

Size does not matter after all:

No evidence for a size-sinking relationship for marine snow

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Running head: Marine snow settling is not determined by size

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Abstract

The biological carbon pump is a critical component for uptake of carbon by the oceans. Most of this is mediated by gravitational sinking of particles and it is generally assumed that there is a positive relationship between sinking velocity and size of particle. Due to the difficulties inherent in measuring the sinking velocity of untouched and undamaged particles, the majority of studies have been based on artificial solid particles or laboratory generated marine snow formed from homogenous material, e.g. phytoplankton cultures. Here, we present results from a newly developed optical method that measures size and settling velocities of undisturbed in situ aggregates in the mesopelagic zone. The measurements were done at depths between 90 and 530 m throughout day and night. In total we measured 55 image sequences of aggregate size and sinking velocities, resulting in measurements of 1060 individual aggregates. Only 10 sequences showed significant correlations between aggregate size and sinking velocity. Furthermore, only 8 of the 10 significant correlations between size and settling were positive. Despite similar optical appearance, similar sized aggregates had different sinking velocities, suggesting that aggregates formed in situ are heterogeneous with different compositions, structure and densities. This complicates estimates of sinking velocity from aggregate size only and one has to be careful when estimating downward particle flux based on in situ size-distribution and abundance of aggregates and theoretical relationships between size and sinking velocity. Hence, this study forces the conclusion that estimates of downward particle flux which use particle size distributions must also include information about aggregate composition, compactness and density from in situ optics or direct particle and aggregate sampling.

Introduction

Understanding the nature of downward flux of organic matter remains a key goal of oceanography. The sinking rate of a marine snow particle relative to its surrounding water will change over time partly due to externalities in the water through which it is sinking (grazing pressure, particle concentration, water density (temperature and salinity) and turbulence) and partly as a result of internal autochthonous modification (aggregation, disintegration, porosity, stickiness, chemistry, hydrated density, surface roughness, internal diffusivity and biotic assemblage). The influence of the externalities will be dependent on its size in most instances and a clear understanding of size and sinking is therefore essential.

Large sinking aggregates such as zooplankton faecal pellets and marine snow transport organic matter to depth in the ocean. These particles affect nutrient distribution in the water column, feed life in the dark ocean, control carbon dioxide removal from the atmosphere, and determine deposition rates of surface material in the sediments several kilometres deep (Trull et al. 2008). More than 90% of the organic matter sinking below the euphotic zone is respired before it reaches a depth of a thousand meters (Robinson et al. 2010) and only organic matter sinking to depths greater than a thousand meters can be considered to be stored in the ocean for more than 100 years (Lampitt et al. 2008a). Most flux attenuation occurs in the upper few hundred meters of the water column where zooplankton grazing and microbial degradation is higher (Iversen et al. 2010; Jackson and Checkley 2011). It therefore seems reasonable that particles sinking more rapidly will make a greater contribution to the flux to the deep ocean than those which sink more slowly, these being recycled at shallow depths. The broader implication of this is that reduced attenuation in flux with depth will lead to a reduction in atmospheric carbon dioxide concentration (Kwon et al. 2009).

We know very little about particle settling behaviour in the ocean. This is because it is

extremely difficult to measure the sinking velocity of individual untouched and undamaged particles in the water column where horizontal flows are typically several orders of magnitude higher than the sinking velocities of particles. Several in situ estimates of particle sinking velocities have been made using a variety of approaches such as settling chambers that excluded ambient water movements (Diercks and Asper 1997; Nowald et al. 2009; Pilskaln et al. 1998), by measuring the arrival time of peak fluxes at traps deployed at different depths (Fischer and Karakas 2009), from the arrival times of material on the deep-sea floor (Billett et al. 1983) or by relating concentrations of particles obtained with in situ cameras with fluxes of particles collected in gel-traps (McDonnell and Buesseler 2010). Only very few direct measurements of undisturbed aggregates while still sinking in an unrestricted water column have been done and those measurements have all been obtained using SCUBA diving and hence confined to the surface ocean (Alldredge and Gotschalk 1988; Alldredge and Gotschalk 1989).

