

1 Slow particle remineralization, rather than  
2 suppressed disaggregation, drives efficient  
3 flux transfer through the Eastern Tropical  
4 North Pacific Oxygen Deficient Zone

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17 ***1 Key Points***

18 The upper mesopelagic of the oligotrophic Eastern Tropical North Pacific Oxygen Deficient Zone (ODZ)  
19 has low flux attenuation.

20 Comparison of particle size observations to models suggests that the breakdown of particles of all sizes is  
21 slow throughout the ODZ.

22 Zooplankton appear to transport organic matter into, and disaggregate particles within, the ODZ above  
23 500 m.

## 24 **2 Abstract**

25 Models and observations suggest that particle flux attenuation is lower across the mesopelagic zone of  
26 anoxic environments compared to oxic environments. Flux attenuation is controlled by microbial  
27 metabolism as well as aggregation and disaggregation by zooplankton, all of which also shape the relative  
28 abundance of differently sized particles. Observing and modeling particle spectra can provide information  
29 about the contributions of these processes. We measured particle size spectrum profiles at one station in  
30 the oligotrophic Eastern Tropical North Pacific Oxygen Deficient Zone (ETNP ODZ) using an  
31 underwater vision profiler (UVP), a high-resolution camera that counts and sizes particles. Measurements  
32 were taken at different times of day, over the course of a week. Comparing these data to particle flux  
33 measurements from sediment traps collected over the same time-period allowed us to constrain the  
34 particle size to flux relationship, and to generate highly resolved depth and time estimates of particle flux  
35 rates. We found that particle flux attenuated very little throughout the anoxic water column, and at some  
36 time-points appeared to increase. Comparing our observations to model predictions suggested that  
37 particles of all sizes remineralize more slowly in the ODZ than in oxic waters, and that large particles  
38 disaggregate into smaller particles, primarily between the base of the photic zone and 500 m. Acoustic  
39 measurements of multiple size classes of organisms suggested that many organisms migrated, during the  
40 day, to the region with high particle disaggregation. Our data suggest that diel-migrating organisms both  
41 actively transport biomass and disaggregate particles in the ODZ core.

## 42 **3 Plain Language Summary**

43 Marine snow are microscopic particles that form in the surface of the ocean and sink into the deep ocean.  
44 Most of these particles are the remains of dead algae and feces of tiny animals (zooplankton). The deeper  
45 the particles sink into the ocean before microbes or animals consume them, the longer it takes before the  
46 carbon in those particles can return to the atmosphere. In parts of the ocean where there is no oxygen,  
47 more particles sink to greater depths, for reasons that are not well-understood. We used an underwater  
48 camera to observe marine snow particles in the ocean just west of Mexico where there is little to no  
49 oxygen at depth. We compared the observations to predictions from several computer simulations  
50 representing hypothesized mechanisms to explain why particles are consumed less in water without  
51 oxygen. Our measurements suggest that one reason that particles sink to deeper depths here is because  
52 microbes consume the particles slowly when there is no oxygen. Meanwhile, zooplankton still break large  
53 particles into smaller ones and produce fecal pellets in these low oxygen waters.

## 54 **4 Introduction**

55 The biological pump, in which sinking microaggregate (< 500  $\mu\text{m}$ ) and marine snow (> 500  $\mu\text{m}$ ) particles  
56 (Simon et al., 2002) transport carbon from the surface into the deep ocean, is a key part of the global  
57 carbon cycle (Neuer et al., 2014; Turner, 2015). Organic matter flux into the deep ocean (>1000 m) is a  
58 function both of export from the photic zone into the mesopelagic (export flux), and the fraction of that  
59 flux that crosses through the mesopelagic (transfer efficiency) (Francois et al., 2002; Passow & Carlson,  
60 2012; Siegel et al., 2016). While definitions vary between studies, we define “mesopelagic” as the region  
61 between the base of the photic zone, and 1000 m (following Francois et al., 2002; Cram et al., 2018). The  
62 transfer efficiency of the biological pump may affect global atmospheric carbon levels (Kwon & Primeau,  
63 2008). Thus, understanding the processes that shape organic matter degradation in the mesopelagic is  
64 critical.

65 Oxygen concentrations, and especially the geographic and vertical extent of anoxic ocean regions, appear  
66 to modulate particle flux through the mesopelagic. Observations of particle flux in the Eastern Tropical  
67 North Pacific near the Mexican coast (Hartnett & Devol, 2003; Van Mooy et al., 2002; Weber & Bianchi,  
68 2020), the Eastern Tropical South Pacific (Pavia et al., 2019), and Arabian Sea (Keil et al., 2016; Roullier  
69 et al., 2014) have suggested lower flux attenuation in these ODZ systems. Models have shown that  
70 accounting for oxygen limitation in ODZs is necessary to fit global patterns of particle transfer (Cram et  
71 al., 2018; DeVries & Weber, 2017). Analysis of remineralization tracers has also shown evidence of slow  
72 flux attenuation in the ODZs (Weber & Bianchi, 2020). Understanding the driving mechanisms of these  
73 patterns is important because the oxygen content of the ocean is decreasing (Ito et al., 2017; Schmidtko et  
74 al., 2017), and the spatial extent and depth range of ODZs, including the Eastern Tropical North Pacific  
75 (ETNP) Oxygen Deficient Zone (ODZ), are likely to change, though there is disagreement over whether  
76 they are expanding or undergoing natural fluctuation (Deutsch et al., 2014; Horak et al., 2016; Stramma et  
77 al., 2008). Recent data informed models suggest that ODZs may enhance carbon transport to the deep  
78 ocean, by inhibiting microbial degradation of sinking marine particles (Cram et al., 2018). However,  
79 biological organic matter transport is also modulated by zooplankton whose interactions with particle flux  
80 in pelagic ODZs are only beginning to be quantitatively explored (Kiko et al., 2020).

81 Zooplankton modulate carbon flux through the mesopelagic (Jackson & Burd, 2001; Steinberg & Landry,  
82 2017; Turner, 2015), and by extension the transfer efficiency of the biological pump (Archibald et al.,  
83 2019; Cavan et al., 2017), in three key ways that could be affected by ocean oxygen concentrations:

84 (1) *Active transport*: Zooplankton migrate between the surface and mesopelagic, consuming plankton and  
85 particles in the surface and producing particulate organic carbon (POC), dissolved organic carbon (DOC),

86 respiratory CO<sub>2</sub>, and zooplankton carcasses at depth (Archibald et al., 2019; Bianchi et al., 2013;  
87 Hannides et al., 2009; Steinberg et al., 2000; Stukel et al., 2018, 2019). This manuscript focuses on  
88 particles, so we only consider POC and carcass production, which cause particles to “appear” in the  
89 midwater.

90 (2) *Repackaging*: Zooplankton fecal pellets have different physical properties than the particles and  
91 plankton that they ingest (Wilson et al., 2008). In this paper we define repackaging as zooplankton  
92 feeding in the mesopelagic and producing fecal pellets, effectively aggregating POM.

93 (3) *Disaggregation*: Zooplankton break large particles into smaller ones in two ways – by Coprorhexy  
94 (also sometimes called sloppy feeding) in which they break particles apart while feeding on them  
95 (Lampitt et al., 1990; Noji et al., 1991; Poulsen & Kiørboe, 2005), and by generating turbulence while  
96 they swim (Dilling & Alldredge, 2000; Goldthwait et al., 2005). Disaggregation can reduce particle  
97 transfer efficiency, because smaller particles sink more slowly and so reside longer in mesopelagic,  
98 allowing them to be consumed before reaching deep waters (Goldthwait et al., 2005; Lampitt et al., 1990;  
99 Noji et al., 1991; Poulsen & Kiørboe, 2005). In some cases, disaggregation can explain around 50% of the  
100 particle flux attenuation over depth (Briggs et al., 2020).

101 The migratory zooplankton that drive these mesopelagic processes spend the night in the surface layer  
102 and migrate into the core of the OMZ during the day (Bianchi et al., 2014). These organisms likely survive  
103 in ODZs by slowing their metabolic processes, but may supplement these with very efficient oxygen  
104 uptake and anaerobic metabolism (Seibel, 2011). Acoustic data suggest that zooplankton do not migrate  
105 as deeply into ODZs as they do into regions where ODZs are absent (Bianchi et al. 2011). New evidence  
106 suggests that in ODZ regions with shallower oxyclines, night-time migration depth remains the same but  
107 the depth where the organisms spend the day is compressed (Wishner et al., 2020). The rates at which  
108 zooplankton transport, repackage and disaggregate particles in ODZs are difficult to measure and  
109 therefore poorly constrained. Despite the importance of zooplankton mediated processes to global carbon  
110 flux, zooplankton are often missing from models of particle transfer.

111 Current models of particle transfer through the mesopelagic ocean predict that particle size, ocean  
112 temperature, and oxygen concentrations are the dominant factors controlling particle flux attenuation  
113 (Cram et al., 2018; DeVries & Weber, 2017). These models, however, do not account for active transport  
114 or disaggregation by zooplankton. As a result of this assumption, the models predict that small particles  
115 preferentially attenuate with depth, which is often not borne out by observations (Durkin et al., 2015).  
116 Therefore, these models’ predictions provide a useful null hypothesis of expected particle size  
117 distributions in the absence of zooplankton effects, which can be compared to observed distributions of  
118 particles to explore the magnitude of zooplankton effects.

119 Underwater vision profilers are cameras that can count and size many particles over large water volumes  
120 (Picheral et al., 2010) and provide valuable information about particle distributions and transport. When  
121 deployed in concert with particle traps in some regions, they can be used to predict flux in other regions  
122 where traps have not been deployed (Guidi et al., 2008; Kiko et al., 2020). Connecting UVP and trap data  
123 can furthermore inform about total particle flux variability across space and time, relationships between  
124 particle size, biomass, composition, and sinking speed, as well as the contributions of the different  
125 particle sizes to flux (Guidi et al., 2008; Kiko et al., 2017). Combined particle trap flux and UVP data  
126 from the North Atlantic suggest active transport by zooplankton into hypoxic water (Kiko et al., 2020),  
127 but the authors suggest that in more anoxic and larger ODZs, such as the modern day ETNP, there might  
128 be reduced active transport into the mesopelagic, since many migratory organisms would presumably not  
129 migrate into the anoxic water and would be less active. In this manuscript we provide the first combined  
130 flux measurement and UVP data from such a fully anoxic region, the ETNP ODZ.

131 In addition to being fully anoxic, the ETNP ODZ is primarily oligotrophic: most of the volume of the  
132 ETNP ODZ is below regions of very low surface productivity (Fuchsman et al., 2019; Pennington et al.,  
133 2006). Meanwhile most flux data have been measured in more coastal, higher productivity regions of the  
134 ETNP (Hartnett & Devol, 2003; Van Mooy et al., 2002).

135 A recent modeling study posed three hypotheses to explain why particle flux attenuates slowly in ODZs  
136 (Weber & Bianchi, 2020), which are susceptible to testing with UVP data. These are: **H1:** All particles in  
137 ODZs remineralize more slowly than in oxic water, regardless of their size, due to slower carbon  
138 oxidation during denitrification than aerobic respiration. **H2:** Breakdown of large particles into small  
139 particles is suppressed in the ODZ because there is less disaggregation by zooplankton than elsewhere.  
140 **H3:** Large particles remineralize more slowly in ODZs, but smaller ones do not, because carbon oxidation  
141 in large particles can become limited by the diffusive supply of oxygen and nitrate. In this case,  
142 respiration can only proceed by thermodynamically inefficient sulfate reduction (Bianchi et al., 2018;  
143 Lam & Kuypers, 2011). Sulfide and organic matter sulfurization have been found on particles at this site  
144 at nanomolar concentrations (Raven et al., 2021). Microbial analysis of particles found sulfate reducers  
145 and S-oxidizing denitrifiers at low abundances (Fuchsman et al., 2017; Saunders et al., 2019). Each of the  
146 hypotheses outlined above were predicted to leave distinct signatures in particle size distributions in the  
147 core of ODZ regions (Weber & Bianchi, 2020). The model with slow remineralization of all particles,  
148 predicts an increase in the abundance of small particles in the ODZ core relative both to overlying waters  
149 and to similar, oxygenated environments (**H1**). The model with suppressed disaggregation predicts a large  
150 decrease in small particle biomass in the ODZ, both relative to the surface and to oxygenated water (**H2**).  
151 The model in which remineralization is depressed only in large particles predicts a small decrease with

152 depth in small particle abundance, similar to that seen in oxygenated environments (**H3**). However, the  
153 necessary particle size data from an ODZ was not previously available to support any hypothesis at the  
154 exclusion of the others. In this manuscript we present a new dataset that is sufficient to test these three  
155 hypotheses.

156 To provide the data to test hypotheses **H1-H3** and illuminate zooplankton particle interactions in  
157 oligotrophic ODZs, we collected particle size data at high temporal resolution over the course of a week  
158 in an anoxic site typical of the oligotrophic ETNP ODZ, well away from the high productivity zone in the  
159 coast. We integrated this size data with observed flux measurements, and acoustic data. We quantified,  
160 throughout the water column, how changes in size distribution deviate from changes that would be  
161 predicted by remineralization and sinking only models.

162 We ask the following four questions:

163 **Question A:** How does the particle size distribution at one location in the oligotrophic Eastern Tropical  
164 North Pacific vary with respect to depth and time?

165 **Question B:** Do our data support any of the three Weber and Bianchi (2020) models (**H1-H3**)?

166 **Question C:** Do our data suggest that regions of the oxygen deficient zone harbor disaggregation-like  
167 processes, and if so, do these co-occur with migratory zooplankton?

168 **Question D:** How do particle size distribution spectra in the ODZ compare to those seen in the oxic  
169 ocean?

170 By addressing these four questions, we demonstrate that our dataset from the ETNP supports Weber and  
171 Bianchi's first hypothesis, that microbial remineralization of all particles slows in the ODZ, while  
172 disaggregation continues unabated. Additionally, disaggregation-like processes do appear to co-occur  
173 with acoustic measurements of migratory zooplankton, suggesting that exclusion of zooplankton is not a  
174 major contributor to slow flux attenuation.

## 175 **5 Methods**

176 Unless specified otherwise, measurements were taken on board the R/V *Sikuliaq*, cruise number  
177 SKQ201617S, from 07 January 2017 through 13 January 2017 at a single station 16.5°N 106.9°W, which  
178 was located in an oligotrophic region of the Eastern Tropical North Pacific Oxygen Deficient Zone  
179 (ETNP Station P2; Figure 1A). Data are compared against measurements taken at 16.5°N 152.0°W on 08  
180 May 2015, collected on the GO-SHIP CLIVAR/CARBON P16N Leg 1 Cruise (CCHDO Hydrographic  
181 Cruise 33RO20150410). This station was at the same latitude as ETNP Station P2, west of the ODZ, but  
182 was not anoxic (P16 Transect Station 100; Figure S1).

## 183 **5.1 Water property measurements**

184 We measured water properties of temperature, salinity, fluorescence, oxygen concentration and turbidity  
185 using the shipboard SeaBird 911 CTD. Auxiliary sensors included a WetLabs C-Star (beam attenuation  
186 and transmission) and a Seapoint fluorometer. Data were processed with Seabird Software, (programs–  
187 data conversion, align, thermal mass, derive, bin average and bottle summary) using factory supplied  
188 calibrations. Data was analyzed and visualized in *R* (Team 2011). Processed data are available under  
189 NCEI Accession number 1064968 (Rocap et al., 2017).

## 190 **5.2 Water mass analysis**

191 Evans et al. (2020) previously employed optimum multiparameter analysis to map the percent identity of  
192 the water observed at each depth to three water masses: the 13 Degree Celsius Water (13CW), North  
193 Equatorial Pacific Intermediate Water (NEPIW), and Antarctic Intermediate Water (AAIW). We subset  
194 and examine only the portion of these data that correspond to our site.

## 195 **5.3 Acoustic Measurements**

196 Backscattering signals from the ship-board EK-60 were collected and archived by UNOLS as raw data  
197 files. We used Echopype software (Lee et al., 2021) to convert these raw files to netcdf files, which were  
198 down-sampled to five minute time-step resolution, saved as a text file, and later visualized in *R*. The  
199 acoustic data appeared to be off by one hour and so one hour was subtracted from all time measurements.  
200 This correction resulted in zooplankton vertical migrations being synchronized with the diel light cycle as  
201 was recorded on board the ship by JAC.

