular) and dissolved (extracellular organic carbon) production rates. To assure complete removal of non-assimilated inorganic labeled carbon the samples were additionally bubbled with nitrogen gas for 5 min. After adding 12 ml of scintillation cocktail (Insta-Gel Plus, Packard), the samples were vigorously shaken and kept tightly capped for 14 to 16 hours before radioactivity was measured. A Canberra Packard Tri-Carb 2500 TR liquid scintillation counter (LSC) was used for all radioactivity measurements, corrected for quenching by internal standards ratio using the direct counting method.

Bacterial secondary production

Bacterial activity was estimated by measuring the incorporation of 3H-thymidine (final concentration 20 nM) as a measure for DNA synthesis. Incubations of 5 ml of ambient water and 2 ml of unpreserved aggregate samples were carried out for 45 min at in situ temperature conditions and stopped with formalin (0.3% final concentration). Samples were filtered onto a 0.45 µm pore-size cellulose nitrate filter (Millipore HA, Ø 25 mm) and rinsed twice with 5 ml of 5% chilled TCA. I used 1.1 x 10^{18} as a commonly used conservative factor to achieve the actual number of bacterial cells produced per mol thymidine incorporated (RIEMANN *et al.,* 1987). Carbon production was calculated assuming 20 fg C $cell^{-1}$ (FUHRMAN & AZAM, 1982).

Dissolved organic carbon

Dissolved organic carbon concentrations were determined by the high-temperature (680°C) catalytic oxidation (platinum/quartz)

using a Shimadzu TOC 5000 analyzer. All samples were first filtered through precombusted (500°C) Whatman GF/F glass fiber filters and the filtrates were sealed in precombusted glass ampoules. The samples were stored frozen at -20ºC until analysis. The filtrates were acidified to pH 2 with reagent-grade HCl and sparged with C-free synthetic air immediately before analysis. Standards (potassium hydrogenphthalate) were prepared immediately before analysis according to Benner & Storm (BENNER & STROM, 1993). The overall precision of analysis of three to five replicate injections was always better than 1.5%.

Statistical methods

Minitab 16 and Grapher 1.23 (Golden Software) software programs were used for statistical analyses and calculations.

RESULTS

During the 1.5-month period of the study cyanobacteria in the outer zone of the investigated aggregates remained fairly constant in cell numbers (mean 14.8 ± 5.5 10^5 cells ml^{-1}) while concentrations in the inner zone (mean 86.2 ± 42.1 10^5 cells ml^{-1}) significantly increased ($y = 1.8x - 323.2$, $r^2 = 0.69$, $P < 0.002$), (Table 1 in MÜLLER *et al.*, 1998).

The outer parts (~ 3-5 cm thick "coating" surrounding the inner darker core) of the investigated aggregates were oxygenated while inner parts appeared to be almost-anoxic/anoxic to toxic (MÜLLER *et al.*, 1998; Table 1, this study). All parts of the aggregates were of a sticky, organic matrix consistency. The outer oxygenated organic mat included both autotrophic and heterotrophic communities dominated by diatoms Chaetoceros ssp. and Nitzschia ssp., cyanobacteria, coccolithophorid Emiliania huxleyi, sporadic intact and empty frustules of dinoflagellates and heterotrophic microflagellates. Species composition was similar to that of ambient water. Scavenged detritus consisted of intact zooplankton fecal pellets and cuticle and larvae of different invertebrates. The almost-anoxic/anoxic central core included both autotrophic cyanobacteria (the only living autotroph), heterotrophic bacteria and detritus consisting of empty frustules of diatoms, coccoliths, fecal matter and unidentifiable material scavenged from the water column.