Settling velocities of similar types of aggregates generally increase with aggregate size (Alldredge and Gotschalk 1988; Alldredge and Gotschalk 1989; Iversen and Ploug 2010). However, aggregate size alone is not a good indicator for sinking velocity (Kiørboe et al. 1998), which mainly depends on the aggregate composition, shape and porosity (Iversen and Ploug 2010). Still, many processes can alter the sinking velocity of aggregates while they sink through the water column, such as zooplankton feeding (Iversen et al. 2010; Stemmann et al. 2004) transforming marine snow into faecal pellets, fragmentation by zooplankton (Dilling and Alldredge 2000; Iversen and Poulsen 2007; Lampitt et al. 1990) and disaggregation due to physical shear, resulting in smaller and possibly slower settling aggregates.

In an attempt to obtain in situ settling velocities from undisturbed aggregates in an unrestricted water column at depths down to 530 m, we modified a neutrally buoyant platform to carry an optical system. Our study was over the Porcupine Abyssal Plain in the Northeast

Atlantic (49°N 16.5°W) (Lampitt et al. 2001) at the PAP Sustained Observatory (PAP-SO) during the research cruise with James Cook (JC087) from the 31st May to the 18th June 2013. We choose this site because it has little horizontal input of particles (Weaver et al. 2000), less eddy activity than most other marine regions (Chelton et al. 2007), and generally has weak currents (Lampitt et al. 2001) with limited lateral advection (Hartman et al. 2010; Williams et al. 2006).

Material and methods

PELAGRA – neutrally buoyant sediment traps

We equipped two PELAGRA sediment traps (neutrally buoyant platforms) with camera systems to image settling aggregates in the free water column. The PELAGRAS are neutrally buoyant sediment traps based on an APEX float (Webb Research Corporation, USA), which has been equipped with four funnel traps (Lampitt et al. 2008b; Saw et al. 2004). The APEX floats provide active buoyancy control that enables the PELAGRAS to maintain a level of constant pressure or density (according to the protocol adopted before deployment). This is achieved by changing the volume of an external oil-filled bladder associated with the APEX float. Expansion of the bladder decreases the density of the PELAGRA causing it to rise and vice versa. Once the PELAGRA is in weight equilibrium with the surrounding water, it will only adjust its buoyancy by 1 cm³ changes in the oil-filled bladder volume if two consecutive 5 minute measurements are out of a pre-defined range. The PELAGRAS were fitted with two CTD sensors (Conductivity, Temperature and Depth), one at the top end of the APEX float (APEX CTD) and one near the bottom part (Idronaut CTD) of the PELAGRA. An additional temperature probe (combined pressure (RBRcoda³ D) and temperature (RBRcoda³ T) sensor from RBR Ltd., Canada) was placed at the top of the structure. We removed two of the funnel traps in order to image settling particles in an undisturbed water parcel. The camera systems consisted of a Canon EOS 6D DSLR camera equipped with a 50 mm macro lens, a Canon Speedlite 600EX-RT flash gun, a Quantum Turbo 3 battery pack, and a Hahnel Giga T Pro II remote timer. The camera, battery pack, and timer were mounted in one pressure housing and the flash gun in another. The two housings were arranged perpendicular to each other providing side-illumination. The illuminated water parcel for each image had dimensions of 14.9 cm, 22.3 cm, and 10 cm (height, width, and depth), equivalent to a volume of 3.32 litres (Fig. 1). The camera systems captured an image sequence of 10 images with two seconds between each

image. During the PELAGRA deployments we obtained one image sequence every hour with a pause of 59 min and 42 seconds between the sequences. Two modified PELAGRAs were deployed simultaneously three times in June 2013 on the 3rd (48.7°N 16.1°W), the 6th (48.6°N 16.1°W) and the 9th (48.7°N 16.1°W).

