

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

5 20 December 2021

6 Jacob A. Cram¹, Clara A. Fuchsman¹, Megan E. Duffy², Jessica L. Pretty³, Rachel M. Lekanoff³,
7 Jacquelyn A. Neibauer², Shirley W. Leung², Klaus B. Huebert¹, Thomas S. Weber⁴, Daniele Bianchi⁵,
8 Natalya Evans⁶, Allan H. Devol², Richard G. Keil², Andrew M.P. McDonnell³

9 ¹Horn Point Laboratory, University of Maryland Center for Environmental Science, Cambridge, MD,
10 USA.

11 ²School of Oceanography, University of Washington Seattle, Seattle, WA, USA.

12 ³College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK, USA.

13 ⁴School of Arts and Sciences, University of Rochester, Rochester, NY, USA.

14 ⁵Department of Atmospheric and Oceanic Sciences, University of California Los Angeles, Los Angeles,
15 CA, USA.

16 ⁶Department of Biological Sciences, University of Southern California, Los Angeles, CA, USA.

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 μm) and marine snow (> 500 μm) 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 CO₂, 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
103 survive in ODZs by slowing their metabolic processes, but may supplement these with very efficient
104 oxygen uptake and anaerobic metabolism (Seibel, 2011). Acoustic data suggest that zooplankton do not
105 migrate as deeply into ODZs as they do into regions where ODZs are absent (Bianchi et al. 2011). New
106 evidence suggests that in ODZ regions with shallower oxyclines, night-time migration depth remains the
107 same but the depth where the organisms spend the day is compressed (Wishner et al., 2020). The rates at
108 which 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 μm 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 Zooprocess 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 Particles were categorized into bins starting at 102-128 μm in size, with the width of each particle size bin
221 1.26 times larger than the previous bin. We observed particles in 26 distinct size bins, with largest, mostly
222 empty, bin covering particles from 26-32 mm.

223 The instrument is capable of observing smaller particles (down to 60 μm), but these tend to be
224 underestimated and so we only consider particles $\geq 102 \mu\text{m}$ in this analysis. The instrument can in
225 principle also measure larger particles (up to the field of view of the camera), though these tend to be
226 scarce enough to be not detected. In this paper, we do not have an upper size cut-off for our analysis and
227 rather implement statistics that are robust to non-detection of scarce large particles (section 5.5.1). Visual
228 inspection of images larger than 1 mm suggests that these large particles are primarily “marine snow” but
229 about 5% are zooplankton. We did not quantify the size distribution of these images.

230 **5.5 Flux measurements**

231 Free floating, surface tethered particle traps were used to quantify carbon fluxes from sinking particles.
232 Arrays, consisting of a surface float and two traps, were deployed and allowed to float freely during
233 which time they collected particles. Trap deployments began on 07 January, concurrently with the
234 beginning of the UVP sampling, and continued through 12 January. Trap recovery began on 08 January
235 and continued through 13 January. Trap depths spanned the photic zone and mesopelagic, with the
236 shallowest at 60 m and the deepest at 965 m. Trap deployments lasted between 21 and 91 hours, with
237 deeper traps left out for longer, to collect more biomass. Two types of traps were deployed. One set of
238 traps, generally deployed in shallower water, had a solid cone opening with area 0.46 m². The second set
239 had larger conical net with opening of 1.24 m² area made of 53 μm nylon mesh similar to the description
240 in Peterson et al. (2005). All equipment were combination incubators and particle traps, but in this study
241 we only use trap data. No poisons were used, and both living and dead zooplankton, or ‘swimmers’, were
242 manually removed prior to POC analysis.

243 Sediment trap material was filtered immediately upon trap recovery onto pre-combusted GF-75 45 mm
244 filters (nominal pore size of 0.3 μm) and preserved until further analysis at -80°C. These filters were split
245 into several fractions for other analyses not discussed here. Total carbon content of particles in each trap
246 were measured by isotope ratio mass spectrometry. Elemental analyses for particulate carbon and nitrogen
247 quantities as well as ¹³C and ¹⁵N isotopic compositions were conducted at the U.C. Davis Stable Isotope

248 Facility (<http://stableisotopefacility.ucdavis.edu>) on acidified freeze-dried trap samples to capture organic
249 elemental contributions. Carbon was below mass spectrometry detection limits in four traps – these traps
250 were excluded from further analysis. Traps at similar depths did detect carbon, lending confidence to the
251 idea that these non-detections were technical in nature, due to splitting of samples for multiple analyses,
252 rather than reflecting environmental conditions.

253 **5.6 Analysis**

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

261 Two normalized values of particle numbers were calculated. In the first, particle numbers were divided by
262 volume sampled, to generate values in *particles/m³*. In the second, particles were divided by both volume
263 sampled and the width of the particle size-bins to generate values in *particles/m³/mm*.