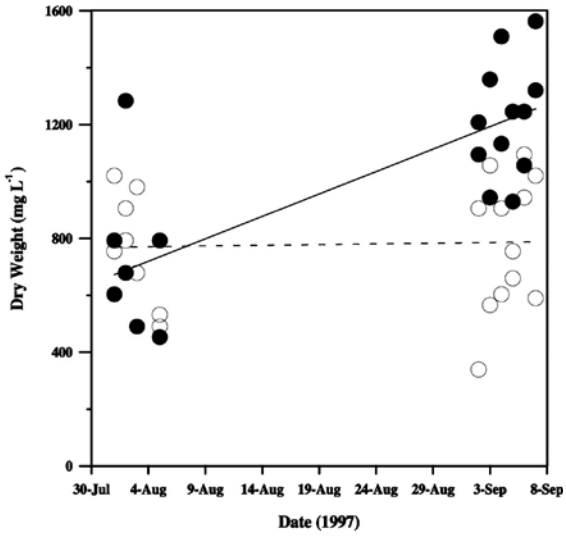

Fig. 3. Dry weight values of inner (full circles) and outer (empty circles) zones of aggregates sampled during the whole investigation period from July (sampling stations 1-4) to September 19 (sampling stations 5-10)

Dry weight values (Fig. 3) revealed that the inner aggregate gradually increased in density as a function of time, while the outer areas maintained a more or less constant density throughout the investigation period.

The depth of the pycnocline varied from 12 to 24 m. During the course of the study aggregates retained their buoyancy and did not sink below the pycnocline until a storm event in mid September.

Primary productivity measurements revealed active uptake of inorganic carbon and synthesis of organic matter in the dark. Primary productivity was in all measurements significantly higher in the aggregates by up to two orders of magnitude than in an equal volume of ambient seawater and more pronounced in the inner part of the aggregates than in the outer zone (Fig. 4).

Rates of primary productivity, bacterial secondary production and dissolved organic carbon (DOC) concentration within the aggregates did not undergo any significant changes over time in contrast to changing trends in the ambient water during the investigation period (Figs. 4,

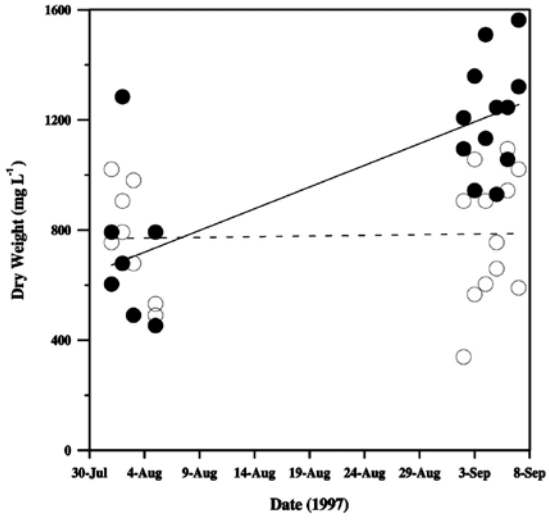

Fig 4. Primary productivity given as mg C L^{-1} h^{-1} in the inner (full circles), outer (empty circles) zone of aggregates plotted with primary productivity measurements in the ambient water surrounding the aggregates (crosses)

5a, 5b, 5c). Beside significant differences in the amounts of DOC, primary productivity and bacterial secondary production measured in marine snow and ambient water, there was a noticeable opposite trend in primary productivity in marine snow as compared to ambient water. While primary productivity in marine snow followed a positive trend (outer zone $Y = 0.008 \cdot X - 1.42$; inner zone $Y = 0.02 \cdot X - 4.12$), measurements in ambient water had a decreasing trend ($Y = -0.0004 \cdot X + 0.1$, $r^2 = 0.94$) during the investigated period (Fig. 4).

Amounts of DOC were remarkably higher in the aggregate's interior than in ambient water (Fig. 5c). Plotting DOC against primary productivity brought at least three clusters forward: ambient water, outer zone and inner zone (Fig. 5a). The measurements also indicate a very high correlation between the primary productivity and bacterial secondary production measurements both in aggregates and ambient water (Fig. 5b). Correlations between cyanobacterial density (Table 1 in MÜLLER *et al.*, 1998) and primary production (Fig. 6) proved to cluster the outer and inner zones of aggregates, respectively, following a distinct gradient inwards with increasing values ($r^2 = 0.42$; $n = 40$; $P < 0.005$).