## 202 **5.4 Particle size measurements**

203 Particle size data were collected by an Underwater Vision Profiler 5 (UVP) that was mounted below the  
204 CTD-rosette and deployed for all CTD casts shallower than 2500 m. A UVP is a combination camera and  
205 light source that quantifies the abundance and size of particles from 100  $\mu\text{m}$  to several centimeters in size  
206 (Picheral et al., 2010). UVP data were processed using the Zooprocess software, which prepares the data  
207 for upload to the Ecotaxa database (Picheral et al., 2017); data from all UVP instruments are located on  
208 this online database for ease of access. Detailed descriptions for installation of the Zooprocess software  
209 can be found on the PIQv website (<https://sites.google.com/view/piqv/zooprocess-uvpapp>). Zooprocess  
210 uses the first and last image number selected by the user in metadata to isolate the downcast and process  
211 this subset for both particle size distribution and image data. The processed files and metadata are then  
212 uploaded to a shared FTP database where it is available for upload to Ecotaxa. This project required the  
213 extra step of filtering out images due to the discovery of an issue with the lighting system, where only one  
214 of the two LEDs would illuminate, resulting in an incomplete sample. The filtering procedure is

215 documented in a link available at the same location as the Zooproduct download. Images where only a  
216 single light illuminated were removed from the dataset before it was uploaded on to Ecotaxa. Once  
217 uploaded to Ecotaxa, data were downloaded from EcoPart (the particle section of the database) in detailed  
218 TSV format, and analyzed in R. The UVP provided estimates of abundances of particles in different size-  
219 bins, as well as information about the volumes over which those particle numbers had been calculated.

220 The instrument is capable of observing smaller particles (down to 60  $\mu\text{m}$ ), but these tend to be  
221 underestimated and so are excluded from the analysis. The instrument can in principle also measure larger  
222 particles (up to the field of view of the camera), though these tend to be scarce enough to be not detected.  
223 In this paper, we do not have an upper size cut-off for our analysis and rather implement statistics that are  
224 robust to non-detection of scarce large particles (section 5.5.1). Visual inspection of images larger than  
225 1 mm suggests that these large particles are primarily “marine snow” but about 5% are zooplankton. We  
226 did not quantify the size distribution of these images.

## 227 **5.5 Flux measurements**

228 Free floating, surface tethered particle traps were used to quantify carbon fluxes from sinking particles.  
229 Arrays, consisting of a surface float and two traps, were deployed and allowed to float freely during  
230 which time they collected particles. Trap deployments began on 07 January, concurrently with the  
231 beginning of the UVP sampling, and continued through 12 January. Trap recovery began on 08 January  
232 and continued through 13 January. Trap depths spanned the photic zone and mesopelagic, with the  
233 shallowest at 60 m and the deepest at 965 m. Trap deployments lasted between 21 and 91 hours, with  
234 deeper traps left out for longer, to collect more biomass. Two types of traps were deployed. One set of  
235 traps, generally deployed in shallower water, had a solid cone opening with area 0.46  $\text{m}^2$ . The second set  
236 had larger conical net with opening of 1.24  $\text{m}^2$  area made of 53  $\mu\text{m}$  nylon mesh similar to the description  
237 in Peterson et al. (2005). All equipment were combination incubators and particle traps, but in this study  
238 we only use trap data. No poisons were used, and both living and dead zooplankton, or ‘swimmers’, were  
239 manually removed prior to POC analysis.

240 Sediment trap material was filtered immediately upon trap recovery onto pre-combusted GF-75 45 mm  
241 filters (nominal pore size of 0.3  $\mu\text{m}$ ) and preserved until further analysis at  $-80^\circ\text{C}$ . These filters were split  
242 into several fractions for other analyses not discussed here. Total carbon content of particles in each trap  
243 were measured by isotope ratio mass spectrometry. Elemental analyses for particulate carbon and nitrogen  
244 quantities as well as  $^{13}\text{C}$  and  $^{15}\text{N}$  isotopic compositions were conducted at the U.C. Davis Stable Isotope  
245 Facility (<http://stableisotopefacility.ucdavis.edu>) on acidified freeze-dried trap samples to capture organic  
246 elemental contributions. Carbon was below mass spectrometry detection limits in four traps – these traps  
247 were excluded from further analysis. Traps at similar depths did detect carbon, lending confidence to the

248 idea that these non-detections were technical in nature, due to splitting of samples for multiple analyses,  
249 rather than reflecting environmental conditions.

## 250 **5.6 Analysis**

251 Particles were binned by depth with 20 m resolution between the surface and 100 m, 25 m resolution  
252 between 100 m and 200 m depths and 50 m resolution below 200 m. This increasing coarseness of the  
253 depth bins helped account for more scarce particles deeper in the water column, while maintaining higher  
254 depth resolution near the surface. To perform this binning, particle numbers, and volumes of water  
255 sampled of all observations within each depth bin were summed prior to other analyses. Most analyses  
256 focused on the mesopelagic, defined here as the region between the base of the secondary chlorophyll  
257 maximum layer (160 m — hereafter the base of the photic zone), which is within the ODZ, and 1000 m.

258 Two normalized values of particle numbers were calculated. In the first, particle numbers were divided by  
259 volume sampled, to generate values in *particles/m<sup>3</sup>*. In the second, particles were divided by both volume  
260 sampled and the width of the particle size-bins to generate values in *particles/m<sup>3</sup>/mm*.

### 261 **5.6.1 Particle size distribution**

262 We determined the slope and intercept of the particle size distribution spectrum by fitting a power law to  
263 the data, which is a common function for fitting particle size distributions (Buonassissi & Dierssen,  
264 2010). Because large particles were infrequently detected, we used a general linear model that assumed  
265 residuals of the data followed a negative-binomial (rather than normal) distribution. We fit the equation

$$266 \ln\left(\frac{E(\text{Total Particles})}{\text{Volume} \cdot \text{Binsize}}\right) = b_0 + b_1 \ln(\text{Size}) \quad (\text{Eqn 1}).$$

267 to solve for the Intercept ( $b_0$ ) and particle size distribution slope (PSD =  $b_1$ ). On the left-hand side of  
268 Eqn 1,  $E(\text{Total Particles})$  refers to the expected number of particles in a given depth and particle size bin  
269 assuming a negative binomial distribution of residuals (Date, 2020; Ooi, 2013).  $\text{Volume}$  indicates the  
270 volume of water sampled by the UVP, or in the case of depth-binned data, the sum of the volumes of all  
271 UVP images in that depth interval.  $\text{Binsize}$  indicates the width of the particle-size bin captured by the  
272 UVP. Thus, if particles between 0.1 and 0.12 mm are in a particle size bin, the  $\text{Binsize}$  is 0.02 mm. On the  
273 right-hand side of Eqn 1,  $\text{Size}$  corresponds to the lower bound of the particle size-bin. We use the lower  
274 bound of a particle size-bin, rather than its midpoint, because, due to the power-law particle size  
275 distribution slopes, the average size of particles in each size-bin is closer to the size-bin's lower bound  
276 rather than its midpoint.

## 277 5.6.2 Estimating particle flux

278 We estimated particle flux throughout the water column, by fitting particle data to trap measurements. We  
279 assumed that particle flux in each size bin ( $j$ ) followed the equation

$$280 \text{ Flux} = \sum_j \left[ \frac{\text{Total Particles}_j}{\text{Volume} * \text{Bin size}_i} * C_f * (\text{Size}_j)^A \right] \quad (\text{Eqn. 2})$$

281 Such that flux at a given depth is the sum of all size-bin specific values.

282 We used the *optimize()* function in R's stats package to identify values for the  $C_f$  and  $A$  coefficients in  
283 Eqn 2. that yielded closest fits of the UVP estimated flux to each particle trap.

284 We also estimated the exponent of the particle size to biomass exponent  $\alpha$  and size to sinking speed  
285 exponent  $\gamma$  per the equations  $\text{Biomass}_j \sim \text{Size}_j^\alpha$  and  $\text{Speed}_j \sim \text{Size}_j^\gamma$ . This is done by assuming a  
286 spherical drag profile, in which case  $A = \alpha + \gamma$  and  $\gamma = \alpha - 1$  (Guidi et al., 2008); with “A” referring to  
287 the exponent in Eqn 2.

## 288 5.6.3 Size specific information

289 We separately analyzed total particle numbers, particle size distribution, and particle flux for particles  
290 larger than or equal to 500  $\mu\text{m}$ , and those smaller than 500  $\mu\text{m}$ , to determine the relative contributions of  
291 these two particle classes to particle properties. 500  $\mu\text{m}$  was chosen as it has been previously defined as  
292 the cutoff point between microscopic “microaggregates” and macroscopic “marine snow” (Simon et al.,  
293 2002).

## 294 5.7 Variability

295 To explore the timescales of temporal variability in the POC flux, we determined how well the flux at  
296 each depth horizon can be described by the sum of daily and hourly temporal modes. This was achieved  
297 by fitting the general additive model of form

$$298 \text{ Flux}^{1/5} \sim s(\text{Depth}) + s(\text{Day}) + s(\text{Hour}) \quad (\text{Eqn. 3})$$

299 This model explored whether estimated flux levels appeared to vary by decimal day and decimal hour,  
300 holding the effects of depth constant, in the 250 m to 500 m region. The smooth terms  $s$  for *Depth* and  
301 *Day* were thin plate splines, while the  $s$  term for *Hour* was a cyclic spline of 24-hour period.

## 302 5.8 Smoothing for Comparison to Model Results

303 Normalized particle abundance data, from the only UVP cast that traversed the top 2000 m of the water  
304 column, taken on January 13 at 06:13, was smoothed with respect to depth, time, and particle size using a  
305 general additive model of the form

306  $\ln\left(\frac{E(\text{Total Particles})}{\text{Volume} \cdot \text{Binsize}}\right) \sim s(\text{Depth}, \ln(\text{Size}))$  (Eqn. 4)

307 In this case, there is a single, two-dimensional, smooth term, rather than additive one-dimensional terms  
308 as in Eqn. 3 so that the smooth term can consider interactions between the two parameters, rather than  
309 assuming that the terms are additive. The predicted particle numbers at each particle size and depth, as  
310 well as particle size distribution spectra, and estimated particle masses of all particles smaller than  
311 500  $\mu\text{m}$  and all particles larger than or equal to 500  $\mu\text{m}$  were then compared to each of Weber and  
312 Bianchi's (2020) models, corresponding to our **H1-H3**.

### 313 **5.9 Modeling remineralization and sinking**

314 To quantify disaggregation, our goal was to compare the particle size-abundance spectrum at each depth  
315 to a prediction of the null hypothesis, that it is simply governed by the effects of sinking and  
316 remineralization reshaping the spectrum observed shallower in the water column. This prediction is  
317 generated using the particle remineralization and sinking model (PRiSM), modified from DeVries et al.  
318 (2014), which we applied to the shallower spectrum as an initial condition. The difference between the  
319 null hypotheses prediction and observation indicates the role of processes not accounted for in PRiSM,  
320 such as disaggregation, aggregation, and active or advective transport of particles with a different size  
321 spectrum than the ones seen at the deeper depth.

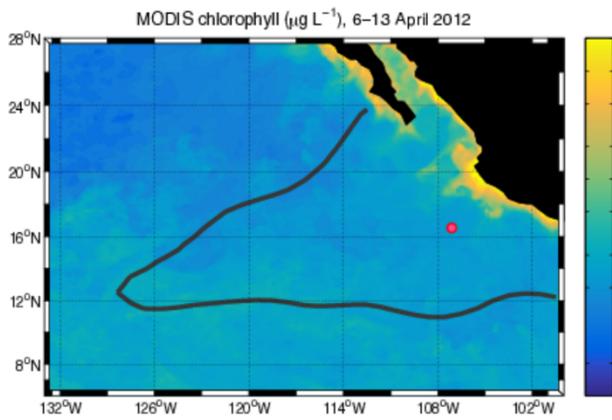
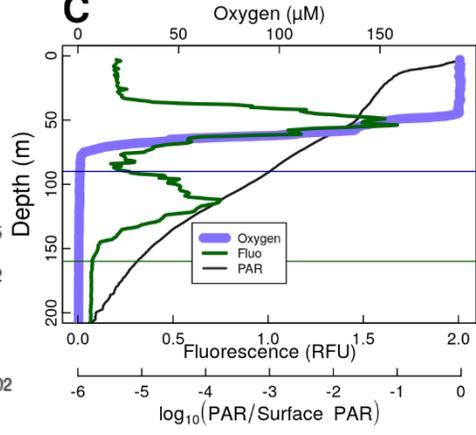
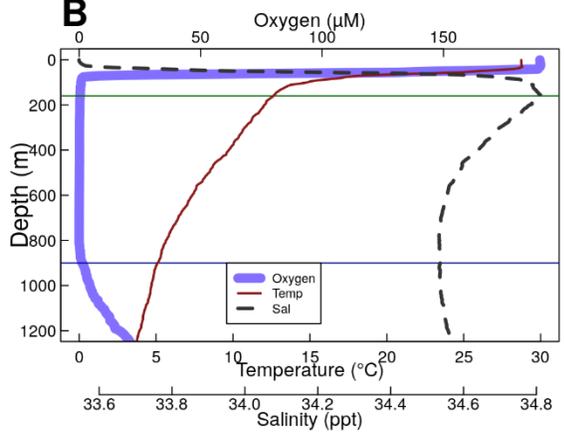
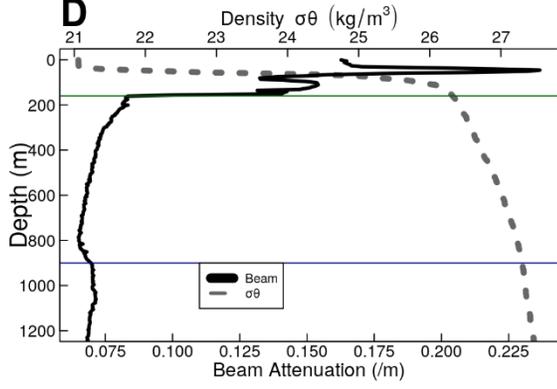
322 In practice we expanded the previous numerical implementation of PRiSM to allow for particle size  
323 distribution spectra with particle-size bins that match those obtained by the UVP, and to return estimates  
324 of the number of particles in those same size bins (Text S1). The model accepts inputs of particle size  
325 distributions at each depth, and changes in particle flux between each depth-bin and the next, deeper,  
326 depth-bin. The model optimizes a particle remineralization rate that would result in that observed flux  
327 loss. It finally returns a "predicted" particle size distribution spectrum that has total flux equal to the flux  
328 of the observed deeper spectrum that would be expected if the shallower spectrum only sank and  
329 remineralized. In cases where flux increased with depth, particles are assumed to put on mass rather than  
330 lose mass following a negative remineralization rate. Here, "negative remineralization" stands in for  
331 chemoautotrophy, active transport, and other processes that result in flux increases with depth. While  
332 these processes likely have more complex effect on the particle size distribution than is accounted for in  
333 our model, we note that flux increases with depth are very rare, and that allowing for negative  
334 remineralization allows our null model to be robust in those rare cases.

## 335 **6 Results**

### 336 **6.1 Physical and Chemical Data**

337 The ODZ, characterized in this study by oxygen levels less than 1  $\mu\text{M}$ , as measured by the CTD, extends  
338 from 90 m to 900 m depth, with a sharp upper oxycline and a gradual lower oxycline (Figure 1B-C). This  
339 station has been previously proven to be anoxic with a STOX sensor (Tiano et al., 2014). The upper  
340 oxycline tracks a sharp pycnocline (Figure 1B-1D), set by the high salinity of the 13CW water mass  
341 (Figure S2), and is characterized by an abrupt drop in temperature below the mixed layer and an increase  
342 in salinity (Figure 1B). Water mass analysis indicated that water in the top part of the ODZ is dominated  
343 by the 13CW water mass, while water between 275 and 500 m is primarily from the NEPIW, with water  
344 from the AAIW dominating in the lower 500 m (Figure S2) (Evans et al., 2020). The site is characterized  
345 by two fluorescence maxima (Figure 1C). The larger, shallower fluorescence peak is positioned just  
346 above the oxycline, with fluorescence from this peak and oxygen attenuating together. The smaller, lower  
347 peak is inside of the ODZ. Turbidity tracks the two chlorophyll peaks in the surface and has a tertiary  
348 maximum at the lower oxycline (Figure 1D). The cyanobacteria at the secondary chlorophyll maximum  
349 are known to be photosynthesizing and producing organic matter in the ODZ (Fuchsman et al., 2019;  
350 Garcia-Robledo et al., 2017). To avoid complication due to this source of organic matter production, we  
351 focus our further analysis below 160 m.