264 **5.6.1 Particle size distribution**

265 We determined the slope and intercept of the particle size distribution spectrum by fitting a power law to
266 the data, which is a common function for fitting particle size distributions (Buonassissi & Dierssen,
267 2010). Because large particles were infrequently detected, we used a general linear model that assumed
268 residuals of the data followed a negative-binomial (rather than normal) distribution. We fit the equation

$$269 \ln\left(\frac{E(\text{Total Particles})}{\text{Volume} * \text{Binsize}}\right) = b_0 + b_1 \ln(\text{Size}) \quad (\text{Eqn 1}).$$

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

279 5.6.2 Estimating particle flux

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

$$282 \text{ Flux} = \sum_j \left[\frac{\text{Total Particles}_j}{\text{Volume} * \text{Bin size}_i} * C_f * (\text{Size}_j)^A \right] \quad (\text{Eqn. 2})$$

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

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

286 We also estimated the exponent of the particle size to biomass exponent α and size to sinking speed
287 exponent γ 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
288 spherical drag profile, in which case $A = \alpha + \gamma$ and $\gamma = \alpha - 1$ (Guidi et al., 2008); with “A” referring to
289 the exponent in Eqn 2.

290 5.6.3 Size specific information

291 We separately analyzed total particle numbers, particle size distribution, and particle flux for particles
292 larger than or equal to 500 μm , and those smaller than 500 μm , to determine the relative contributions of
293 these two particle classes to particle properties. 500 μm was chosen as it has been previously defined as
294 the cutoff point between microscopic “microaggregates” and macroscopic “marine snow” (Simon et al.,
295 2002).

296 5.7 Variability

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

$$300 \text{ Flux}^{1/5} \sim s(\text{Depth}) + s(\text{Day}) + s(\text{Hour}) \quad (\text{Eqn. 3})$$

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

304 5.8 Smoothing for Comparison to Model Results

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

308 $\ln\left(\frac{E(\text{Total Particles})}{\text{Volume} \cdot \text{Bin size}}\right) \sim s(\text{Depth}, \ln(\text{Size}))$ (Eqn. 4)

309 In this case, there is a single, two-dimensional, smooth term, rather than additive one-dimensional terms
310 as in Eqn. 3 so that the smooth term can consider interactions between the two parameters, rather than
311 assuming that the terms are additive. The predicted particle numbers at each particle size and depth, as
312 well as particle size distribution spectra, and estimated particle masses of all particles smaller than
313 500 μm and all particles larger than or equal to 500 μm were then compared to each of Weber and
314 Bianchi's (2020) models, corresponding to our **H1-H3**.

315 **5.9 Modeling remineralization and sinking**

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

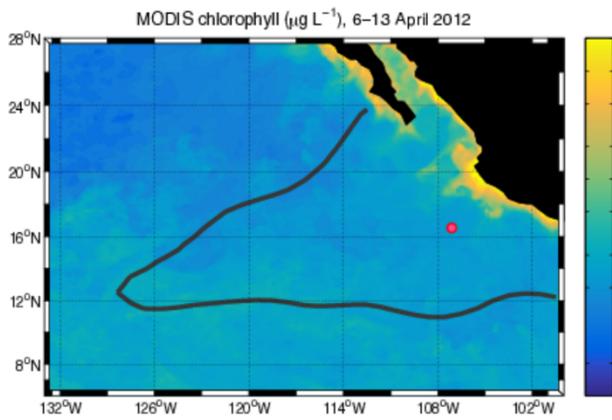
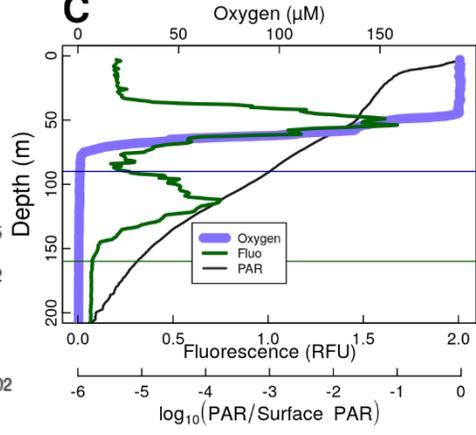
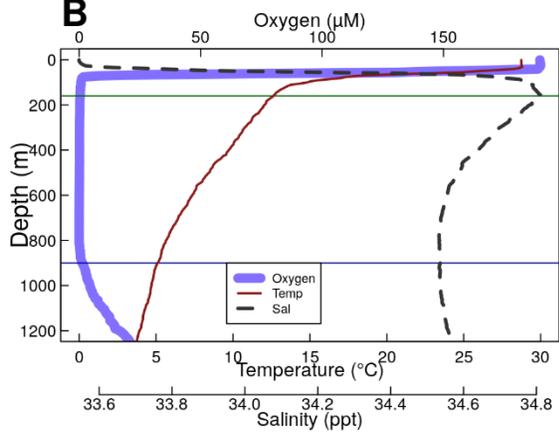
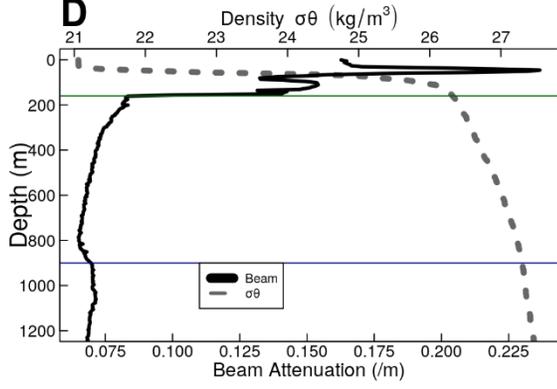
324 In practice we expanded the previous numerical implementation of PRiSM to allow for particle size
325 distribution spectra with particle-size bins that match those obtained by the UVP, and to return estimates
326 of the number of particles in those same size bins (Text S1). The model accepts inputs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