Selection of image sequences

Several sequences were obtained at periods when the PELAGRAs were descending or ascending to its target depth. We discarded those sequences since the PELAGRAs were out of equilibrium with the surrounding water mass and, therefore, not “locked” into the water mass and not moving in a Lagrangian manner. This selection criterion resulted in 55 image sequences where the PELAGRAs appeared to be in equilibrium and no indications of turbulence were observed in the trajectories of the imaged particles. However, we cannot exclude the possibility that slight upward or downward movements of the PELAGRAs occurred. This would increase or decrease the measured sinking velocities equally across all particle sizes and therefore over- or underestimate the absolute sinking velocities but not affect the slope of a regression line (power function) plotted for the relationship between aggregate size and sinking velocity. In order to estimate the absolute sinking velocities as a function of aggregate size, we introduced a second selection criterion and only accepted image sequences from periods where the temperature range measured with the CTDs were within a 3 milli-degrees (C) variation during the 10 min preceding the captured image sequence. This resulted in 12 image sequences from which we obtained absolute sinking velocities as a function of aggregate size.

Image analysis

We analysed the image sequences in C++ with Qt using OpenCV libraries for image processing. This was done by converting the images into grey scales and using the first image in a sequence as a reference image which was subtracted from remaining nine images to remove

the background. Hereafter a threshold value of 17 was used to produce a binary image with each particle projected as white objects on a black background. Optical noise was removed from the images by eroding and dilate each object with a Kernel size of 3x3 pixels. We only accepted a particle if its area was larger than 12 pixels and used the pixel size of 40.8 μm per pixel to get the real size of the particle. This resulted in particles with areas larger than 490 μm^2 . The particle area was converted into equivalent spherical diameter (ESD) and resulted in a minimum particle ESD of 80 μm . In this way, the image analyses returned pixel area, length of the longest axis, length of the shortest axis, and x and y position of each particle captured in an image (we excluded zooplankton).

Laboratory calibrations of particle sizes and sinking velocities

The illuminated depth of field in our optical setup was 10 cm, which will cause particles observed in the front of the illuminated field (close to the camera) to appear larger and sink faster than particles at the back of the illuminated field. To test this uncertainty for our system we made laboratory calibrations using coloured agar beads of know sizes. This was done by comparing sizes and settling velocities for the same agar beads measured at the front, middle and back of the illuminated field of depth. The image analyses returned similar sizes for the beads as those measured microscopically prior to the calibration. However, when using a pixel size determined for center of the illuminated filed of depth (40.8 μm per pixel), the individual beads were either 9% smaller or larger and sank 13% slower or faster when they were measured at the back or the front of the illuminated field of depth, respectively. Hence, our optical system has an uncertainty of $\pm 9\%$ for the sizes and $\pm 13\%$ for the settling velocities, we have added this uncertainty as standard deviations for the ESDs and the sinking velocities.

In situ size-specific sinking velocities

We measured size-specific sinking velocities for 55 image sequences selected for different depths and at different times of the day. This was done using the C++ script to identify an aggregate in one image and searched for the same aggregate in the subsequent image. The identification of the particle in the subsequent image was carried out searching a box with x-position being 100 pixels wide on each side of the previous position and 400 pixels below the previous position, i.e. 200 x 400 pixels (8.16 x 16.32 mm). The program would search for a particle with an area that was only deviating by maximum 20% of the size determined in the previous image. This was performed for all particles in all images and trajectories for each particle were superimposed on a stacked image containing all ten images from the sequence. We then verified each trajectory and removed doubles, zooplankton, and false trajectories. We used the projected area for each particle to calculate the ESDs of the aggregates and the axis-lengths to calculate the aspect ratio (AR), which indicate the roundness of the particles. Only the 12 image sequences that had less than 3 milli-degrees (°C) variation in temperature 10 minutes prior to the start of the image sequences provided absolute size-specific sinking velocities (see above). However, all 55 sequences provided reliable slopes for the regressions between sinking velocity and aggregate ESD.

Statistical analyses

We tested for normality using the Shapiro-Wilk test (SigmaPlot 12.0) and used either the parametric Pearson Correlation or the nonparametric Spearman Rank-Order Correlation (SigmaPlot 12.0). Pearson was used when both the aggregate sizes and sinking velocities for one image-sequence were normally distributed and Spearman was used when one or both of the parameter (size and settling velocity) were not normally distributed.