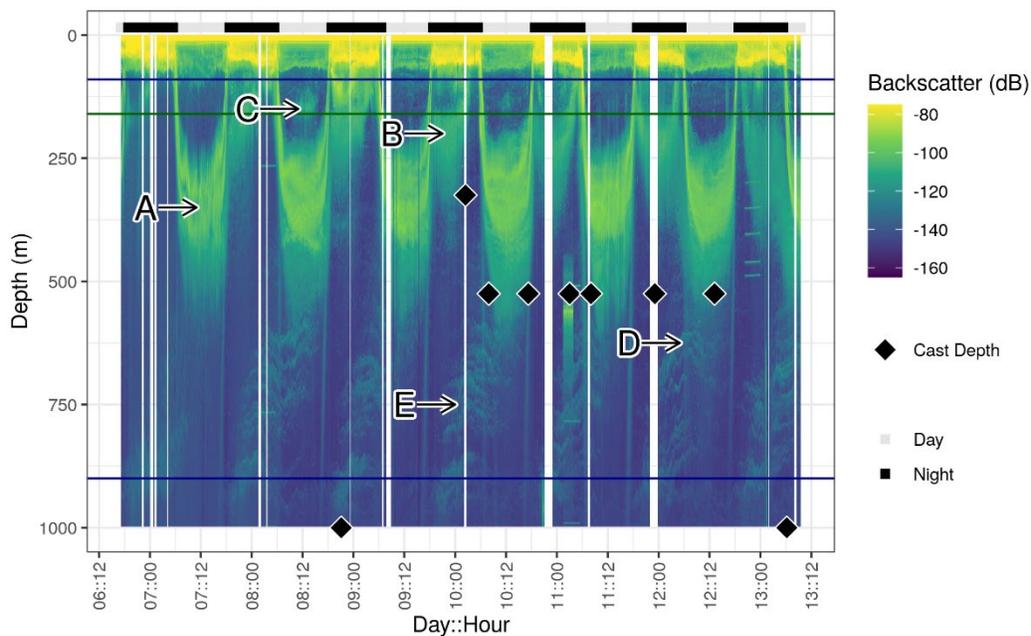
352 For the purposes of this study, we define the photic zone as ending at the base of this deeper fluorescence  
353 layer (160m). This photic zone base corresponds with photosynthetically active radiation (PAR)  $< 10^{-5}$  of  
354 surface PAR levels (Figure 1C). We note that this photic zone depth is deeper than conventional  
355 definitions, in which the base of the photic zone corresponds with  $10^{-2}$  (90 m) or  $10^{-3}$  (120 m) of surface  
356 PAR.

**A****C****B****D**

357

## 371 6.2 Acoustic data reveal diel migration patterns

372 Acoustic data, produced by the shipboard EK60 (Andersen, 2001), at ETNP Station P2, suggest the  
373 presence of multiple cohorts of migratory organisms. We focus initially on backscattering measurements  
374 from the EK60's lowest frequency 18000 Hz signal, corresponding to organisms the size of small fish,  
375 because it travels furthest into the water column and has the best resolution of the channels. Most  
376 migratory organisms appeared to leave the surface at dawn and return at dusk, spending the day between  
377 250 m and 500 m (Figure 2A). There appeared to be two local maxima in backscattering intensity at mid-  
378 day, one at ~300 m and one at ~375 m (Figure 2A). There also appeared to be organisms that reverse  
379 migrated downward at dusk and upward at dawn, spending the night at ~300 m (Figure 2B). Just above  
380 the base of the photic zone, there was a peak of organisms that appeared, at mid-day, on some but not all  
381 days, without any visible dawn or dusk migration. (Figure 2C). Some diel migrators appeared to cross the  
382 ODZ and spend the day below the detection range of the EK60 (Figure 2D), as well as organisms that  
383 appeared between 500 m and 1000 m but did not appear to migrate to or from that depth at our site, but  
384 rather traveled through the EK60's field of view (Figure 2E). Similar patterns were evident in each of the  
385 other measured frequencies, with better resolution by the lower frequencies (Figure S3).

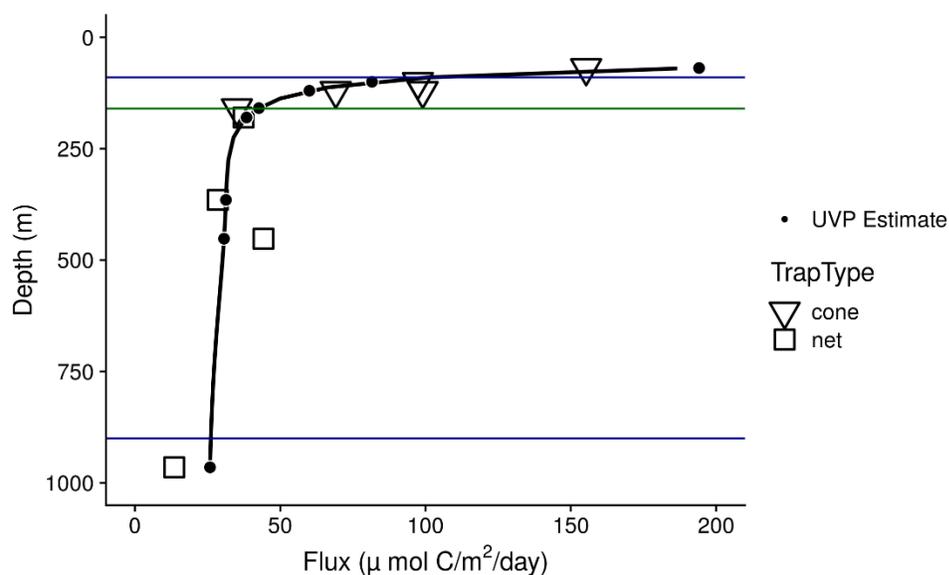


386

392 of the photic zone. Times are local Mexico General Standard time, which is the local time for the  
 393 nearest port of call in Manzanillo and is equivalent to United States Central Standard Time. The  
 394 black and white bar at the top indicates day and night periods, with day defined as times when  
 395 the center of the sun is above the horizon, per the OCE R package. Diamonds indicate the  
 396 depths and times of UVP casts, with casts deeper than 1000 m shown as diamonds on the  
 397 1000 m line. Several patterns are evident **A.** Two bands of organisms can be seen leaving the  
 398 surface at dawn, spending the day between 250 m and 500 m and returning to the surface at  
 399 dusk. **B.** Another group of nocturnally migrating organisms can be seen leaving the surface at  
 400 dusk, spending the night near 250 m and returning at dawn. **C.** Some organisms appear at the  
 401 base of the photic zone, during some, but not all mid days, and then disappear in the evening.  
 402 **D.** A group of very deep migrating organisms appears to leave the surface with the diel  
 403 migrators and pass all the way through the ODZ and out of the EK60's field of view. It returns at  
 404 dusk. **E.** Swarms of organisms appear between 500 m and 1000 m disappearing later in the  
 405 day. Swarms appear in the deepest layers at night and appear progressively shallower as the  
 406 day progresses.

### 407 6.3 Flux data from traps

408 Flux measurements at Station P2 were consistent between the different particle trap types, showing a  
 409 profile that broadly followed a power law with respect to depth, with the exception that flux appeared to  
 410 increase in one trap at 500 m (Figure 3).



412 **Figure 3.** Sinking particle flux, measured from surface-tethered sediment traps (large symbols),  
 413 at ETNP Station P2. Trap types are shown by the shape of the large points. Superimposed are

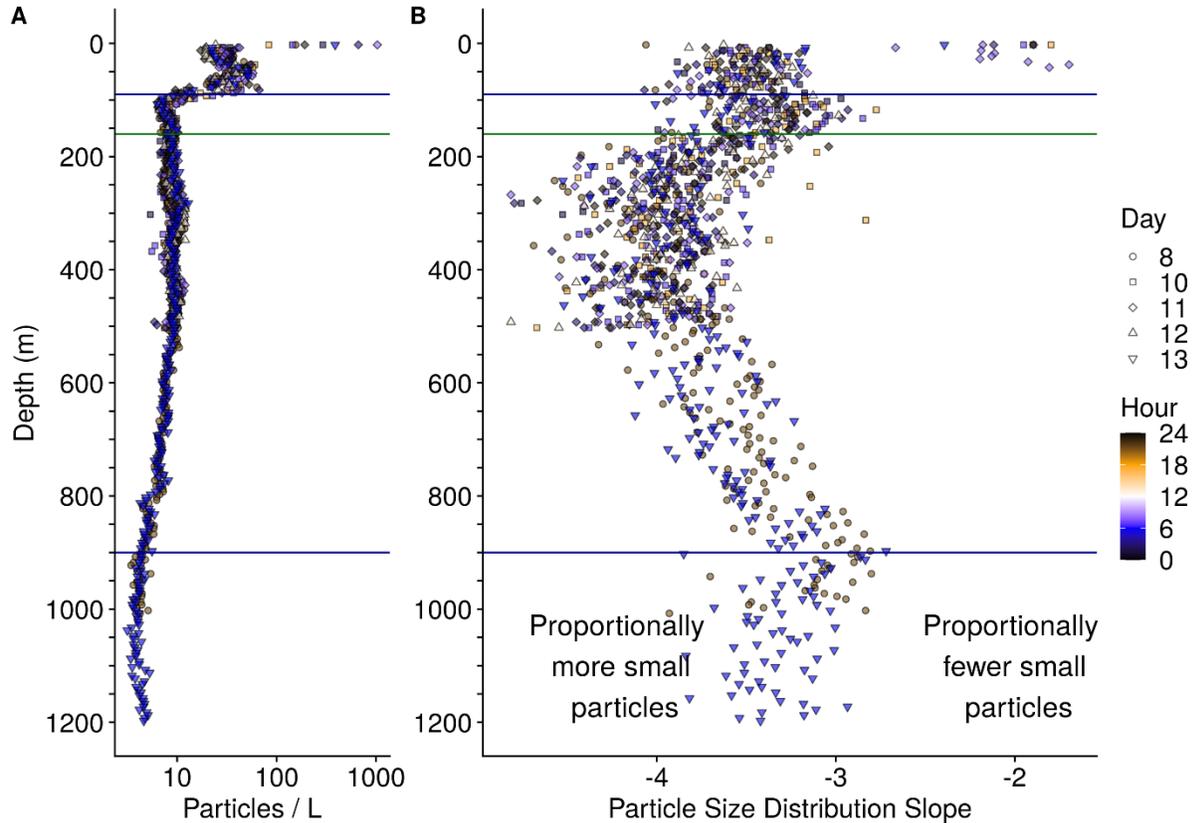
414 estimates of particle flux from the UVP generated by fitting the sum of particle numbers all four  
415 profiles to the trap observed flux. The black line indicates flux predictions made by fitting UVP  
416 observations to the trap data. Black circles indicate regions on the black line corresponding to  
417 the trap observation depths. Horizontal blue lines indicate the top and bottom of the ODZ, while  
418 the horizontal green line indicates the base of the photic zone.

#### 419 **6.4 Particle abundance measurements vary with size and depth**

420 In all profiles, particle abundances were highest at the surface, and highest among the smallest particles  
421 (Figure S4). Visual examination of the relationship between particle number and size suggested a power  
422 law relationship where the log of volume and bin-size normalized particle abundance was proportional to  
423 the log of the particles' size (Figure S5). The exception to this pattern were particles larger than 10  $\mu\text{m}$   
424 (Figure S4, S5), which are rare enough that they are usually not detected by the UVP. Generalized linear  
425 models that assume a negative-binomial distribution of the data accounted for this under-sampling of  
426 large particles to estimate power law slopes, while considering rare occurrences of the large particles at  
427 each depth (Figure S5).

428 Total particle numbers were generally similar between different casts, regardless of which day or hour  
429 they were collected (Figure 4A). Particle numbers were highest in the surface and decreased within the  
430 oxic region, then remained relatively constant from 160 m to 500 m, and gradually decreased between  
431 500 m and the lower oxycline (Figure 4A).

432 The particle size distribution slope generally steepened (became more negative) between the base of the  
433 photic zone (160 m) and 500 m, flattened (became less negative) between 500 m and 1000 m, and then  
434 steepened again below 1000 m (Figure 4B). Steeper, more negative, slopes indicate a higher proportion of  
435 small particles relative to large particles, while flatter, less negative, slopes indicate a more even particle  
436 size distribution. Flatter distributions still have a higher *absolute number* of smaller particles than larger  
437 particles; however, they have a higher *proportion* of larger particles relative to other samples with steeper  
438 distributions.



440 **Figure 4. A.** Observed, volume normalized total particle numbers from 9 casts taken at different  
 441 times of the day at ETNP station P2. **B.** Calculated particle size distribution slopes of those  
 442 particles. These data have not been binned by depth in order to better show sample to sample  
 443 variability. Horizontal blue lines indicate the top and bottom of the ODZ, while the horizontal  
 444 green line indicates the base of the photic zone. Hour corresponds to local, Mexican General  
 445 Standard, time.

### 446 **6.5 Estimated particle flux sometimes increases with depth in the ODZ core**

447 Optimization found best agreement between particle flux measured by traps, and UVP estimated particle  
 448 flux when per particle flux is fit by the equation

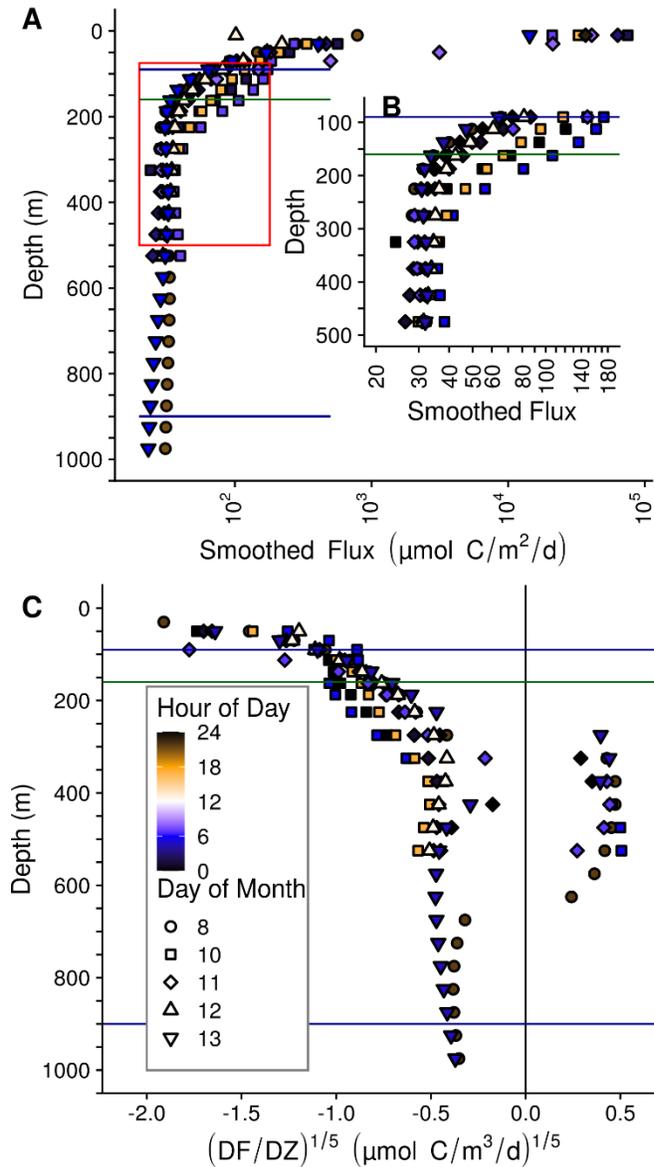
$$449 \text{ Flux} = (133 \mu \text{ mol C} / \text{m}^2/\text{day}) = 133 * \text{Size (mm)}^{2.00} \quad (\text{Eqn 5})$$

450 This equation represents an empirical relationship between particle flux from traps and particle size  
 451 measured by UVP. Applying this fit to the UVP data resulted in a UVP predicted flux profile that broadly  
 452 fit the expected trap observed flux profiles (Figure 3).

453 Particle flux profiles, predicted from the above particle size abundances and fit, varied between casts  
 454 between the base of the photic zone and 500 m (Figure 5A-5B). To examine the rate of change of flux and

455 to identify regions and time points where flux appeared to increase with depth, we examined the rate of  
456 change of flux. This rate of change was fifth root transformed to normalize the data and to allow us to  
457 focus on the cases where flux attenuation varied about zero, since we were interested in identifying  
458 factors that related to whether flux was positive or negative. Between 250 m and 500 m, particle flux  
459 appeared to increase on some, but not all, casts, while attenuating slowly on the other casts (Figure 5C).  
460 Below 500 m, there were not enough casts to measure variability between casts.