337 **6 Results**

338 **6.1 Physical and Chemical Data**

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

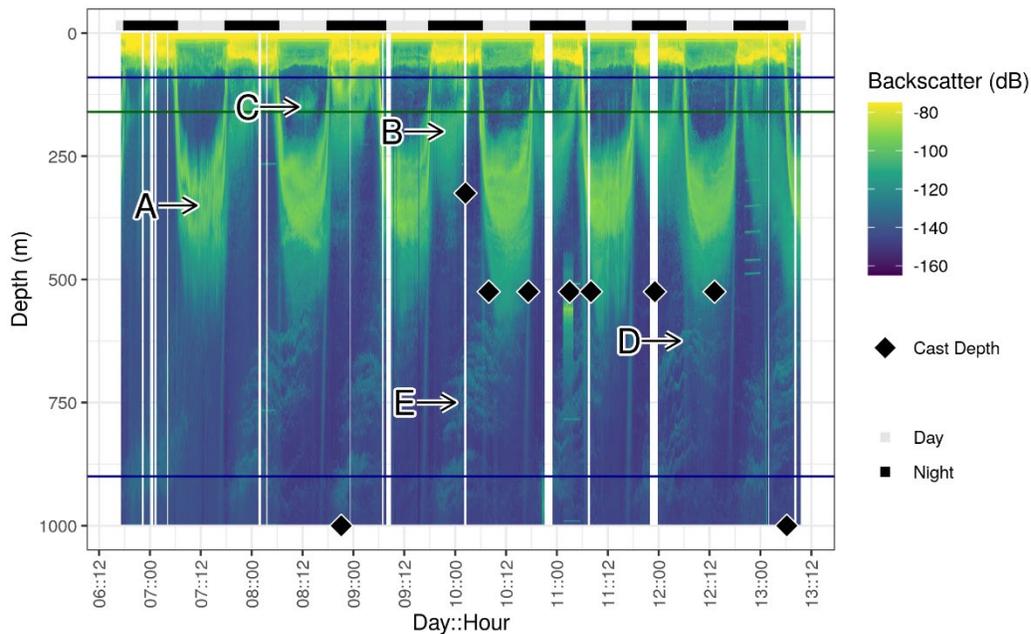
354 For the purposes of this study, we define the photic zone as ending at the base of this deeper fluorescence
355 layer (160m). This photic zone base corresponds with photosynthetically active radiation (PAR) $< 10^{-5}$ of
356 surface PAR levels (Figure 1C). We note that this photic zone depth is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