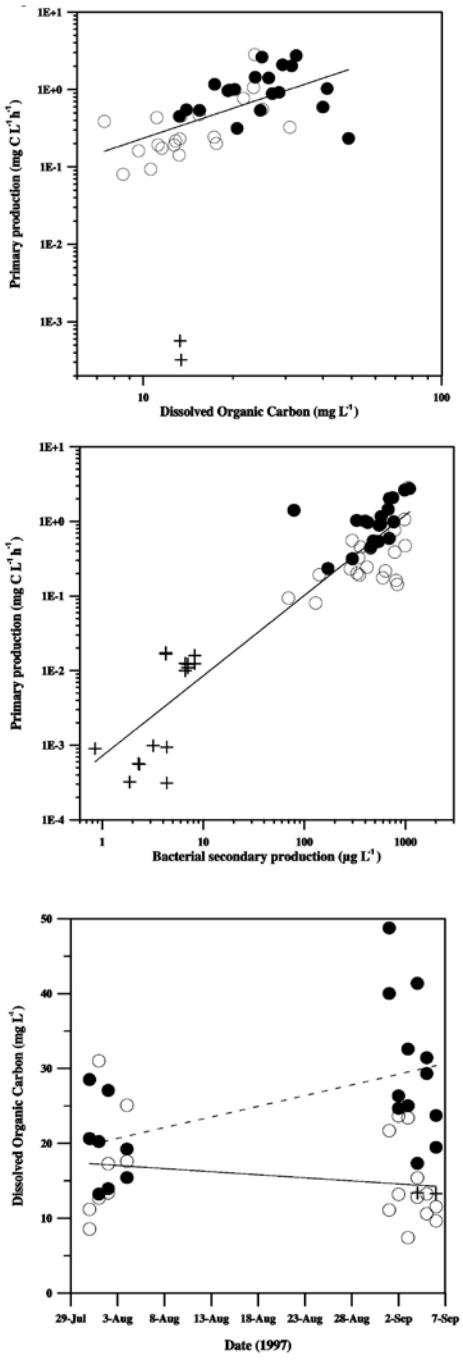

Fig. 5. Correlation between primary production given as mg C L^{-1} h^{-1} and a) dissolved organic carbon (mg L^{-1}), b) bacterial secondary production given as µg C L^{-1} h^{-1} for the inner (full circles) and outer (empty circles) aggregate zone as well as in ambient water (crosses) and c) dissolved organic carbon (mg L^{-1}) of ambient water (crosses), inner (full circles) and outer (empty circles) zones of aggregates sampled during the whole investigation period from July (sampling stations 1-4) to September 19 (sampling stations 5-10)

DISCUSSION

Marine snow aggregates harbor a wide range of particulate and dissolved compounds during their residence time in the water column. Several studies have demonstrated that marine aggregates can contain interstitial nutrients and DOC in concentrations significantly higher than in surrounding water (GOLDTHWAIT *et al.*, 2005; ALLDREDGE, 2000; KALTENBÖCK & HERNDL, 1992) thus being an important lateral and vertical route for both particulate and dissolved compounds. Aggregates only 3-6 mm diameter are capable of storing dissolved compounds longer than expected, based on their specific sticky, gel-like nature (GOLDTHWAIT *et al.,* 2005). The aggregates investigated in this report were so large (e.g. Fig. 2b) that diffusion in and out of them is likely to be much smaller. Even 4 mm aggregates develop measurable oxygen gradients (ALLDREDGE & COHEN, 1987) as it was found on a much larger scale in this study (Table 1). Slow diffusion was likely the primary mechanism maintaining the internal microhabitat in these huge aggregates.

Marine snow does not necessarily originate from cell growth, but also from direct aggregation of extracellular polysaccharide particles, known as transparent exopolymeric particles (TEP) (ALLDREDGE *et al.,* 1993; CHIN *et al*., 1998; PASSOW, 2002; ENGEL *et al*., 2004). The availability of surface area stimulates the production of exopolysaccharides by bacteria (VANDEVIVERE & KIRCHMAN, 1993) and the production of fibrillar capsules is an important mechanism for attachment and the formation of larger aggregates (HEISSENBERGER *et al*., 1996). My results confirm these findings, suggesting that marine snow aggregates act as a retention mechanism for newly produced organic matter. The initial aggregation of the event reported in this study most probably resulted from the spontaneous aggregation of large amounts of TEP that escaped sedimentation and bacterial degradation since the initial aggregation occurred after the phytoplankton bloom clearing the water column as shown in Fig. 2a.