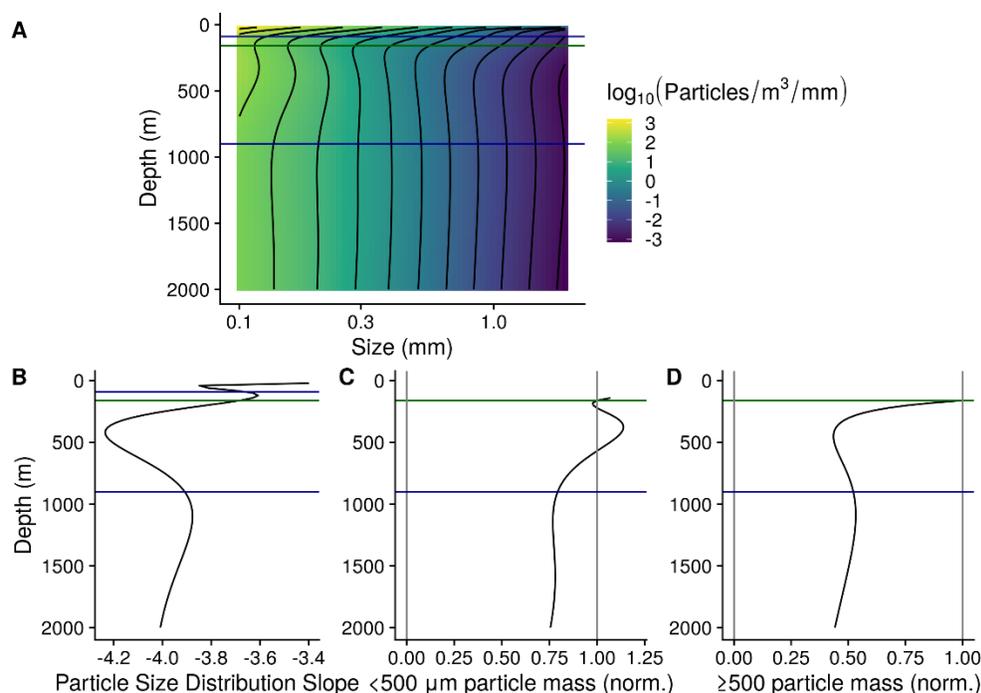
461 The general additive model that quantified how the of change of flux between 250 m and 500 m varied  
462 with depth, decimal study day and decimal hour found that depth ( $p = 0.061$ ) and hour of the day ( $p =$   
463  $0.196$ ) did not statistically associate with the fifth root transformed rate of change of flux while day of  
464 study did ( $p = 0.019$ ,  $R^2 = 0.264$ , Figure S6). There were generally increases in flux over this region  
465 towards the beginning and end of the sampling period and decreases in flux nearer to day 10 (Figure  
466 S6B). A general additive model that looked only at the relationship between study day and rate of change  
467 of flux (fifth root transformed) in this region suggested that day accounted for 14% of the variance in this  
468 value, as determined by adjusted  $R^2$  ( $p = 0.040$ ). If the fifth root transformation was not applied to the rate  
469 of change of flux, there was a statistically significant relationship between depth and rate of change ( $p =$   
470  $0.001$ ), but not study day ( $p = 0.062$ ) or hour ( $p = 0.719$ ,  $R^2 = 0.341$ ). This pattern indicated that, without  
471 the transformation, any temporal signal is swamped by the substantial changes in rate of change in depth,  
472 with shallower depths losing flux faster than deeper ones.



474 **Figure 5.** Within and between day variability in UVP predicted particle flux at ETNP Station P2.  
 475 All profiles are depth binned with higher resolution towards the surface (methods). Horizontal  
 476 blue lines indicate the top and bottom of the ODZ, while the horizontal green line indicates the  
 477 base of the photic zone. **A.** Flux profiles in the top 1000 m of the water column. **B.** A more  
 478 detailed depiction of the area enclosed by the rectangle in **A.** -- **C.** The rate of change of flux,  
 479 divided by the rate in change in depth. The fifth root of these values are shown to highlight  
 480 differences between values close to zero. Hour corresponds to local, Mexican General  
 481 Standard, time.

## 482 6.6 Smoothed and averaged data

483 At the ETNP ODZ site, highly smoothed particle abundance data suggested that particle size, averaged  
484 across all casts, followed a pattern in which the abundance of  $<500 \mu\text{m}$  particles increased between the  
485 oxycline and 350 m (Figure 6A), which corresponded with steepening of the particle size distribution  
486 slope (Figure 6B), and an increase in microaggregate ( $<500 \mu\text{m}$ ) particle biomass (Figure 6C), but not of  
487  $> 500 \mu\text{m}$  particle biomass (Figure 6D). Deeper in the ODZ, the microaggregate ( $<500 \mu\text{m}$ ) particle  
488 number and biomass, and the particle size distribution slope declined.



490 **Figure 6. A.** GAM smoothed, bin-size and volume normalized particle numbers across the  
491 particle size spectrum, at ETNP Station P2. Data are from the only cast that traversed the top  
492 2000 m of the water column, collected on January 13 beginning at 06:13. Horizontal blue lines  
493 indicate the top and bottom of the ODZ, while the horizontal green line indicates the base of the  
494 photic zone. **B.** Particle size distribution slope. **C-D.** Estimated biomass of **(C)** microaggregate  
495 ( $<500 \mu\text{m}$ ) and **(D)** marine snow ( $\geq 500 \mu\text{m}$ ) particles, normalized to biomass at the base of the  
496 photic zone. In these two biomass panels, data from above the base of the photic zone are not  
497 shown.

498 At the oxic site, particle size distributions generally steepened with depth, while both microaggregates  
499 ( $<500 \mu\text{m}$ ) and  $\geq 500 \mu\text{m}$  estimated particle biomass followed a power law decrease with depth (Figure  
500 S10).

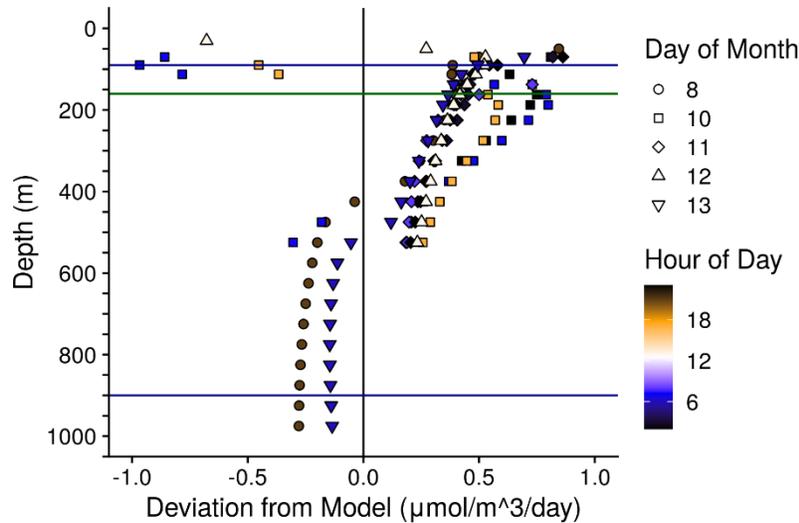
## 501 **6.7 Particle number dynamics differ from model expectations**

502 The modified particle remineralization and sinking model predicted particle size distributions at each  
503 depth from the particle size distribution one depth-bin shallower and the calculated flux attenuation  
504 between the two depths. At the ETNP ODZ site, we found that the observed particle size distributions  
505 usually deviated from model expectations (Figure S11). In the model, remineralization rates are  
506 optimized, to ensure that the total predicted flux at each depth matches the observed total flux. However,  
507 the predicted size spectrum will diverge from the observed spectrum if the assumptions of the model (i.e.,  
508 sinking and remineralization are the only particle transformations) are violated. The difference between  
509 the observed and predicted flux of *microaggregate particles* (100 - 500  $\mu\text{m}$ ), normalized to depth,  
510 therefore serves as a metric of observed deviations from the size distribution expected from sinking and  
511 remineralization alone. We call this value *Deviation from Model* (DFM).

$$512 \text{DFM} = \frac{(<500 \mu\text{m Flux Observed} - <500 \mu\text{m Flux Modeled})}{\Delta Z} \quad (\text{Eqn. 6})$$

513 In the above equation  $\Delta Z$  is the distance, in meters, between the current depth bin and the previous depth  
514 bin, whose particle size distribution is fed into the predictive model.

515 DFM was positive between the base of the photic zone (160 m) and 500 m, meaning that less  $<500 \mu\text{m}$   
516 particle flux attenuated than would be expected from the *PRiSM* model in this region (Figure 7). There  
517 was some variability in the DFM parameter between casts. A general additive model (GAM) that showed  
518 that the variability in DFM was statistically significantly related to depth ( $p < 10^{-5}$ ), day of the study  
519 ( $p = 0.002$ ), but not to hour of the day ( $p = 0.051$ ), with these factors together explaining 41.6% of the  
520 variance, as measured by  $R^2$ . DFM was highest shallower in the water column (Figure S12A), highest  
521 near day 10 and lower at the beginning and end of the study (Figure S12B). A GAM that only explored  
522 the effect of depth accounted for 27.4% of the variance. Comparing a GAM that accounted for study day  
523 and depth to one that only accounted for depth effects showed an increase in  $R^2$  value of 10.4%,  
524 suggesting that study day accounts for an additional 10.4% of the variance, after accounting for depth.  
525 Comparing the model that accounts for depth, day and hour to one that only accounts for depth and day,  
526 suggests that hour of the day, while not statistically significant, could explain an additional 3.4% of the  
527 variance. Below 500 m, DFM was negative. There were only two casts that reached below 500 m at this  
528 station, and so an analysis of the dynamics of DFM in this region is not possible. At P16 Station 100,  
529 DFM was positive between the base of the photic zone and 350 m and negative below 350 m (Figure  
530 S9C).



532 **Figure 7.** *Deviation from Model (DFM)* indicates the difference between the observed flux of  
 533 small particles (< 500  $\mu\text{m}$ ), and the flux of small particles that would be estimated by a model,  
 534 which assumes that particles in the depth bin above only remineralized and sank, following the  
 535 PRiSM model. Values are normalized to the change in depth and are in units of  
 536  $\mu\text{mol Carbon m}^{-3}\text{d}^{-1}$ . This value serves as a metric of processes that cannot be captured by a  
 537 null model, which assumes that particles only sink and remineralize. Positive values suggest an  
 538 excess of <500  $\mu\text{m}$  particles, suggesting disaggregation or advection of small particles, while  
 539 negative values suggest a dearth of small particles, suggesting repackaging or aggregation.  
 540 DFM is only reported for <500  $\mu\text{m}$  particles (<500  $\mu\text{m}$ ), because it is the inverse of the deviation  
 541 from expected flux of  $\geq 500 \mu\text{m}$  particles. *DFM* is reported for all casts at ETNP Station P2.  
 542 Horizontal blue lines indicate the top and bottom of the ODZ, while the horizontal green line  
 543 indicates the base of the photic zone.

## 544 **6.8 ETNP particle dynamics differ from those seen at an oxic site**

545 The ODZ data were compared to an oxic water column in order to identify the spectral signatures that are  
 546 particular to oxygen deficient waters. The oxic site, P16 Station 100, was characterized by a more  
 547 gradually sloping pycnocline, and an oxygen minimum at 500 m of 19.7  $\mu\text{M}$ , which is hypoxic (Figure  
 548 S1B). There was no working fluorescence sensor on that cruise, but data from World Ocean Atlas (Boyer  
 549 et al., 2018) suggest that the photic zone is characterized by a single fluorescence peak with a maximum  
 550 at 110 m and which disappeared at 200 m (Figure S1C). Thus, we define the mesopelagic as beginning at  
 551 200 m at the oxic site. Turbidity followed chlorophyll concentration and did not have a peak in the  
 552 mesopelagic (Figure S1D), unlike the ODZ site. There was a salinity peak at 150 m (Figure S1B).

553 Particle numbers were higher between the base of the photic zone through 1000 m at the ETNP ODZ site,  
554 than at the same-latitude, oxygenic, P16 Station 100 (Figure S7A). Particle size distributions were similar  
555 between the two sites above 500 m, being characterized by overlapping confidence intervals generated by  
556 a general additive model. From 500 m to 1000 m, particle size distributions were flatter at the ETNP site,  
557 being characterized by a smaller proportion of smaller particles, relative to larger ones (Figure S7B).

558 Microaggregate particles (100  $\mu\text{m}$  - 500  $\mu\text{m}$ ) at the ETNP ODZ site were about two orders of magnitude  
559 more common than marine snow particles ( $\geq 500 \mu\text{m}$ ) (Figure S8).  $\geq 500 \mu\text{m}$  particle numbers appeared  
560 to attenuate more quickly than  $<500 \mu\text{m}$  particles, and more generally follow a power law decrease, while  
561  $<500 \mu\text{m}$  particles appeared to increase around 500 m depth. Flux was predicted to be predominantly  
562 from  $<500 \mu\text{m}$ , rather than  $\geq 500 \mu\text{m}$  particles, at all depths except the shallowest depth bin in the surface  
563 of the photic zone. The particle size distribution, calculated only on  $\geq 500 \mu\text{m}$  particles, was more variable  
564 between depths than calculated for  $<500 \mu\text{m}$  particles. Data from the oxic P16 Station 100 suggested  
565 more particles, steeper particle size distribution, and more flux at this station than at the ETNP station.  
566 They also suggested that differences between  $<500 \mu\text{m}$  and  $\geq 500 \mu\text{m}$  particles, with respect to number,  
567 flux and size distribution that were broadly similar to the ones seen at ETNP Station P2. In contrast to the  
568 anoxic station, at the oxic station flux always decreased with depth (Figure S9A+B).

## 569 **7 Discussion**

### 570 **7.1 Diel migrators spend time in the ODZ core**

571 Organisms of all sizes appear to migrate into the core of the ODZ at our site. Most migrators appear to  
572 leave the surface at dawn, spend the day in the top 500 m of the ODZ and return to the surface at dusk  
573 (Figure 2A), while others show the opposite pattern, leaving the surface at dusk and returning at dawn  
574 (Figure 2B). Diel migration is prevalent throughout the oceans (Cisewski et al., 2010; Hays, 2003;  
575 Heywood, 1996; Jiang et al., 2007; Rabindranath et al., 2011; Sainmont et al., 2014; Yang et al., 2019),  
576 including at other ODZ sites (Antezana, 2009; Kiko et al., 2020; Riquelme-Bugueño et al., 2020),  
577 including highly anoxic sites with secondary, anoxic, deep chlorophyll maxima, like this one (Bianchi et  
578 al., 2014; Hidalgo et al., 2005), and much of the ETNP ODZ (Herrera et al., 2019). Sampling efforts in  
579 the Costa Rica Dome, a unique system in the ETNP, find that euphausiids and fish migrate into the ODZ  
580 (Maas et al., 2014; Wishner et al., 2013), but that diel migrators are primarily 2 mm–5 mm in size  
581 (Wishner et al., 2013). Krill in the Humboldt current OMZ similarly spend the day at depth and migrate to  
582 the surface at night (Riquelme-Bugueño et al., 2020). The presence of organisms that appear and  
583 disappear just above the base of the photic zone, in the region of the deeper anoxic fluorescence peak  
584 region, but absence of a tell-tale signature of mass migration before or after they appear (Figure 2C) may

585 suggest that these organisms migrate at different times of the day to this deep region, rather than all at  
586 once. Another possibility is that they pass through our station at this depth in mid-day, but migrate to  
587 depth at another location.

588 The organisms that appear between 500 m and 1000 m (Figure 2E) have acoustic signatures that resemble  
589 those of jellyfish (Kaartvedt et al., 2007), but could also represent other organisms such as salps (Maas et  
590 al., 2014; Ressler, 2002). That they appear in horizontal bands that do not appear to trend upwards over  
591 time suggests that these swarms are traveling through our site at progressively shallower depths over the  
592 course of the day, but that the individual swarms are not themselves moving upward at this station. This  
593 pattern suggests that any vertical migration by these organisms happens elsewhere or occurs more slowly  
594 than the advection seen at this site. That they appear at different depths at different times of the day  
595 suggest that these organisms have some sort of vertical migration pattern. Future work may consider more  
596 highly resolved spatial and temporal monitoring of this phenomenon. Indeed molecular surveys have  
597 found evidence of both Cnidarians and Ctenophores both within and below the ETSP ODZ near Chile  
598 (Parris et al., 2014).

## 599 **7.2 Flux is lower at this site than previous measurements in the ETNP**

600 Flux at P2 was lower at all depths, ranging from 10–100  $\mu\text{mol}/\text{m}^2/\text{day}$ , than was seen in previous  
601 measurements by traps at other, more productive, ODZ sites, which ranged from 1000–  
602 10000  $\mu\text{mol}/\text{m}^2/\text{day}$  (Hartnett & Devol, 2003; Van Mooy et al., 2002).

## 603 **7.3 The flux to size relationship is typical of other sites**

604 The exponent of the particle size to flux relationship that we saw at our site (2.00) is of a similar  
605 magnitude to, but slightly smaller than, those seen by other studies that compare UVP flux to trap flux  
606 (Guidi et al., 2008; Kiko et al., 2020). Differences in the size-flux relationship could indicate that this  
607 relationship truly varies between sites, or that imprecision in flux measurements leads to differences in  
608 these values between studies. The single fit and relationship that we carried out does not account for  
609 variation in the size to flux ratio across time and depth, nor does it account for differences in particles of  
610 different origin. In practice, this value could change over depth and time. Setting up, deploying and  
611 retrieving each trap array is a large effort. However, coupled particle flux and size measurements that are  
612 more resolved with respect to depth, space or time might allow for further exploration of the  
613 spatiotemporal variability of this relationship. In other systems, combined image analysis and gel traps  
614 (McDonnell & Buesseler, 2010, 2012) have provided opportunities to explore particle size to flux  
615 relationships and how they vary between particle types in more detail.