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

359

373 **6.2 Acoustic data reveal diel migration patterns**

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

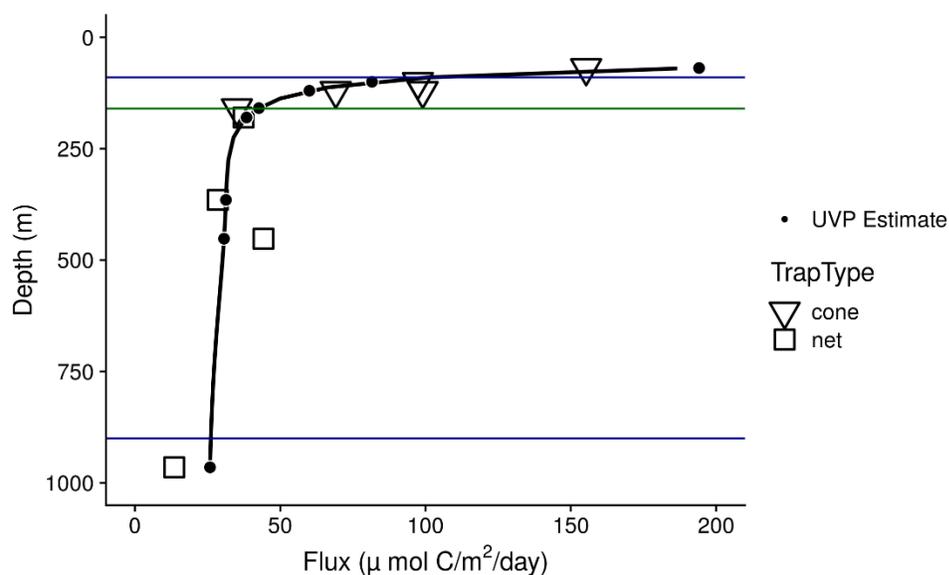


388

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

409 6.3 Flux data from traps

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



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

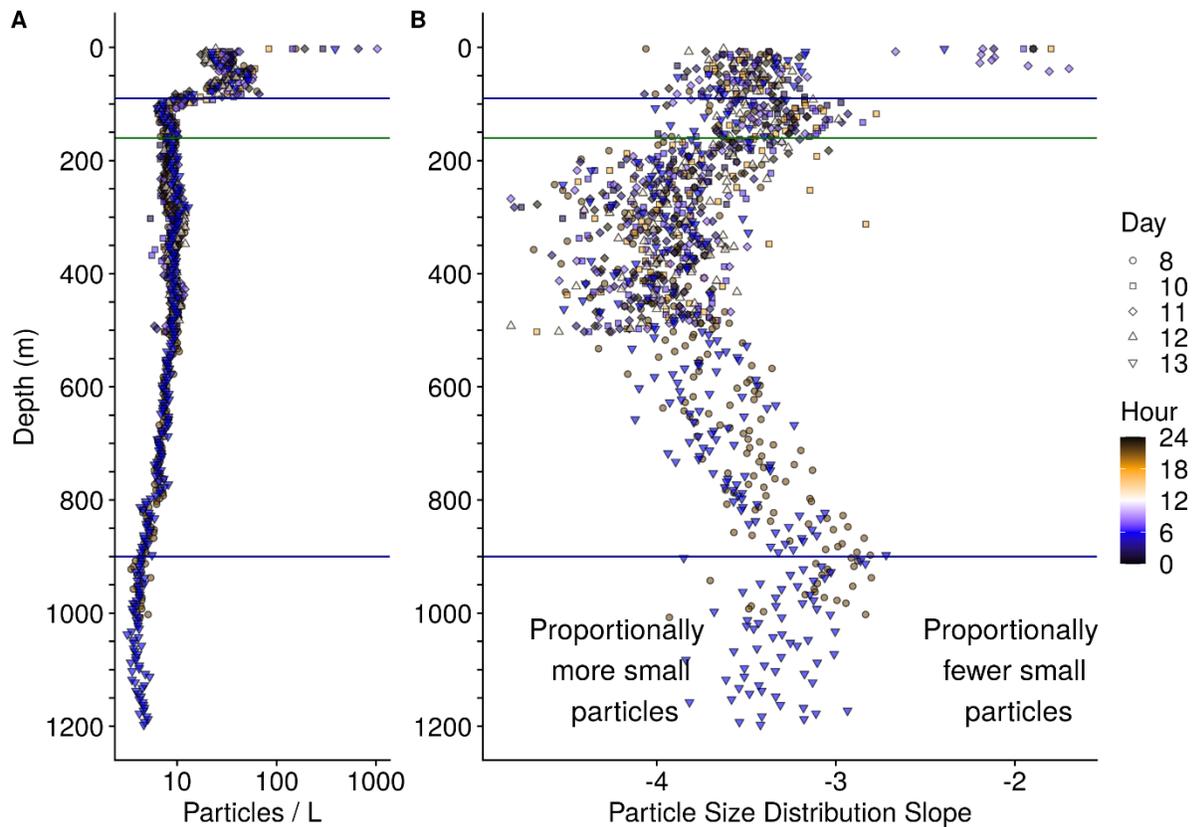
416 estimates of particle flux from the UVP generated by fitting the sum of particle numbers all four
417 profiles to the trap observed flux. The black line indicates flux predictions made by fitting UVP
418 observations to the trap data. Black circles indicate regions on the black line corresponding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

421 **6.4 Particle abundance measurements vary with size and depth**

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

430 Total particle numbers were generally similar between different casts, regardless of which day or hour
431 they were collected (Figure 4A). Particle numbers were highest in the surface and decreased within the
432 oxic region, then remained relatively constant from 160 m to 500 m, and gradually decreased between
433 500 m and the lower oxycline (Figure 4A).