Results

The 55 image sequences provided direct observations of size-specific sinking velocities

for 1060 individual aggregates, n.b. only 12 sequences provided absolute sinking velocities, i.e. 158 individual aggregates. The 1060 particles varied in ESD from 0.04 to 2.98 mm (Mean 0.69 ± 0.40 mm). The aspect ratios of the aggregates averaged 1.40 ± 1.21 , suggesting that the majority of the aggregates were ellipsoidal. Generally, the aggregates were similar in appearance and apart from a few faecal pellets from krill, amphipods, and copepods, most aggregates appeared flocculent and amorphous with a white colour, which is typical for phytodetrital aggregates and marine snow.

Considering first the larger collection of 55 sequences some of which may not have been obtained by a completely “locked” PELAGRA (i.e. during periods when the PELAGRAS were out of equilibrium with the surrounding water mass), only ten of the 55 sequences had significant correlations between aggregate ESDs and sinking velocities ($p < 0.05$), eight of which were positively correlated and two that were negatively correlated. The absolute sinking velocities were derived from the 12 sequences that were obtained during periods when the PELAGRAS were in equilibrium with the surrounding water masses. These 12 sequences had a range in sinking velocities from 4 to 416 m d^{-1} (Mean: $156 \pm 98 \text{ m d}^{-1}$, Fig. 2) and had ESDs in a range between 0.1 and 1.9 mm (Mean: 0.6 ± 0.3 mm, Fig. 2). None of the 12 sequences had significant correlations between ESDs and sinking velocities (Fig. 2). The 18% and 26% variability in size and sinking velocity estimates, respectively, which was caused by the optical configuration of the camera systems (see Material and Methods), were less than the variability in the size-specific sinking velocities measured for the aggregates in situ. The aggregates sank in a stable orientation without rotating or spinning. The relationship between sinking rate and AR did not reveal significant correlations ($p > 0.05$) (Fig. 3). The same was observed for other shape descriptors: i) projected aggregate area, ii) circularity (ratio between perimeter estimated from the ESD and the actual perimeter), iii) longest axis perpendicular to the settling direction and iv) the Corey shape factor (Dietrich 1982), data not shown. It therefore seemed that neither

aggregate size nor shape controlled the settling velocity. There was no clear trend when plotting average settling velocity for each image sequence against their capture time or depth (Fig. 4), suggesting that there was no vertical or diel pattern in the settling velocities.

Discussion

We first consider the 12 sequences which were obtained during periods when the PELAGRAAs were in equilibrium with the surrounding water mass. These sequences provided absolute sinking velocities of the aggregates (Fig. 2). We observed some variation in size-specific sinking velocities between the 12 image sequences. The majority of the aggregates had sinking velocities in the range from 20 m d⁻¹ to 300 m d⁻¹ which is typical for in situ measurements of aggregates smaller than 1.5 mm (Alldredge and Gotschalk 1988; Alldredge and Gotschalk 1989; Nowald et al. 2009). Further, on-board flow-chamber measurements of sinking velocities using in situ formed aggregates that were collected with Marine Snow Catchers during the same cruise provided velocities ranging from 10 to 450 m d⁻¹ for aggregate sizes between 0.2 and 1.7 mm. This supports that the PELAGRAAs measured sinking velocities and aggregate sizes in a realistic range.

For the larger collection of 55 sequences with 906 particles, we cannot exclude the possibility that the PELAGRA platforms were gently ascending or descending during image capture. This would have caused a general increase or decrease in apparent sinking velocities. It would not, however, affect the regression between size and sinking velocity for a sequence as the apparent velocity of all particles would be equally affected. With that in mind, only 8 of the 55 sequences had significant positive correlations between sizes and sinking velocities ($p < 0.05$) and one can state with some confidence that during this particular time period at PAP-SO “size does not matter after all”.