## 616 **7.4 Remineralization rates of all particles decrease in the ODZ, but** 617 **disaggregation does not**

618 Particle size profiles, particle size distribution slopes, and estimated biovolume, averaged across all casts  
619 and smoothed, are all similar to the predictions made by Weber and Bianchi's (2020) "Model 1".  
620 (Figure 5), and therefore our hypothesis **H1**, that all particles are remineralized more slowly than in oxic  
621 sites. This suggests that the low oxygen at this site decreases the remineralization rate of all particles,  
622 including <500  $\mu\text{m}$  microaggregates. It does not support the **H2** in which disaggregation is suppressed in  
623 the ODZ, nor **H3** in which only the very large particles' remineralization is slowed due to sulfate  
624 reduction. The data at the oxic site generally conformed to Weber and Bianchi's null model, "Model 0",  
625 which was their prediction for particle distributions at oxic sites (2020). However, one difference was that  
626 the observed particle size distribution, while essentially constant from the base of the photic zone through  
627 1000 m, appeared to steepen between 1000 m and 2000 m, suggesting an increase in the abundance of  
628 <500  $\mu\text{m}$  particles, relative to Model 0. This could indicate increased disaggregation in this region or  
629 horizontal transport of small particles through advection in this region. One possible source of  
630 disaggregation are zooplankton communities that have been found to specialize in feeding in the lower  
631 oxycline (Saltzman & Wishner, 1997; Wishner et al., 1995). These communities actively seek out the  
632 lower oxycline and feed on particles that have escaped remineralization in the ODZ, potentially resulting  
633 in the increased disaggregation we observe in this depth interval. Such a community would likely be  
634 comprised primarily of small organisms which the EK60 is not able to measure at this depth. One  
635 possible source of horizontal transport is colloids in a deep iron plume (Homoky et al., 2021; Lam et al.,  
636 2020).

## 637 **7.5 Zooplankton likely transport organic matter into the ODZ core**

638 Predicted flux levels sometimes increase between 275 m and 625 m, and at all other times attenuate very  
639 slowly in this region. The EK60 data suggest the diel migration of all sizes of organisms to this region,  
640 agreeing with previous analysis of copepods collected with nets (Wishner et al., 2020). Taken together,  
641 the concurrent intermittent increases in flux with diel migration in the top 500 m suggests that  
642 zooplankton are transporting organic matter. The observation that the rate of change in flux changes with  
643 depth suggests some day-to-day variability in this transport. That this rate does not vary statistically  
644 significantly between day and night suggests that any diel release of particles is relatively small compared  
645 to the particles already present in situ. Indeed, it suggests that particle sinking is slow enough that any  
646 particles that are transported to depth during the day are retained at night. Furthermore, nocturnal  
647 migrators are likely playing a role in carbon transport which may smooth out any diel signal. Another  
648 possibility, given that the magnitude of the day-to-day variability in apparent particle flux is small, is that

649 the zooplankton themselves, which likely make up about 5% of what the UVP counts as particles, may be  
650 driving this apparent pattern and that particle flux itself does not vary. More likely, especially given the  
651 observation that this flux variability did not track well with the within day backscattering patterns seen by  
652 the EK60 and the small number of particles that are zooplankton, is that this factor accounts for some, but  
653 not all, of the observed variability in flux. An additional source of temporal variability in flux is variation  
654 in particle export from the photic zone. Zooplankton, if they are more common in large particle size bins,  
655 or even if they have a flatter size distribution spectrum than non-living particles, may flatten the particle  
656 size spectrum, where they are present. However, this effect, if present at our site, appears to be  
657 overpowered by the disaggregation effect, since the particle size spectra appear to be steeper where  
658 zooplankton are present.

659 Zooplankton are also known to congregate at the lower boundaries of ODZs (Wishner et al., 2018, 2020)  
660 and high urea concentrations in the lower oxycline of the ETNP have been suggested to be due to these  
661 zooplankton (Widner et al., 2018). Beam attenuation indicates a third peak in the oxycline below the  
662 ODZ. We do not see this congregation in the EK60 data. However, it is possible that small organisms do  
663 congregate here, but are not detected by the EK60's 12000 and 20000 kHz signals, which do not  
664 penetrate to 1000 m in our data. The EK60 data do however suggest that larger, krill to fish sized  
665 organisms are not abundant in the lower oxycline.

## 666 **7.6 Zooplankton likely disaggregate particles in the ODZ core**

667 The observation that there is greater flux by microaggregate particles ( $< 500 \mu\text{m}$ ) than would be predicted  
668 by remineralization and sinking alone (Figure 7), between the photic zone and 500 m suggests that some  
669 process is disaggregating large particles into smaller ones. That this apparent disaggregation corresponds  
670 with the region where migratory organisms are found suggests that some of these organisms, likely small  
671 animals such as copepods and euphausiids (Herrera et al., 2019; Maas et al., 2014), may break down  
672 particles (Dilling & Alldredge, 2000; Goldthwait et al., 2005). While, in principle, other processes such as  
673 horizontal advection of water containing  $<500 \mu\text{m}$  particles (Inthorn, 2005) could be responsible for this  
674 increase in  $<500 \mu\text{m}$  particles, there is no reason to expect horizontal differences at this site, which is at  
675 the core of the ODZ and far from shore.

676 Other deviations from model assumptions could alternatively explain the increase in  $<500 \mu\text{m}$  particles  
677 relative to model predictions. In particular, smaller particles might break down more slowly than larger  
678 ones, or sink more quickly for their size than expected, as has been seen elsewhere (McDonnell &  
679 Buesseler, 2010). Our model assumes a spherical particle drag profile, such that the particle sinking speed  
680 fractal dimension ( $\gamma$ ) is one less than the particle size fractal dimension ( $\alpha$ ) (Cram et al., 2018; Guidi et

681 al., 2008), and that these two values sum to the particle flux fractal dimension. If any of these assumptions  
682 do not hold, the magnitude of the values may differ.

683 In contrast to the upper ODZ core, there is an apparent flattening of the particle size distribution below  
684 500 m, beyond the expected effects generated by particle remineralization. This could suggest  
685 aggregation processes (Burd & Jackson, 2009). Indeed, aggregation could be occurring throughout the  
686 ODZ core, but only exceed disaggregation in the lower ODZ region. Alternatively, in this region,  
687 processes resembling Weber and Bianchi's (2020) Model 3, corresponding to **H3**, in which large particles  
688 remineralize more slowly than larger ones could also occur. Like aggregation, such processes could be  
689 occurring through the ODZ but are overwhelmed by the effects of disaggregation above 500 m.

## 690 **7.7 Water mass changes may affect particle flux and size changes**

691 The observation that particle flux begins to attenuate below 500 m more quickly than it does between the  
692 base of the photic zone and 500 m could be explained in part by a shift in water mass at this depth where  
693 AAIW begins to mix with NEPIW (Figure S2). The AAIW is suggested to have micromolar oxygen  
694 concentrations, as compared to the NEPIW, such that a small contribution of AAIW can raise the oxygen  
695 concentration (Evans et al., 2020). However, measurements taken at this station in 2012 observed zero  
696 oxygen though 800 m with the highly sensitive STOX electrode, suggesting that oxygen, if present, is  
697 below 4 nM (Tiano et al., 2014). It is conceivable that the AAIW has larger particle sizes and lower  
698 particle abundance characteristics due to its having advected from different geographic regions than the  
699 overlying water, but it is difficult to see why this would be the case as these water masses stay in the ODZ  
700 region for years (DeVries et al., 2012) and particles have a much shorter residence time. In any case, the  
701 NEPIW to AAIW transition coincides with the lower limit of the depth to which vertically migrating  
702 zooplankton travel (Figure 2), and so we are not able to deconvolve the effects of water mass changes  
703 from that of changes in zooplankton effects on particle characteristics.

704 The change in water mass between 13CW and NEPIW, around 250 m, in contrast, does not appear to  
705 correspond to any apparent changes in particle flux or size. Thus, we would argue that any historical  
706 effects of these water mass differences are likely to be small, and that active transport differences above  
707 and below 500 m likely have a larger effect.

## 708 **7.8 Oxic site differences**

709 The oxic site provides validation that the patterns that we see at the ETNP are unique to the ODZ region,  
710 and do not apply to a same latitude ODZ site. The particle size distribution slope varied little and there  
711 was not an increase in particle mass in the oxic site, consistent with Weber and Bianchi's (2020) null  
712 model (Figure S10), in which oxygen is not limiting and particle sizes are not affected by anoxia. In this

713 case, small particles break down more quickly in the oxic site than our site and so there is no small  
714 particle excess in this region. Similarly, the higher flux attenuation in the oxic site (Figure S9A) suggests  
715 that the differences in attenuation of all particle sizes by microbes at both sites do indeed drive differences  
716 in flux profiles, and by extension transfer efficiency, between oxic and anoxic regions. The lack of  
717 increases in flux at the oxic site (Figure S9B) suggest that active transport may play a greater role in the  
718 anoxic region than elsewhere. The lack in apparent excess of small particles over model prediction  
719 (Figure S9C) could either indicate less activity by zooplankton in this region, or perhaps that  
720 remineralization of small particles quickly removes any small particles produced by zooplankton in this  
721 region.

## 722 **7.9 Future directions**

723 We advocate exploring the relationships between particle size distribution, flux and acoustic signatures in  
724 other parts of the ETNP and other ODZ regions. Expanded spatial analysis of particle size spectra in  
725 ODZs would allow the community to confirm whether Weber and Bianchi's (2020) model (**H1**), that  
726 particles of all sizes break down more slowly in ODZs, applies elsewhere. Similarly, a clear next step is to  
727 apply our disaggregation model to other ocean regions, perhaps using particle size data already collected  
728 by other groups (Guidi et al., 2008; Kiko et al., 2017, 2020).

729 While the UVP characterizes dynamics of particles  $>100\ \mu\text{m}$ , particles smaller than this range contribute  
730 dramatically to carbon flux (Durkin et al., 2015), and so their size distribution matters as well. However,  
731 at some point particles become small enough that they likely do not sink, and so exploring  
732 remineralization and disaggregation of  $<500\ \mu\text{m}$  microaggregate particles into non-sinking size classes  
733 would provide valuable context to these measurements. In-situ pumped POC data from the GEOTRACES  
734 program have been used to describe the dynamics of smaller particle size classes (Lam et al., 2011; Lam  
735 & Marchal, 2015). Other sensors, such as coulter counters (Sheldon et al., 1972) and Laser In-Situ  
736 Scattering transmissometers (Ahn & Grant, 2007) provide size resolved distribution information about  
737 these smaller size classes of particles. Comparison between UVP data and past and ongoing (Siegel et al.,  
738 2016) studies of the characteristics of  $<100\ \mu\text{m}$  particles provide opportunities to better understand the  
739 dynamics of the full range of particle sizes.

740 The image data collected by the UVP offers opportunities to quantify the abundance and taxonomic  
741 distribution of the zooplankton that migrate into the mesopelagic, as well as the particle types within this  
742 region. Identifying this visual data would have the added benefit of allowing researchers analyze particle  
743 size spectra, rather than the sum of particles and zooplankton as we do here.

## 744 **8 Conclusions**

745 If ODZs expand in response to the changing climate, larger areas of the ocean are likely to resemble this  
746 environment, which is oligotrophic and has an oxygen deficient zone spanning most of the mesopelagic  
747 zone. Previous models and observations have suggested that ODZs are sites of efficient carbon transfer to  
748 the deep ocean (Cram et al., 2018; Hartnett & Devol, 2003; Van Mooy et al., 2002; Weber & Bianchi,  
749 2020), and our data appear to support this contention. Indeed, the mechanism of efficient transfer appears  
750 to be slowing of particle remineralization, presumably from decreased microbial metabolism, with  
751 zooplankton playing an important role in both active particle transport and particle disaggregation.  
752 Our data could potentially be used in conjunction with mechanistic models (e.g. Weber & Bianchi, 2020)  
753 to constrain the relative carbon oxidation rate by nitrate reduction, denitrification and sulfate reduction  
754 processes, which is currently poorly understood (Bristow, 2018). Furthermore, it appears that diel  
755 migratory organisms both disaggregate particles and transport carbon throughout the top 500 m of the  
756 water column. Day-to-day and within day variability in organic matter transport was evident, though  
757 overall patterns in particle size, flux and disaggregation appeared to be consistent over the course of the  
758 time-series. The change in particle abundance and size between 500 m and the bottom of the ODZ has  
759 implications for the free-living microbes living in this region. These microbes are likely particularly  
760 organic matter starved, and so these decaying particles are likely an important energy source for them.  
761 Our data highlights the heterogeneous nature of the ETNP ODZ with depth and indicates that more  
762 detailed sampling should be performed for rate and microbial measurements to properly extrapolate to the  
763 entire ODZ.

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1075

1 Supporting Information for

2 **Slow particle remineralization, rather than suppressed**  
3 **disaggregation, drives efficient flux transfer through the**  
4 **Eastern Tropical North Pacific Oxygen Deficient Zone**

5

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22 Contents of this file

23

24 Figures S1 to S12

25 Caption for Text S1

26

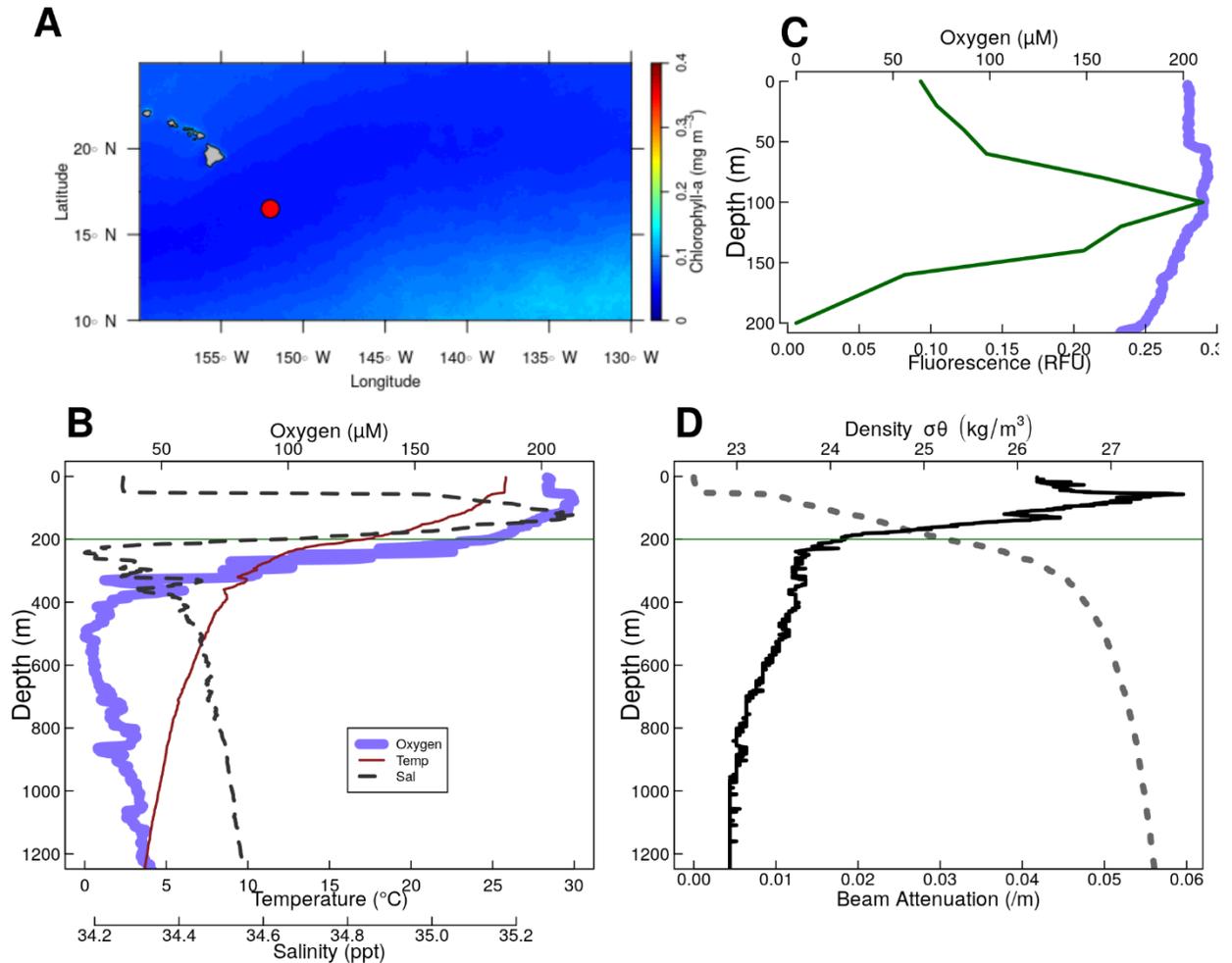
27 Additional Supporting Information (Files uploaded separately)