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



442 **Figure 4. A.** Observed, volume normalized total particle numbers from 9 casts taken at different
 443 times of the day at ETNP station P2. **B.** Calculated particle size distribution slopes of those
 444 particles. These data have not been binned by depth in order to better show sample to sample
 445 variability. Horizontal blue lines indicate the top and bottom of the ODZ, while the horizontal
 446 green line indicates the base of the photic zone. Hour corresponds to local, Mexican General
 447 Standard, time. Particles are binned into 5 m depth increments.

448 **6.5 Estimated particle flux sometimes increases with depth in the ODZ core**

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

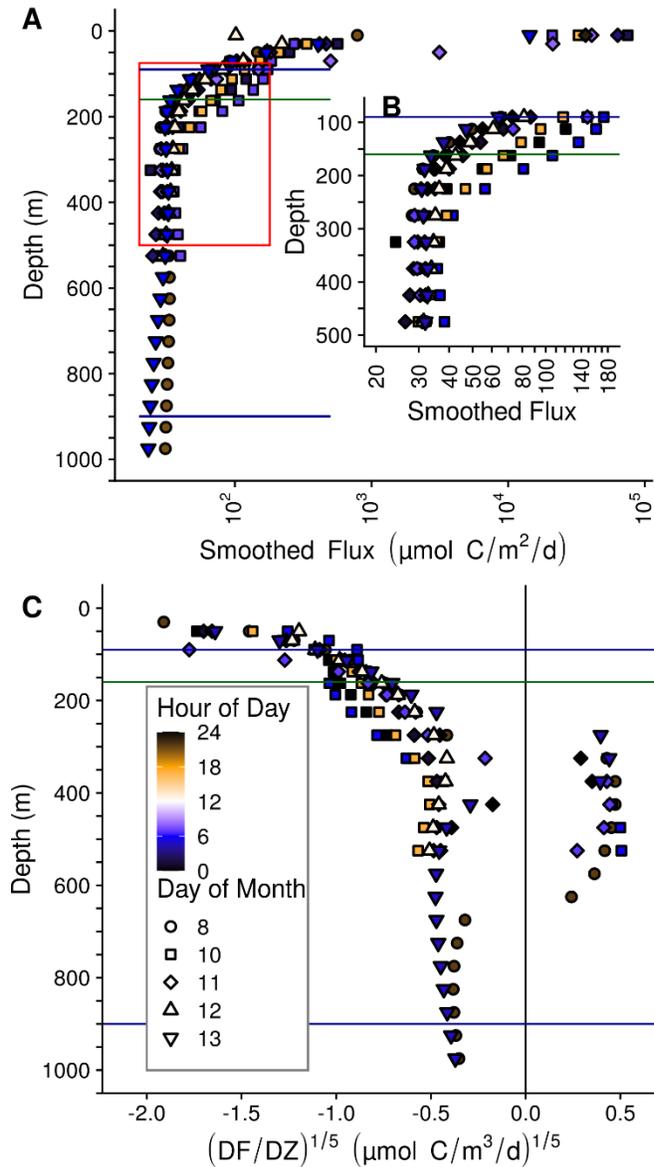
$$451 \text{ Flux} = (133 \mu \text{ mol C} / \text{m}^2/\text{day}) = 133 * \text{Size (mm)}^{2.00} \quad (\text{Eqn 5})$$

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

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

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

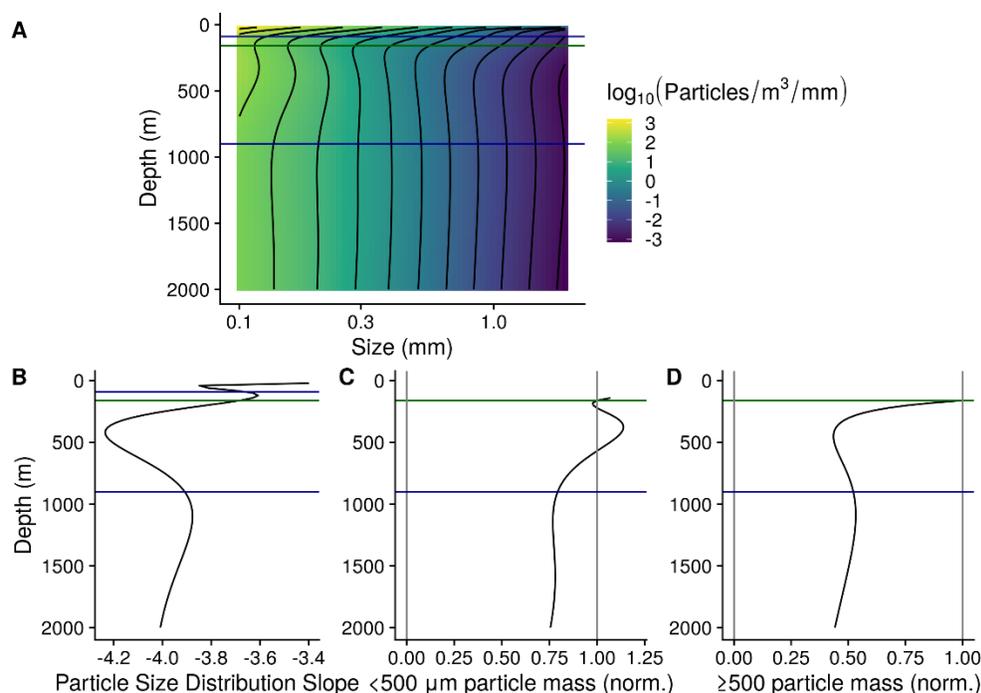
463 The general additive model that quantified how the of change of flux between 250 m and 500 m varied
464 with depth, decimal study day and decimal hour found that depth ($p = 0.061$) and hour of the day ($p =$
465 0.196) did not statistically associate with the fifth root transformed rate of change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