Cyanobacteria constituted the only autotrophic fraction actively growing and increasing in cell abundance within the aggregates during their presence in July-September 1997. However, active growth and decay of diatoms and dinoflagellates dominating flocs has been previously reported in the northern Adriatic aggregates (REVELANTE & GILMARTIN, 1991; NAJDEK, 1996). Separate from a possible effect of variable photosynthetic activities in different species of cyanobacteria (CARPENTER *et al*., 1993) in outer and inner zones of the aggregates, a spatial community shift including phytoplankton species other than cyanobacteria variably contributing to the synthesis of new organic matter may have influenced this clustering. Nevertheless, a significant contribution of cyanobacteria to the overall synthesis of organic matter within the aggregate matrix was evident during this unique event (Fig. 6), as other living autotrophs were not found in the aggregate interstices. Furthermore, the time-dependent development of gel-like aggregates considered to be in senescent stages (MÜLLER-NIKLAS *et al.,* 1994) implies an enhanced aggregation due to cell surface stickiness through an increased release of high molecular weight substances from senescent phytoplankton communities (KIØRBOE *et al.,* 1990). Dry weight persistence and the presence of chemosensitizers of multixenobiotic resistance as very

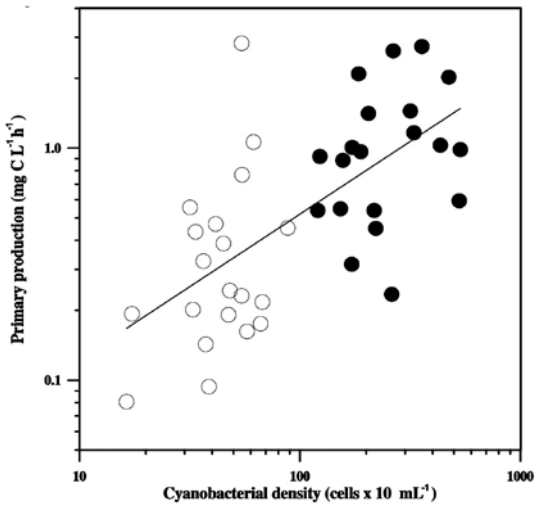

Fig. 6. Correlation between phytoplankton primary production given as mg C L^{-1} h^{-1} and cyanobacterial density given as 105 cells ml^{-1} in the inner (full circles) and outer (empty circles) zone of aggregates sampled

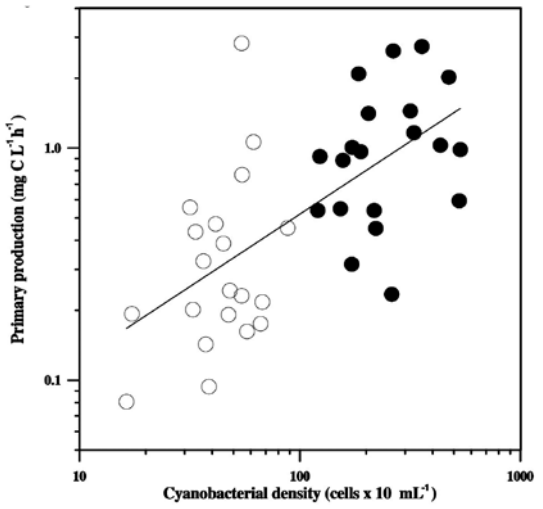

Fig. 7. Primary production measurements in the light plotted against the primary production measurements in the dark, values given as mg C L^{-1} h^{-1} for inner (full circles) and outer (empty circles) aggregate zones

primordial mechanisms of biological defense (MÜLLER *et al.* 1996) suggest that the outer zones of such mega aggregates act as a coating or protective layer against outward disturbances. In this regard, primary productivity, bacterial secondary production and dissolved organic carbon (DOC) concentration within the aggregates did not reflect any significant changes to the same parameters, which occurred in the ambient water during the investigation period.

Aggregate buoyancy proved to be under steady control throughout the study. RIEBESELL, (1992) has shown that photosynthesis and bacterial degradation, generating gas bubbles trapped within the matrix due to a reduced diffusion rate between aggregate and ambient water can maintain steady aggregate buoyancy. Mediating a diel, bidirectional flux of aggregates between the surface and pycnocline layer (HERNDL, 1992) metabolic gases change the aggregate's residence time within the water column and long-distance transport through the interaction with pycnoclines and ocean currents. Metabolic gasses were not observed to regulate either buoyancy or the sinking of aggregates. The high gel content alone in the aggregates may have been responsible for their neutral buoyancy during the entire study.