Typically in laboratory studies with aggregates of similar composition, there is a positive relationship between particle size and sinking velocity (see Turner 2002). However, previous measurements of in situ aggregate settling showed poor correlations between sinking velocity and aggregate size (Alldredge and Gotschalk 1988; Alldredge and Gotschalk 1989),

which is most likely due to the heterogeneity of in situ aggregates (Iversen and Ploug 2010; Ploug et al. 2008a; Ploug et al. 2008b). Similarly, Laurenceau-Cornec et al. (2015) observed that particulate samples from two different sites formed aggregates with different structure, composition, and size-specific sinking velocities and that relationships between size and settling only occurred for very compact aggregates. Iversen and Ploug (2010) observed that aggregates of similar composition showed clear size to settling relationships, while this relationship was lost when plotting many aggregate types together.

The sinking velocities of similar-sized aggregates are controlled by their excess density, which is determined by their composition and compactness (Ploug et al. 2008a). Zooplankton faecal pellets and gelatinous aggregates are generally more compact than large porous phytoplankton aggregates, such as marine snow (Iversen and Ploug 2010). This suggests that part of the variable sinking velocities for similar-sized aggregates within individual sequences was caused by different aggregate types having similar sizes (Fig. 2).

We only observed a few target particles which had the characteristics of faecal pellets and the majority were phytodetrital aggregates that looked very similar. However, we deduce that they were of a heterogeneous nature with different composition, internal structure, and densities, leading to the variability in size-specific sinking velocities. Marine snow ballasted with minute minerals such as liths from coccolithophores or lithogenic material deposited as airborne dust will increase the density and sinking velocity of an aggregate, compared to a non-ballasted aggregate, without changing its appearance significantly (Iversen and Robert 2015; Passow and De La Rocha 2006; Ploug et al. 2008a; van der Jagt et al. 2018). This complicates any attempts to estimate export flux from in situ observations of aggregate size-distribution and abundance alone. Without direct measurements of in situ sinking velocities, it is not possible to differentiate slow sinking from fast sinking aggregates of similar sizes.

It would be unlikely to find aggregates only formed from similar particles under identical conditions in the ocean and we therefore have to assume that any depth in the ocean contains a pool of heterogeneous aggregates with different age, composition, density, structure, and porosity. This suggests that no universal scaling between aggregate sizes and sinking velocities exists in the ocean, which also explains why this and many other in situ studies did not observe increasing sinking velocities with increasing aggregate sizes (Diercks and Asper 1997; Karakas et al. 2009; Nowald et al. 2009), as is generally found for similar composed laboratory aggregates (Iversen and Ploug 2010; Iversen and Ploug 2013; Iversen and Robert 2015). In the past, fluxes have been calculated from in situ aggregate size-distribution and abundance by assuming that aggregate settling velocity increase with increasing aggregate size (Guidi et al. 2008; Iversen et al. 2010; Jackson et al. 2005). This is of course true for aggregates of similar composition, but will vary between different aggregate types (Iversen and Ploug 2010; Ploug et al. 2008a) and especially for a heterogeneous pool of in situ aggregates (Fig. 2). We therefore need improved optical systems that can differentiate aggregates and pool similar aggregate types. This will allow implementation of different scaling-relationships between size and sinking velocity and help us to understand the aggregate characteristics, which control in situ settling.

Microbial carbon-specific degradation rate is similar across different types of sinking aggregates irrespective of their composition and size (Belcher et al. 2016; Iversen and Ploug 2010; Ploug et al. 2008a). If both sinking velocity and microbial carbon-specific degradation rate are size-independent for an in situ pool of aggregates, then one would assume that all aggregate sizes are equally likely to be exported to the deep ocean. This suggests that the remineralization length scale is similar for all aggregate sizes and that particles size-spectra will change little with increasing depth, which indeed seems to be the case in the mesopelagic and bathypelagic zones (Iversen et al. 2010). However, zooplankton interactions with settling

aggregates have caused large variations in average particle size, slopes of particle size-spectra and aggregate abundance in the upper water column, especially at the base of the euphotic zone (Iversen et al. 2010; Jackson and Checkley 2011; Lampitt et al. 1993). This suggests that the biological activity taking place at the transition zone between the upper mixed layer and the mesopelagic zone determines the magnitude and efficiency of the biological carbon pump (Jackson and Checkley 2011). Better understanding of aggregate dynamics in that transition zone is paramount to our understanding and prediction of organic matter export and biogeochemistry. The ability of neutrally buoyant systems to ‘park’ at this critical depth and obtain simultaneous measurements of aggregate size, abundance, type, and sinking velocity provides a powerful tool to study how aggregate type and structure influence sinking velocity and affects total export of organic matter to the deep ocean.