28

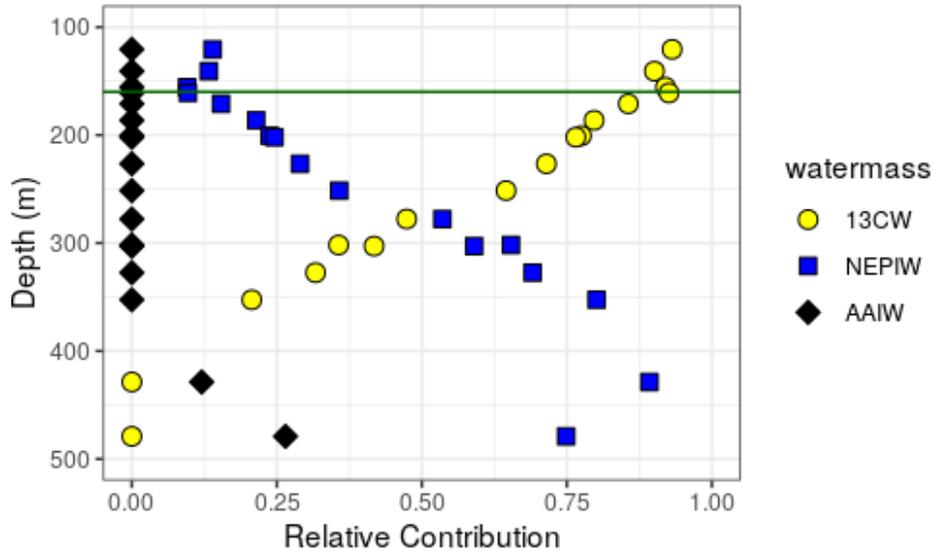
29 Text S1

30 Introduction

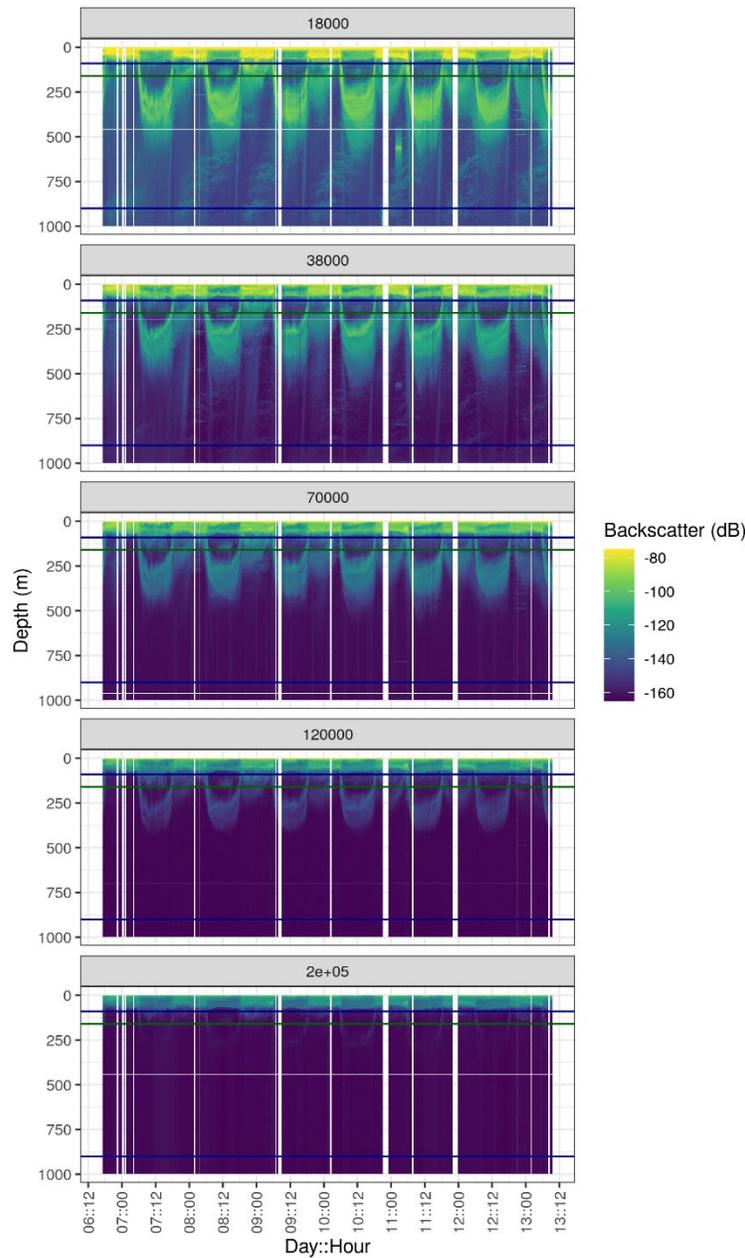
31 This file contains supplemental figures referenced in the manuscript. It also contains a  
32 caption for a .PDF file containing mathematical equations underpinning the particle  
33 remineralization model used.



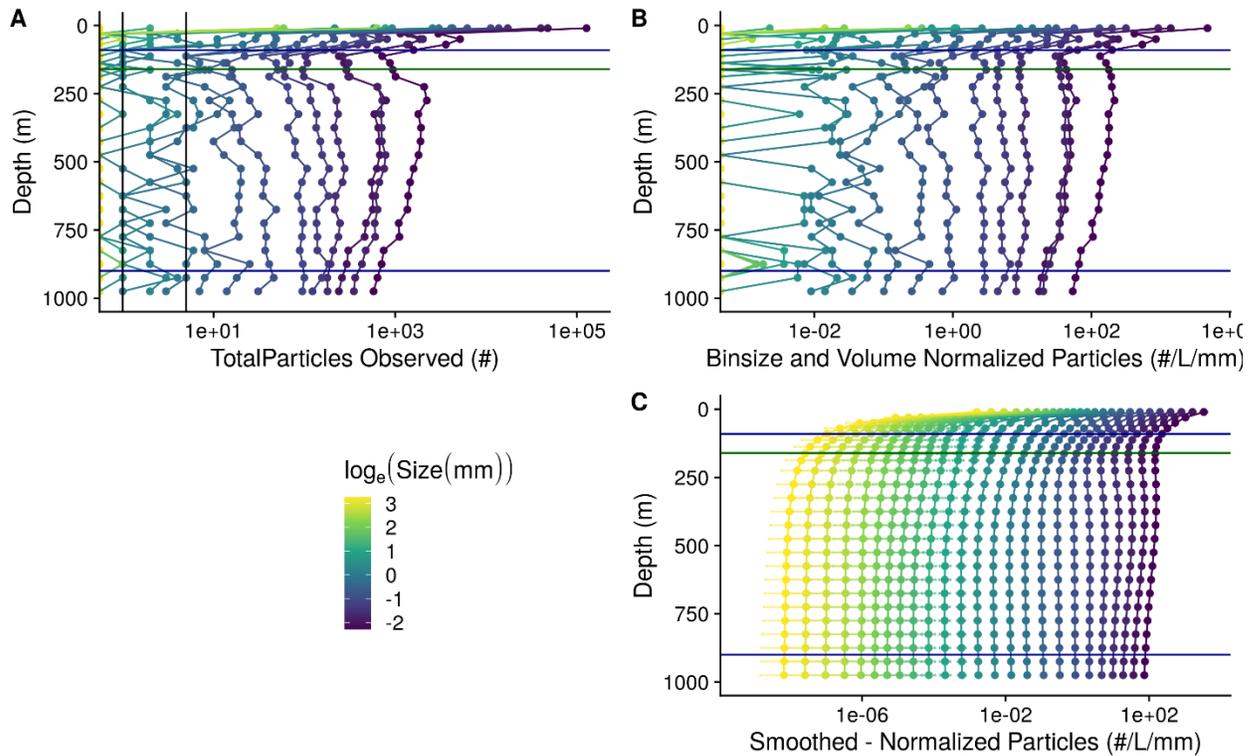
36 Figure S1. Physical and chemical data from P16 Station 100. Located at 16.5°N  
 37 152.0°W. (A) Map of the nearby tropical Pacific station P16 Station 100. Colors indicate  
 38 chlorophyll concentrations at the surface, averaged over all MODIS images. The red  
 39 circle indicates the location of P16 Station 100. (B-D) Oceanographic parameters. The  
 40 thin horizontal green line shows the location of the base of the photic zone (200 m). (B)  
 41 Oxygen temperature and salinity. (C) Oxygen, and fluorescence. Because the fluorometer  
 42 was broken on this cruise, fluorescence data were pulled from world ocean atlas (Garcia  
 43 et al. 2014). (D) Beam attenuation and density, calculated from the salinity temperature  
 44 and pressure data.



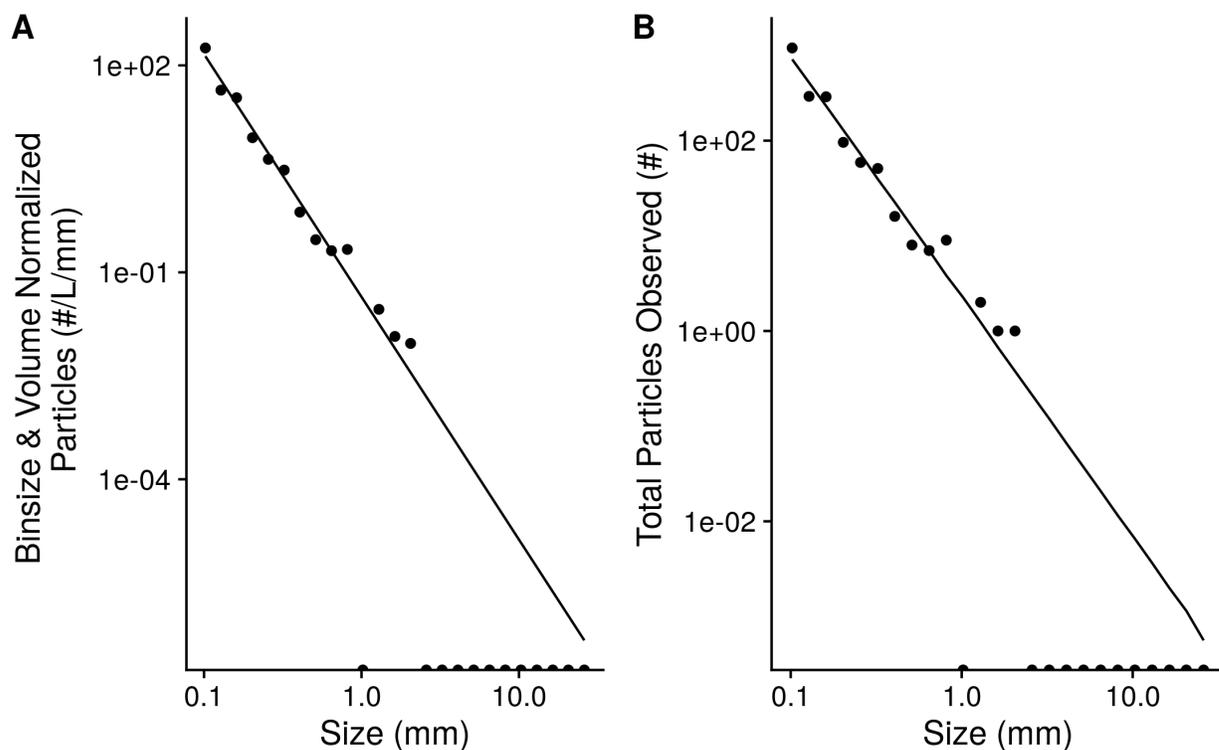
46 Figure S2. Water mass analysis at ETNP Station P2 indicates the relative contributions  
 47 proportions of the three primary water masses at this site, **13°C** water (13CW), North  
 48 Equatorial Pacific Intermediate Water (NEPIW) and Antarctic Intermediate Water  
 49 (AAIW). Values indicate relative contributions of each water mass and are scaled so as to  
 50 sum to one. The horizontal green line indicates the base of the photic zone (160m). Data  
 51 are taken directly from Evans et al. (2020).



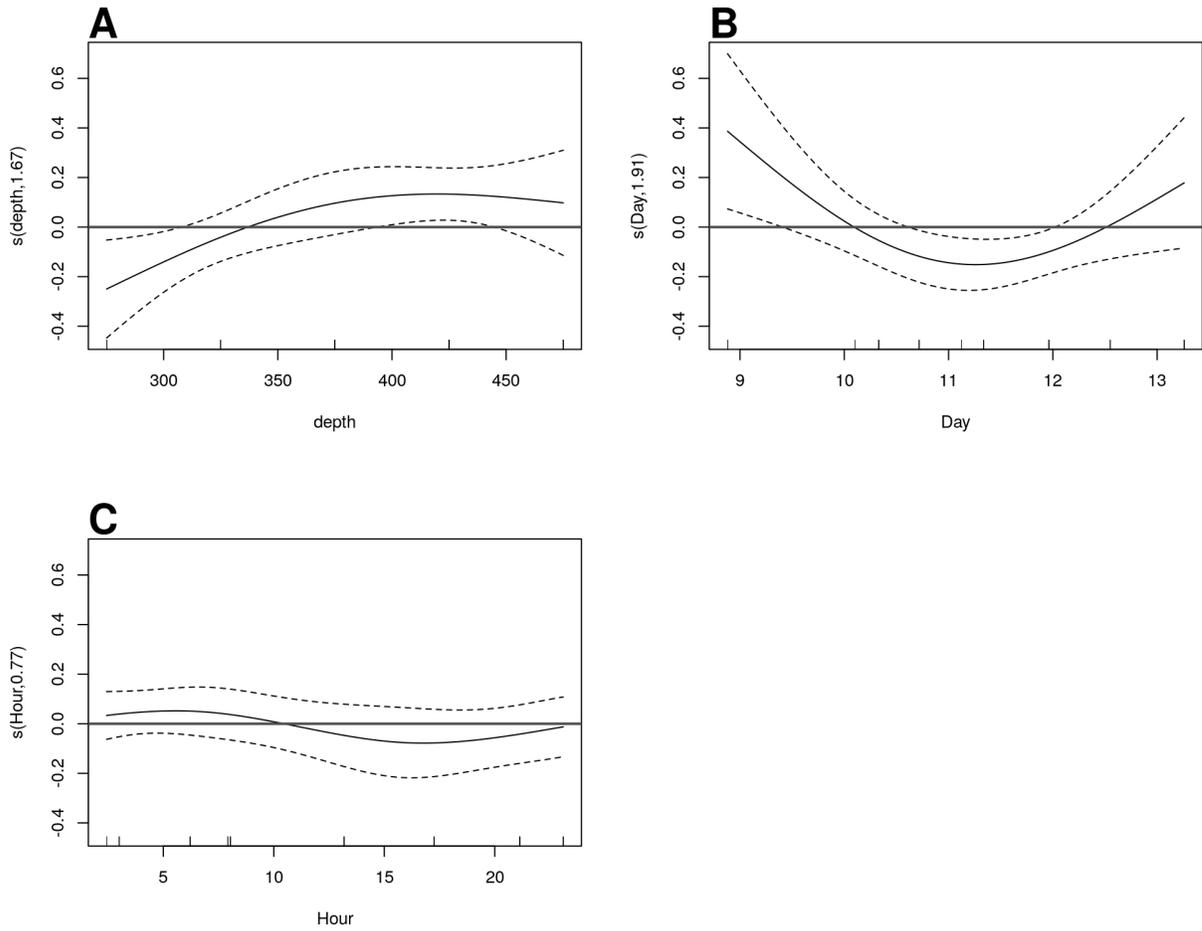
53 Figure S3. Acoustic data, measured by EK60, measured over the course of the  
 54 experiment, at ETNP Station P2. Shown are data from all frequency bands. Values are in  
 55 return signal intensity and have not been normalized to observed biomass. Horizontal  
 56 blue lines indicate the surface and bottom of the ODZ, while the horizontal green line  
 57 indicates the base of the photic zone.