Resources needed to maintain an autotrophic-heterotrophic community include light and both organic and inorganic nutrients. Light may become a limiting factor especially within the center of gel-like aggregates due to shading by the nontransparent central parts of the aggregates as observed by SCUBA divers. However, my measurements demonstrate an efficient fixation of inorganic carbon and synthesis of organic matter occurring even in the dark within the 15 min incubations (Fig. 7) proving the presence of phosphoenolpyruvate carboxylase, a ubiquitous cytosolic enzyme in cyanobacteria (LEPINIEC *et al.,* 1994) that plays a major role in fixation of CO_2 in light limiting conditions (MORTAIN-BERTRAND *et al.,* 1988). Both Calvin cycle and ß-carboxylation are light-independent reactions (also called "dark reactions"), which in autotrophs continue assimilating carbon even after "the light is off". This argues against the subtraction of the dark bottle values from the values obtained in the transparent bottles. This also confirms the adaptation of cyanobacteria to low irradiances (MOORE *et al*., 1995) and the active growth in the organic matrix. Such adaptation is due to the availability of all required energy sources and the fact that cyanobacteria possess the systems for the active transport of both CO_2 and HCO_3^- (ESPIE *et al*., 1991).

One of the most recent reports on the physiology of extracellular release of organic carbon by marine diatom *Skeletonema costatum* (PUŠKARIĆ & MORTAIN-BERTRAND, 2003) revealed a very close partnership between phytoplankton and heterotrophic bacteria. In 15 min incubations, the described cycle included the incorporation of inorganic carbon, its release as dissolved organic compounds consequently incorporated by bacteria, and again released by bacteria and reincorporated by phytoplankton. Hence, there seems to be a bacterial preference for immediately released, fresh organic compounds from phytoplankton, while further energy is obtained from the bulk of sticky organic aggregate matrix. My results corroborate the scenario showing a very high correlation between the primary productivity and bacterial secondary production measurements both in aggregates and ambient water (Fig. 5b).

Marine snow aggregates studied in this report could be described as a microbial paradise, functioning as a highly effective, self-contained microhabitat; autotrophic and heterotrophic communities are closely linked, providing mutual benefit. The aggregate's matrix is loaded with organic and inorganic nutrients, unstressed by turbulent forces, and energy is plentiful in practically any required chemical form in the near vicinity for every member of the community.

My results show that amounts of DOC are remarkably higher in the aggregate's interior than in ambient water (Fig. 5c), but there is no visible correlation between DOC and other measured parameters including primary productivity and bacterial secondary production. Plotting DOC against primary productivity brought at least three clusters forward: ambient water, outer zones and inner zones (Fig. 5a). Furthermore, the concentrations of DOC within the interstices of the investigated aggregates (outer zone from 7.4 to 31.01 mg L^{-1}; inner zone from 13.22 to 48.76 mg L^{-1}) are in the range as previously reported for the interstices of the sinking marine snow (HERNDL, 1992; ALLDREDGE, 2000).

Gel-like aggregates can bounce back after disturbances. Only two conditions are a threat for their "survival." (1) Slight disturbances; such as their emergence onto the sea surface as mats. This leads to the partial drying and decay of the matrix, which increases its density. The aggregates rapidly sink down to the sea floor, often in conjunction with the removal of trapped gases by storm-induced turbulence. (2) Heavy disturbances causing disintegration of aggregates with partial sinking (PUŠKARIĆ *et al*., 1992) and partial re-aggregation (personal observations from 1989 -1998 and PUŠKARIĆ *et al*., 1992). Rapid and massive sedimentation of particulate organic matter to the ocean sea floor has been reported previously (NOWALD *et al.,* 2006).

In addition to the well documented enhancement in sedimentation of particulate organic matter (FOWLER & KNAUER,1986) and retardation of sedimentation (RIEBSELL, 1992) microbial communities living within the polysaccharide matrix in large aggregates can significantly enhance sequestration of inorganic carbon and accumulation of newly produced organic matter during their prolonged residence within the surface layers of the oceans.