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

484 6.6 Smoothed and averaged data

485 At the ETNP ODZ site, highly smoothed particle abundance data suggested that particle size, averaged
486 across all casts, followed a pattern in which the abundance of $<500 \mu\text{m}$ particles increased between the
487 oxycline and 350 m (Figure 6A), which corresponded with steepening of the particle size distribution
488 slope (Figure 6B), and an increase in microaggregate ($<500 \mu\text{m}$) particle biomass (Figure 6C), but not of
489 $> 500 \mu\text{m}$ particle biomass (Figure 6D). Deeper in the ODZ, the microaggregate ($<500 \mu\text{m}$) particle
490 number and biomass, and the particle size distribution slope declined.



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

500 At the oxic site, particle size distributions generally steepened with depth, while both microaggregates
501 ($<500 \mu\text{m}$) and $\geq 500 \mu\text{m}$ estimated particle biomass followed a power law decrease with depth (Figure
502 S10).

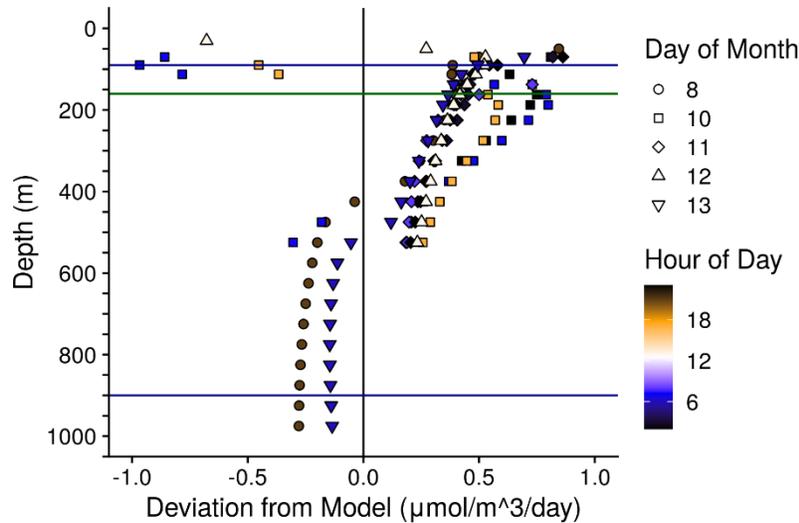
503 **6.7 Particle number dynamics differ from model expectations**

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

$$514 \text{DFM} = \frac{(<500 \mu\text{m Flux Observed} - <500 \mu\text{m Flux Modeled})}{\Delta Z} \quad (\text{Eqn. 6})$$

515 In the above equation ΔZ is the distance, in meters, between the current depth bin and the previous depth
516 bin, whose particle size distribution is fed into the predictive model.

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



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

546 **6.8 ETNP particle dynamics differ from those seen at an oxic site**

547 The ODZ data were compared to an oxic water column in order to identify the spectral signatures that are
 548 particular to oxygen deficient waters. The oxic site, P16 Station 100, was characterized by a more
 549 gradually sloping pycnocline, and an oxygen minimum at 500 m of 19.7 μM , which is hypoxic (Figure
 550 S1B). There was no working fluorescence sensor on that cruise, but data from World Ocean Atlas (Boyer
 551 et al., 2018) suggest that the photic zone is characterized by a single fluorescence peak with a maximum
 552 at 110 m and which disappeared at 200 m (Figure S1C). Thus, we define the mesopelagic as beginning at
 553 200 m at the oxic site. Turbidity followed chlorophyll concentration and did not have a peak in the
 554 mesopelagic (Figure S1D), unlike the ODZ site. There was a salinity peak at 150 m (Figure S1B).