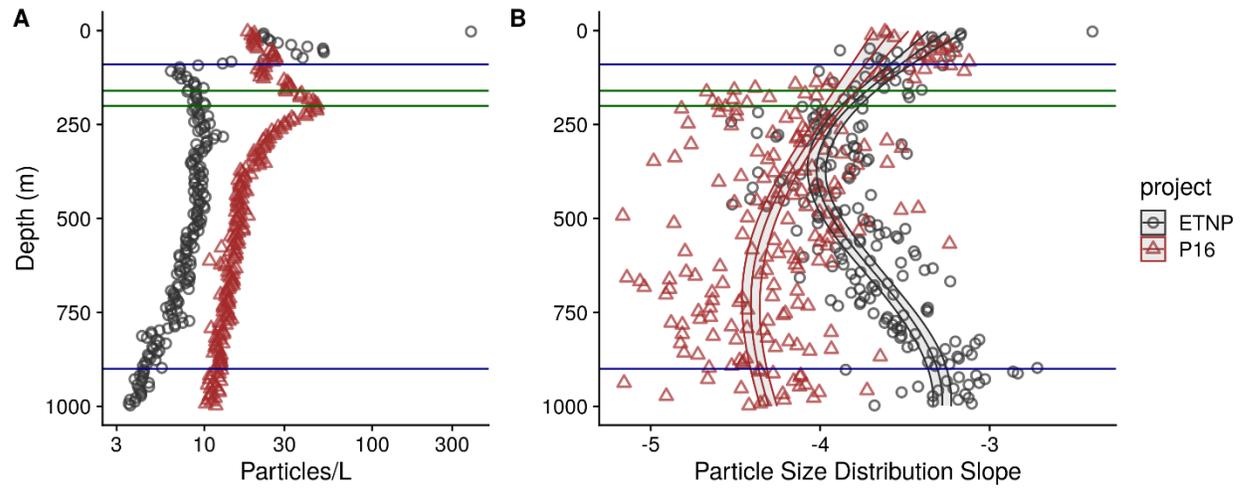
59 Figure S4. A profile of particle abundances at different sizes and depths, collected on  
 60 January 13 beginning at 06:13 at ETNP Station P2. Horizontal blue lines indicate the  
 61 surface and bottom of the ODZ, while the horizontal green line indicates the base of the  
 62 photic zone. (A) Numbers of observed particles. As the x axis is log transformed, zeros  
 63 are indicated as points along the Y axis. Vertical black lines indicate 1 and 5 observed  
 64 particles, respectively. (B) Particle numbers normalized to volume sampled and particle  
 65 size bin width. (C) Smoothed and extrapolated particle abundances, based on a negative  
 66 binomial GAM that predicts particle abundance form size and depth.



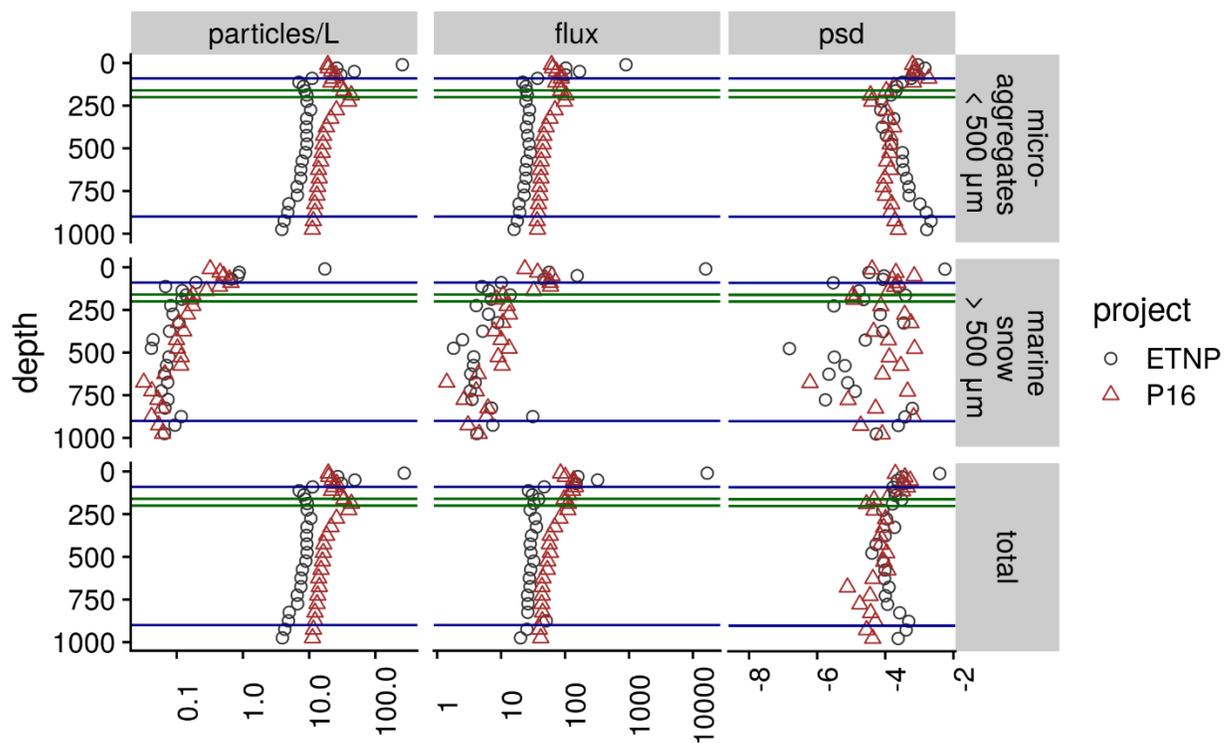
68 Figure S5. An example of observed particle size distribution spectra. These are depth  
 69 binned data from between 150 and 175 m deep in the water column from the cast that  
 70 occurred at *2017-01-13 17:51* local time at ETNP Station P2. This depth bin contains  
 71 total numbers of particles that were seen across 206.8 L of merged UVP image volume.  
 72 Points indicate (A) total numbers of observed particles and (B) particle numbers  
 73 normalized to volume sampled and particle size bin width. Half-dots along the x axis  
 74 correspond to particle size bins in which zero particles were observed. The line indicates  
 75 the predicted best fit line of the data. The line was fit on the binsize and volume  
 76 normalized data by a negative-binomial general linear model. The line in panel A  
 77 indicates predictions from this same model, re-scaled into absolute particle space.

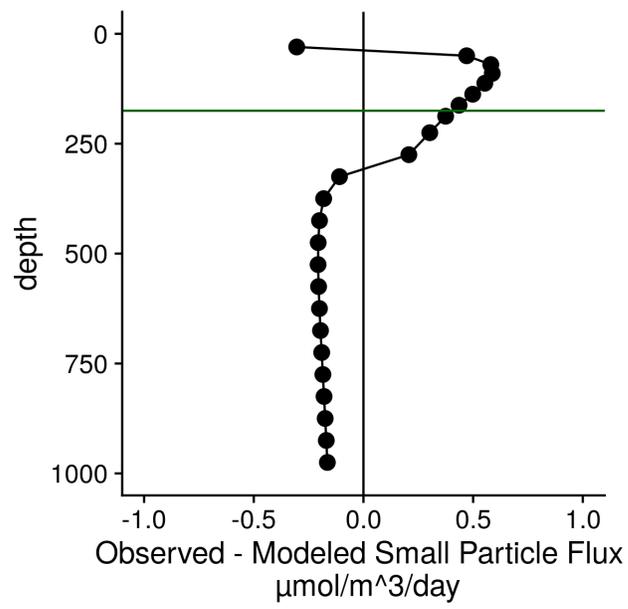
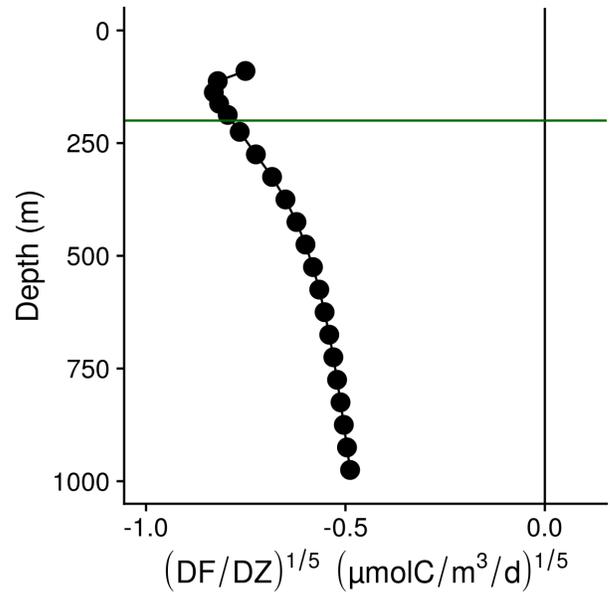
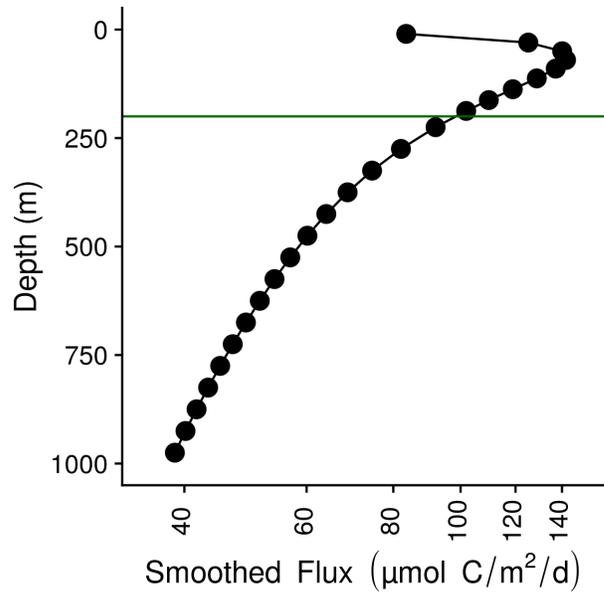


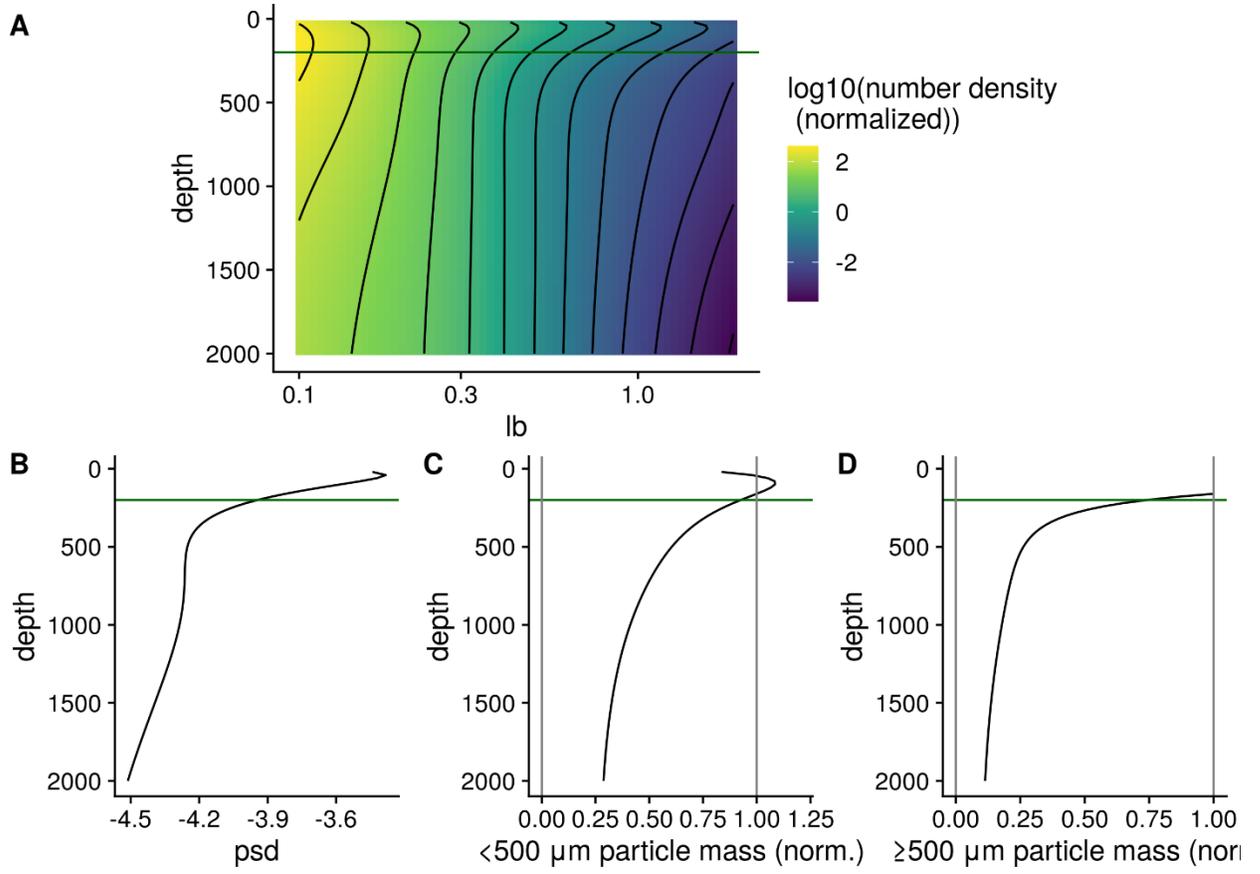
79 Figure S6. GAM predicted effects of A Depth, B Day of the month in January 2017, and  
 80 C hour of the day on the fifth-root transformed, depth normalized, rate of change of flux  
 81 at ETNP Station P2. Y axis indicates the value of the component smooth functions effect  
 82 on Flux. Positive values associate with times and regions of the water column where flux  
 83 is increasing, holding other factors constant, and negative ones where it is decreasing.  
 84 Horizontal gray line indicates  $y = 0$ , corresponding to that parameter having zero effect,  
 85 positive or on the outcome. Only Depth has a statistically significant relationship to rate  
 86 of change of flux (see section 6.5).