Hence, marine snow aggregates are not only an efficient means of transport for particulate and dissolved organic matter to the ocean interior and the sea floor. BURD *et al.* (2010) raised the still burning question of the apparent imbalances of carbon budgets in the world's oceans associated with discrepancies in sources and sinks of both particulate and dissolved matter in the global carbon cycle. Druffel *et al.* (DRUFFEL *et al.,* 1996) suggested that adsorption of DOC to particulate organic carbon caused the loss of DOC in the deep North Pacific. Other reports have shown that vertical particulate flux might not even reach the dark ocean due to high demands and consumption of the residential biota of the twilight zone (HANSEL & CARLSON, 1998; BUESSELER *et al.,* 2007). From the perspective of this study large marine snow aggregates might be seen to play a significant role in lateral advection of particulate and dissolved carbon due prolonged residence times in the surface waters above the pycnocline (up to 1.5 months as shown in this study) favoring primary production and bacterial growth by making readily available marine organic moieties present in the gel's matrix. Being so large they have high inertia (tendency to resist any change in motion) so the residing biota on their sinking routes will not have sufficient time for solubilization of the particulate fraction and consumption of DOC entrapped in the aggregate matrix. Our observations indicate that when disrupted by a storm event, aged aggregates can very rapidly sink through the pycnocline to the sea floor thus bringing most of this stored particulate and dissolved organic matter into the realm of deep ocean consumers.

Consequences of present global warming trends will be pronounced ocean stratification, geographical shifts and decrease in nutrient supply with phytoplankton community shifts towards small phytoplankton and ocean acidification as a consequence of increased concentrations of atmospheric CO_2 (MARINOV *et al.,* 2010). Such conditions could increase the production

of TEP by phytoplankton, prolonged periods of surface ocean stratification would enhance TEP aggregation and allow aging and colonization of aggregates as shown in this study. Small phytoplankton might find preferable conditions in the interstices of marine snow balancing the gap in the reduced production as a consequence of warming and acidification. It might therefore be possible that we will have to look at the oceans from a very different perspective - from the perspective of marine snow.

ACKNOWLEDGEMENTS

Grateful acknowledges are expressed to N.V. QUERIC and G. MÜLLER-NIKLAS for close collaboration and considerable contribution to experimental work as well as R. ALBERT who finally made this study possible. I thank the Institute Ruđer Bošković, Center for Marine Research (Rovinj, Croatia) for hospitality and especially its staff for invaluable help onboard the vessels "Burin" and "Vila Velebita". Autor also thanks to anonymous reviewers for their suggestions and constructive comments, which helped to improve the quality of this manuscript.

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Received: 3 May 2012
Accepted: 2 September 2012

Ekologija pojave sluzavog morskog snijega u sjevernom Jadranu

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SAŽETAK

U ovom radu je opisan razvoj, nakupljanje i starenje amorfnih nakupina morskog snijega u sjevernom Jadranu tijekom jedinstvene pojave u smislu trajanja i veličine organskih nakupina tijekom ljeta 1997. Istraživanja su provedena od lipnja do rujna 1997. u sjevernom Jadranu sa postajama uzorkovanja dvije nautičke milje od Rovinja, Hrvatska. Da bi se prikazao razvoj odvajanja unutrašnjih zona unutar čestica morskog snijega, SCUBA ronioci su uzorkovali nakupine sličnih oblika. Uzorci nakupina i mora oko agregata su prikupljeni za određivanje brojnosne koncentracije bakterija i cijanobakterija, mjerenje otopljenog kisika, primarne proizvodnje, bakterijske sekundarne produkcije, otopljenog organskog ugljika i suhe tvari. Čestice morskog snijega imaju karakteristike nezavisnih i samoodržavajućih i mogu značajno doprinijeti nakupljanju i taloženju novoproizvedene organske tvari iz vodenog stupca. U specifičnim uvjetima nakupine ne podliježu razgradnji, remineralizaciji ili kolonizaciji zooplanktona. Tijekom tonjenja ispod piknokline čestice učinkovito zaobilaze biološke zajednice srednjeg sloja vodenog stupca i tako postaju možda najvažniji čimbenik sekvestracije morske biološke pumpe i puta čvrstog organskog ugljika prema morskom dnu.

Ključne riječi: čestice morskog snijega, želatinozne nakupine, staništa mikroorganizama, ekološke zone, sjeverni Jadran