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

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

571 **7 Discussion**

572 **7.1 Diel migrators spend time in the ODZ core**

573 Organisms of all sizes appear to migrate into the core of the ODZ at our site. Most migrators appear to
574 leave the surface at dawn, spend the day in the top 500 m of the ODZ and return to the surface at dusk
575 (Figure 2A), while others show the opposite pattern, leaving the surface at dusk and returning at dawn
576 (Figure 2B). Diel migration is prevalent throughout the oceans (Cisewski et al., 2010; Hays, 2003;
577 Heywood, 1996; Jiang et al., 2007; Rabindranath et al., 2011; Sainmont et al., 2014; Yang et al., 2019),
578 including at Oxygen Minimum Zone ($<20 \mu\text{M O}_2$) sites (Antezana, 2009; Kiko et al., 2020; Riquelme-
579 Bugueño et al., 2020), and highly anoxic ODZ sites (Bianchi et al., 2014; Herrera et al., 2019; Hidalgo et
580 al., 2005). Sampling efforts in the Costa Rica Dome, a unique system in the ETNP, find that euphausiids
581 and fish migrate into the ODZ (Maas et al., 2014; Wishner et al., 2013), but that diel migrators are
582 primarily 2 mm–5 mm in size (Wishner et al., 2013). Krill in the Humboldt current OMZ similarly spend
583 the day at depth and migrate to the surface at night (Riquelme-Bugueño et al., 2020). The presence of
584 organisms that appear and disappear just above the base of the photic zone, in the region of the deeper
585 anoxic fluorescence peak region, but absence of a tell-tale signature of mass migration before or after they
586 appear (Figure 2C) may suggest that these organisms migrate at different times of the day to this deep

587 region, rather than all at once. Another possibility is that they pass through our station at this depth in
588 mid-day, but migrate to depth at another location.

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

600 **7.2 Flux is lower at this site than previous measurements in the ETNP**

601 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
602 measurements by traps at other, more productive, ODZ sites, which ranged from 1000–
603 10000 $\mu\text{mol}/\text{m}^2/\text{day}$ (Hartnett & Devol, 2003; Van Mooy et al., 2002).

604 **7.3 The flux to size relationship is typical of other sites**

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

617 **7.4 Remineralization rates of all particles decrease in the ODZ, but** 618 **disaggregation does not**

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

639 **7.5 Zooplankton likely transport organic matter into the ODZ core**

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

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

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

667 **7.6 Zooplankton likely disaggregate particles in the ODZ core**

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

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

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

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

691 **7.7 Water mass changes may affect particle flux and size changes**

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

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

709 **7.8 Oxic site differences**

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

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

723 **7.9 Future directions**

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

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

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

745 **8 Conclusions**

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

765 **9 Acknowledgements**

766 The authors thank the captain and crew of the RV *Sikuliaq* for making field collection possible. The
767 authors also thank Gabrielle Rocap and Curtis Deutsch for assistance in the field and valuable insight.
768 Jacquelyn Burchfield provided helpful insights about the mathematical underpinnings of the particle
769 remineralization model. We thank two anonymous reviewers, whose comments dramatically improved
770 this manuscript.

771 Funding for this project was provided by NSF Grant Number DEB-1542240, as well as startup funds to
772 JAC and CAF provided by University of Maryland Center for Environmental Science. The McDonnell
773 laboratory acknowledges support from NSF-OCE 1654663.

774 Data for this research, as well as analysis and model code are available on FigShare at
775 <https://figshare.com/articles/software/POMZ-ETNP-UVP-2017/14589435>.

776 **10 References**

- 777 Ahn, J. H., & Grant, S. B. (2007). Size Distribution, Sources, and Seasonality of Suspended Particles in
778 Southern California Marine Bathing Waters. *Environmental Science & Technology*, *41*(3), 695–
779 702. <https://doi.org/10.1021/es061960+>
- 780 Andersen, L. N. (2001). The new Simrad EK60 scientific echo sounder system. *The Journal of the*
781 *Acoustical Society of America*, *109*(5), 2336–2336. <https://doi.org/10.1121/1.4744207>
- 782 Antezana, T. (2009). Species-specific patterns of diel migration into the Oxygen Minimum Zone by
783 euphausiids in the Humboldt Current Ecosystem. *Progress in Oceanography*, *83*(1), 228–236.
784 <https://doi.org/10.1016/j.pocean.2009.07.039>
- 785 Archibald, K. M., Siegel, D. A., & Doney, S. C. (2019). Modeling the Impact of Zooplankton Diel
786 Vertical Migration on the Carbon Export Flux of the Biological Pump. *Global Biogeochemical*
787 *Cycles*, *33*(2), 181–199. <https://doi.org/10.1029/2018GB005983>
- 788 Bianchi, D., Stock, C., Galbraith, E. D., & Sarmiento, J. L. (2013). Diel vertical migration: Ecological
789 controls and impacts on the biological pump in a one-dimensional ocean model. *Global*
790 *Biogeochemical Cycles*, *27*(2), 478–491. <https://doi.org/10.1002/gbc.20031>
- 791 Bianchi, D., Babbín, A. R., & Galbraith, E. D. (2014). Enhancement of anammox by the excretion of diel
792 vertical migrators. *Proceedings of the National Academy of Sciences*, *111*(44), 15653–15658.
793 <https://doi.org/10.1073/pnas.1410790111>
- 794 Bianchi, D., Weber, T. S., Kiko, R., & Deutsch, C. (2018). Global niche of marine anaerobic metabolisms
795 expanded by particle microenvironments. *Nature Geoscience*, *11*(4), 263.
796 <https://doi.org/10.1038/s41561-018-0081-0>
- 797 Boyer, T., Garcia, H. E., Locarini, R. A., Ricardo, A., Zweng, M. M., Mishonov, A. V., et al. (2018).
798 *World Ocean Atlas 2018*. NOAA National Centers for Environmental Information.