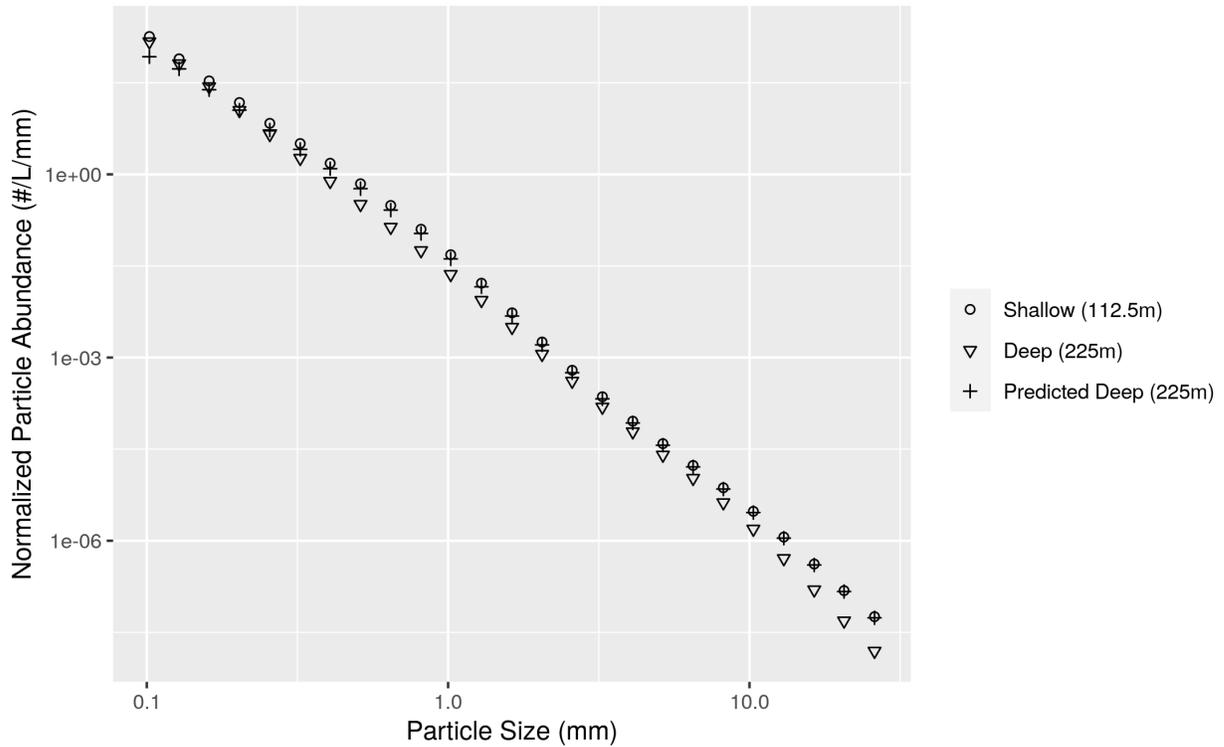


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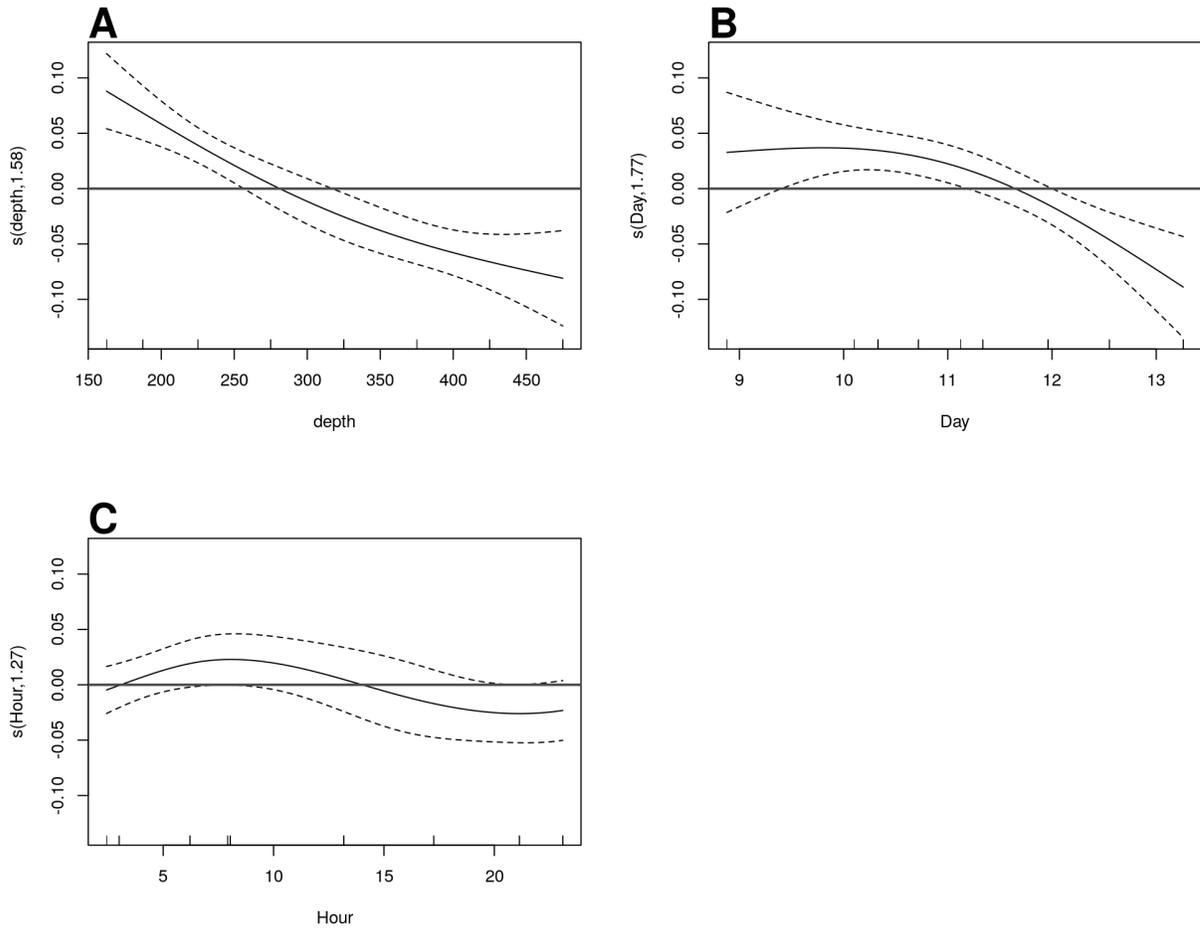








115 Figure S11. An example of differences between modeled and observed particle slope.  
 116 The particle size distribution at a shallow and a deeper depth, from ETNP Station P2, are  
 117 shown. The model generates a prediction of the deep depth profile from the shallow  
 118 depth profile and the flux attenuation between the two profiles. The model predicts more  
 119 attenuation of the smallest particles than is actually observed. In practice the model  
 120 compares depths that are closer together than the two shown here. In particular, the depth  
 121 bin above 225m in our analysis has a midpoint of 187.5m, but we choose in this example  
 122 to compare the 225m particle size profile to the profile at 112.5 m. Two depths that are  
 123 far apart are shown so that the flux attenuation is large enough to be seen by eye and to  
 124 provide a conceptual example of the models' function.



126 Figure S12. GAM predicted effects of A Depth, B Day of the month in January 2017, at  
 127 ETNP Station P2. Y axis indicates the value of the component smooth functions effect on  
 128 the difference between observed and modeled flux. Thus higher values correspond with  
 129 greater flux of small particles than predicted by the model. Horizontal gray line indicates  
 130  $y = 0$ , corresponding to that parameter having zero effect, positive or on the outcome.  
 131 Only Depth and Day have a statistically significant relationship to rate of change of flux  
 132 (see Section 6.8).

133

134 Text S1. Full mathematical justification for the Eulerian version of the particle  
 135 remineralization and sinking model (PRiSM) model. Ful document uploaded separately.

# Diagnosed Particle Disaggregation

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## 1 Definitions and Units

$$m = C_m r^\alpha \quad (1)$$

As in DeVries et al. [2014] particle mass  $m$  is a function of radius  $r$  and scales with a fractal dimension  $\alpha$ .  $C_m$  is a constant.

$$w = C_w r^\gamma \quad (2)$$

Sinking speed also scales with mass to another constant  $\gamma$ . According to Guidi et al. [2008]  $\gamma = \alpha - 1$ , but we'll keep things in terms of  $\gamma$  going forward.

$$F = nmw = nC_m C_w r^{\alpha+\gamma} \quad (3)$$

Flux  $F$  is a function of particle numbers, mass, and sinking speed.

Going forward we will determine the calculations for how many particles of size  $j$  in shallow depth  $i-1$  remineralize into smaller particles of size  $j-1$  in deeper depth  $i$ . We will call this term  $\Delta n_j$

## 2 Conservation of particle number flux

In the absence of disaggregation, the number of particles leaving a box of water is equal to the number of particles going into that box from above. In other words, particle "number-flux" is conserved. Thus the number of particles in the box is a function of the number of particles going into that box, and the difference in velocities between when the particle enters and when that particle leaves.

$$n_{i-1,j-1} \frac{w_{j-1}}{w_j} + n_{i-1,j} = n_{i,j-1} \frac{w_{j-1}}{w_j} + n_{i,j} \quad (4)$$

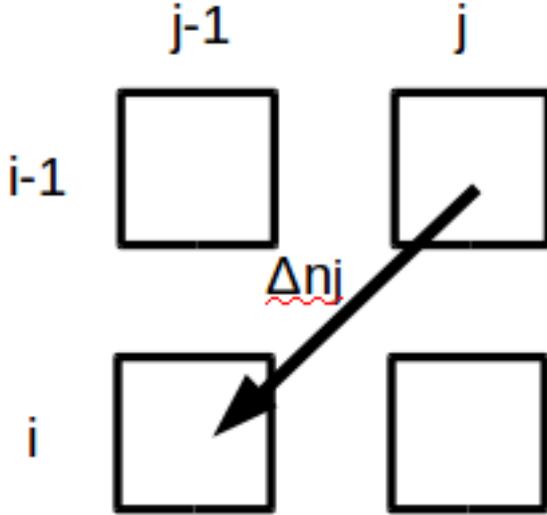


Figure 1: Some number of particles  $\Delta n_j$  of size “j” remineralize to size “j-1” as they sink from depth “i-1” to depth “i”.

Where  $n_{i-1,j}$  is the number of particles of size j (the bigger size) at depth i-1 (the shallower depth). The subscripts correspond to locations in Figure 1.

We can re-arrange equation 4

$$n_{i-1,j-1}w_{j-1} + n_{i-1,j}w_j = n_{i,j-1}w_{j-1} + n_{i,j}w_j \quad (5)$$

Substitute in equation 2 into equation 5.

$$n_{i-1,j-1}r_{j-1}^\gamma + n_{i-1,j}r_j^\gamma = n_{i,j-1}r_{j-1}^\gamma + n_{i,j}r_j^\gamma \quad (6)$$

Rearrange equation 6

$$r_{j-1}^\gamma(n_{i-1,j-1} - n_{i,j-1}) = r_j^\gamma(n_{i,j} - n_{i-1,j}) = \Phi \quad (7)$$

Where  $\Phi$  is a placeholder standing for either side of equation 7, which I will subsequently substitute into things.

Solve for  $\Delta n_j$

$$\Delta n_j = n_{i,j} - n_{i-1,j} = \frac{r_{j-1}^\gamma}{r_j^\gamma}(n_{i-1,j-1} - n_{i,j-1}) \quad (8)$$

### 3 Conservation of Mass Flux

Total flux defined is the sum of flux in each (observed) particle size bin. Particles not in an observed bin don't count towards total flux.

$$\Delta F = \sum_{j=2}^n \Delta f_j + \Delta f_1 \quad (9)$$

Here  $\Delta f_j$  is the flux attenuation from bin of size  $j$  and  $\Delta f_1$  is the loss that comes from particles in bin 1 becoming small enough that you can no longer see them with the UVP.

The flux attenuation in a bin is the product of the rate of flux attenuation with depth of each individual particle  $\frac{\partial f}{\partial z}$ , the depth interval over which the particles attenuate  $\Delta z$  and the number of particles in that bin at the top of the depth interval  $n_{i-1,j}$

$$\Delta f_j = \frac{\partial f}{\partial z} \Delta z n_{i-1,j} \quad (10)$$

Furthermore, the rate of flux attenuation with respect to depth is the product of the rate of mass attenuation with respect to time  $\frac{\partial m}{\partial t}$ , the inverse of the sinking speed  $\frac{\partial t}{\partial z}$ , and the derivative of the flux to mass relationship  $\frac{\partial f}{\partial m}$ .

$$\frac{\partial f}{\partial z} = \frac{\partial m}{\partial z} \frac{\partial f}{\partial m} = \frac{\partial m}{\partial t} \frac{\partial t}{\partial z} \frac{\partial f}{\partial m} \quad (11)$$

In PRiSM, fractional mass loss as a function of time is the same for all particles of all sizes.

Now we are going to come up with the values for each of these terms.

The particle remineralization rate  $C_r$  is the same for particles of all sizes.

$$\frac{\partial m}{\partial t} = C_r * m = C_r C_m r^\alpha \quad (12)$$

Sinking speed definition, substituting from equation 2

$$\frac{\partial t}{\partial z} = \frac{1}{w} = \frac{1}{C_w r^\gamma} \quad (13)$$

Flux for a given size class, substituting equation 1, and finally putting everything in terms of mass (rather than mass and radius, since the two are related)

$$f = mw = m * C_w r^\gamma = m * C_w \left(\frac{m}{C_m}\right)^{\frac{\gamma}{\alpha}} \quad (14)$$

Derriving equation 14 with respect to mass, and substituting equation 1

$$\frac{\partial f}{\partial m} = Cw(1 + \frac{\gamma}{\alpha})(\frac{m}{C_m})^{\frac{\gamma}{\alpha}} = C_w(1 + \frac{\gamma}{\alpha})r^\gamma \quad (15)$$

Finally, we can construct our equation for flux attenuation by substituting equations 12, 13 and 15 into equation 11

$$\frac{\partial f}{\partial z} = C_r C_m r^\alpha (1 + \frac{\gamma}{\alpha}) \quad (16)$$

And now we can solve for equation 17.

$$\Delta f_j = C_r C_m r^\alpha (1 + \frac{\gamma}{\alpha}) \Delta z * n_{i-1,j} \quad (17)$$

We also need to solve for  $\Delta f_1$  the flux “attenuation” that actually comes from particles leaving the smallest bin and escaping from what the UVP sees.

$$\Delta f_1 = \Delta n_1 m_1 w_1 = \Delta n_1 C_m C_w r_1^{\alpha+\gamma} \quad (18)$$

Here,  $\Delta n_1$  is the number of particles leaving bin  $j = 1$ , but we haven’t solved for that yet.

## 4 Solving for $\Delta n_j$

Recall that  $\Delta n_j$  is the number of particles that migrate between bin “j” and bin “j-1” as the particles sink from depth “i-1” to depth “i”.

The flux at the shallower depth is equal to the flux at the deeper depth, plus the flux that attenuated between those two depths. Since  $f = nmw$  and we know m and w

$$n_{i-1,j-1} C_m C_w r_{j-1}^{\alpha+\gamma} + n_{i-1,j} C_m C_w r_j^{\alpha+\gamma} = n_{i,j-1} C_m C_w r_{j-1}^{\alpha+\gamma} + n_{i,j} C_m C_w r_j^{\alpha+\gamma} + \Delta f_j \quad (19)$$

This equation can be re-arranged, and we can substitute in equation 17 for  $\Delta f_j$ .

The  $C_m$  cancel out.

$$C_w r_{j-1}^{\alpha+\gamma} (n_{i-1,j-1} - n_{i,j-1}) = C_w r_j^{\alpha+\gamma} (n_{i,j} - n_{i-1,j}) + C_r (1 + \frac{\gamma}{\alpha}) \Delta z n_{i-1,j} r^\alpha \quad (20)$$

We can then substitute in  $\Phi$  from equation 7.

$$C_w r_{j-1}^\alpha \Phi = C_w r_j^\alpha \Phi + C_r (1 + \frac{\gamma}{\alpha}) \Delta z n_{i-1,j} r^\alpha \quad (21)$$

Rearrange

$$C_w \Phi (r_{j-1}^\alpha - r_j^\alpha) = C_r (1 + \frac{\gamma}{\alpha}) \Delta z r^\alpha n_{i-1,j} \quad (22)$$

solve for  $\Phi$

$$\Phi = \frac{\frac{C_r}{C_w} \Delta z r^\alpha n_{i-1,j} (1 + \frac{\gamma}{\alpha})}{r_{j-1}^\alpha - r_j^\alpha} \quad (23)$$

$$\Delta n_j = \frac{\Phi}{r_j^\gamma} = \frac{\frac{C_r}{C_w} \Delta z r^\alpha n_{i-1,j} (1 + \frac{\gamma}{\alpha})}{r_j^\gamma (r_{j-1}^\alpha - r_j^\alpha)} \quad (24)$$

$$\Delta n_{j-1} = \frac{\Phi}{r_{j-1}^\gamma} = \frac{\Delta n_j r_j^\gamma}{r_{j-1}^\gamma} \quad (25)$$

At this point, the only unsolved variable is  $C_r$ , which we can now calculate.

## 5 Solving for $C_r$

We can calculate  $\Delta F$ , the attenuation of flux and can impose the size spectrum and all of the other constants. Here we find the  $C_r$  that gives us the correct  $\Delta F$

First, to solve equation 9 by substituting in equations 17 and 18

$$\Delta F = \sum_{j=2}^n \Delta f_j + \Delta f_1 = \sum_{j=2}^n \left\{ C_r C_m r_j^\alpha (1 + \frac{\gamma}{\alpha}) \Delta z n_{i-1,j} \right\} + \Delta n_1 C_m C_w r_1^{\alpha+\gamma} \quad (26)$$

Substitute equation 24 for  $\Delta n_j$  when  $j = 1$  for  $\Delta n_1$

$$\Delta F = \sum_{j=2}^n \Delta f_j + \Delta f_1 = \sum_{j=2}^n \left\{ C_r C_m r_j^\alpha (1 + \frac{\gamma}{\alpha}) \Delta z n_{i-1,j} \right\} + \frac{\frac{C_r}{C_w} \Delta z r_1^\alpha n_{i-1,1} (1 + \frac{\gamma}{\alpha})}{r_1^\gamma (r_0^\alpha - r_1^\alpha)} C_m C_w r_1^{\alpha+\gamma} \quad (27)$$

In the above,  $r_0$  is the effective size of the particles smaller than the UVP can see. In principle this is arbitrary. Numbers closer to zero result in fewer particles in the smallest bin disappearing, larger ones to more of those particles disappearing. As  $r_0$  approaches  $r_1$   $C_r$  approaches zero. They cannot be equal or the math breaks.

Pull what I can out of the sum operation, and cancel out  $r^\gamma$  and  $C_w$  from the rightmost term

$$\Delta F = C_r C_m \Delta z \left(1 + \frac{\gamma}{\alpha}\right) \sum_{j=2}^n \{r_j^\alpha n_{i-1,j}\} + \frac{C_r \Delta z r_1^{2\alpha} n_{i-1,1} \left(1 + \frac{\gamma}{\alpha}\right)}{(r_0^\alpha - r_1^\alpha)} C_m \quad (28)$$

Now we can solve for  $C_r$

$$C_r = \frac{\Delta F}{C_m \Delta z \left(1 + \frac{\gamma}{\alpha}\right) \left[ \sum_{j=2}^n \{r_j^\alpha n_{i-1,j}\} + \frac{r_1^{2\alpha} n_{i-1,1}}{r_0^\alpha - r_1^\alpha} \right]} \quad (29)$$

Thus for a pair of profiles, we can estimate the flux attenuation, calculate  $C_r$  from that, and then plug  $C_r$  (and the profile) into the equation 24 for  $\Delta n_j$ . We can thus compute  $\Delta n_j$  for each size class to see how many particles from that bin move to the next bin smaller.