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Figures

Fig. 1: Arrangement of the camera system on the PELAGRA. The left image shows the whole PELAGRA with the mounted camera system during deployment. The right image is a close up of the flash (left pressure housing) mounted perpendicular to the camera pressure housing. The scale bar in the upper left corner of each image is 30 cm long.

Fig. 2: Size (equivalent spherical diameter) and sinking velocities of the aggregates measured during each image sequence with temperature variations less than 3 milli-degrees ($^{\circ}\text{C}$) during the 10 minutes prior to the capture of an image sequence. The deployment number (Dep 1, Dep 2, and Dep 3) is provided in each figure panel for the two PELAGRAs, PA and PB. The standard deviations are representing the uncertainties in the measurements depending on the position of the aggregates in the illuminated field of depth, i.e. 18% in size and 26% in sinking velocities.

Fig. 3: The Aspect Ratio (longest to shortest axis) and sinking velocities of the aggregates measured during each image sequence. The deployment number (Dep 1, Dep 2, and Dep 3) is provided in each figure panel for the two PELAGRAs, PA and PB.

Fig. 4: Box plots of the sinking velocities for each deployment plotted against the water depth (upper panel) and time of day (lower panel) for each image sequence.

Fig 1



Fig 2

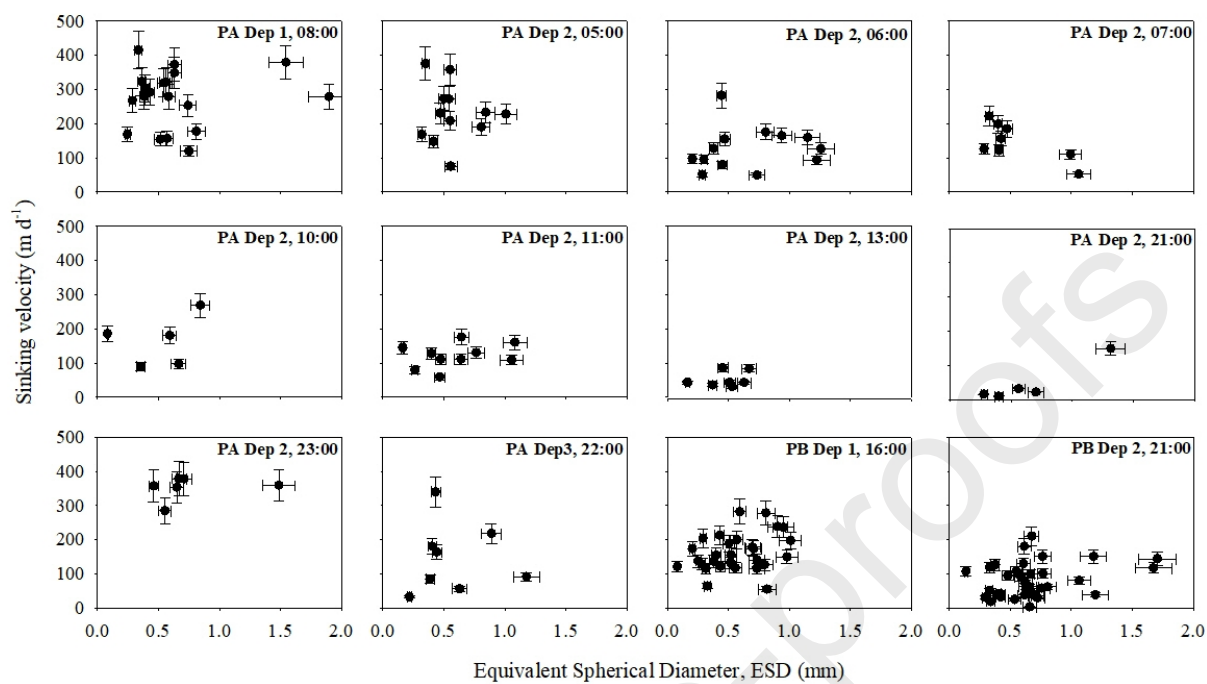


Fig. 3

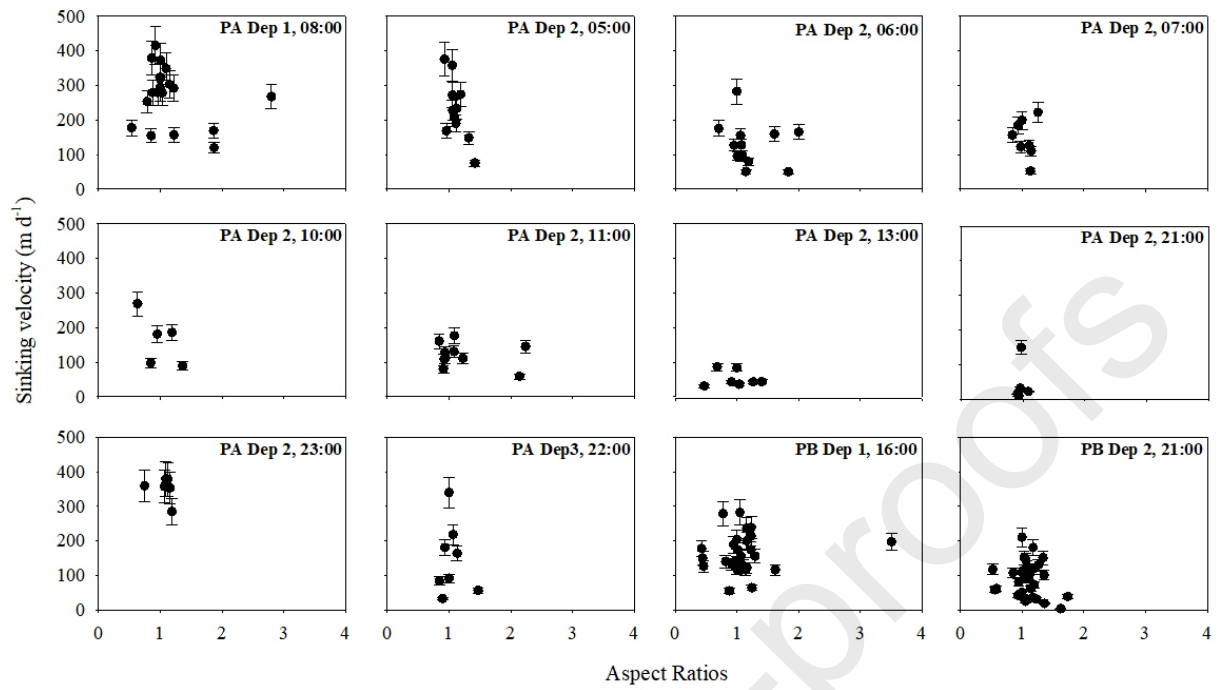
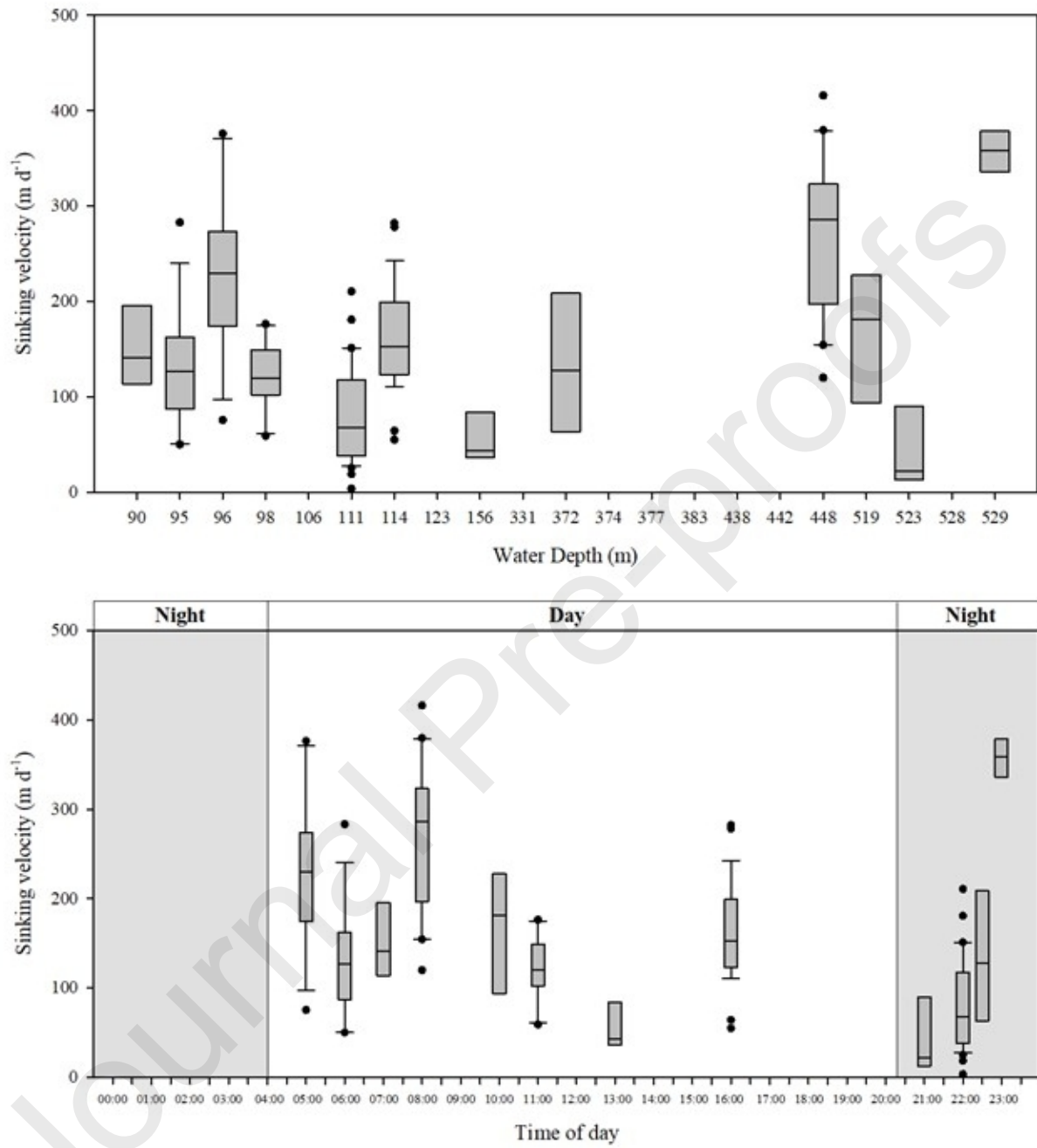


Fig. 4



Highlights to Size does not matter after all: No evidence for a size-sinking relationship for marine snow

There are very few studies of aggregate settling velocities as a function of size from direct and undisturbed measurements in the water column. Mostly the depths for such in situ measurements have been restricted to SCUBA depths in the upper tens of metres. We developed an in situ camera system mounted on a neutrally buoyant platforms and generated the first ever made measurements of size and settling of in situ particles in the mesopelagic. In total we measured the settling velocities of 1060 individual aggregates and discovered that there was surprisingly little effect of particle size, despite that this is main parameter used to estimate aggregate settling from in situ camera observations of aggregate size-distribution. This shows that one has to be very careful when use particle size-spectra to calculate export flux through the water column.

Size does not matter after all:

No evidence for a size-sinking relationship for marine snow

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The authors have no conflict of interest.

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