799 Briggs, N., Dall'Olmo, G., & Claustre, H. (2020). Major role of particle fragmentation in regulating
800 biological sequestration of CO₂ by the oceans. *Science*, 367(6479), 791–793.
801 <https://doi.org/10.1126/science.aay1790>

802 Bristow, L. A. (2018). Anoxia in the snow. *Nature Geoscience*, 11(4), 226–227.
803 <https://doi.org/10.1038/s41561-018-0088-6>

804 Buonassissi, C. J., & Dierssen, H. M. (2010). A regional comparison of particle size distributions and the
805 power law approximation in oceanic and estuarine surface waters. *Journal of Geophysical*
806 *Research: Oceans*, 115(C10). <https://doi.org/10.1029/2010JC006256>

807 Burd, A. B., & Jackson, G. A. (2009). Particle Aggregation. *Annual Review of Marine Science*, 1(1), 65–
808 90. <https://doi.org/10.1146/annurev.marine.010908.163904>

809 Cavan, E. L., Trimmer, M., Shelley, F., & Sanders, R. (2017). Remineralization of particulate organic
810 carbon in an ocean oxygen minimum zone. *Nature Communications*, 8, 14847.
811 <https://doi.org/10.1038/ncomms14847>

812 Cisewski, B., Strass, V. H., Rhein, M., & Krägfesky, S. (2010). Seasonal variation of diel vertical
813 migration of zooplankton from ADCP backscatter time series data in the Lazarev Sea, Antarctica.
814 *Deep Sea Research Part I: Oceanographic Research Papers*, 57(1), 78–94.
815 <https://doi.org/10.1016/j.dsr.2009.10.005>

816 Cram, J. A., Weber, T., Leung, S. W., McDonnell, A. M. P., Liang, J.-H., & Deutsch, C. (2018). The Role
817 of Particle Size, Ballast, Temperature, and Oxygen in the Sinking Flux to the Deep Sea. *Global*
818 *Biogeochemical Cycles*, 32(5), 858–876. <https://doi.org/10.1029/2017GB005710>

819 Date, S. (2020, November 21). Generalized Linear Models. Retrieved May 2, 2021, from
820 <https://towardsdatascience.com/generalized-linear-models-9ec4dfe3dc3f>

821 Deutsch, C., Berelson, W., Thunell, R., Weber, T., Tems, C., McManus, J., et al. (2014). Centennial
822 changes in North Pacific anoxia linked to tropical trade winds. *Science*, 345(6197), 665–668.
823 <https://doi.org/10.1126/science.1252332>

824 DeVries, T., & Weber, T. (2017). The export and fate of organic matter in the ocean: New constraints
825 from combining satellite and oceanographic tracer observations. *Global Biogeochemical Cycles*,
826 2016GB005551. <https://doi.org/10.1002/2016GB005551>

827 DeVries, T., Deutsch, C., Primeau, F., Chang, B., & Devol, A. (2012). Global rates of water-column
828 denitrification derived from nitrogen gas measurements. *Nature Geoscience*, 5(8), 547–550.
829 <https://doi.org/10.1038/ngeo1515>

830 DeVries, T., Liang, J.-H., & Deutsch, C. (2014). A mechanistic particle flux model applied to the oceanic
831 phosphorus cycle. *Biogeosciences Discuss.*, 11(3), 3653–3699. [https://doi.org/10.5194/bgd-11-](https://doi.org/10.5194/bgd-11-3653-2014)
832 [3653-2014](https://doi.org/10.5194/bgd-11-3653-2014)

833 Dilling, L., & Alldredge, A. L. (2000). Fragmentation of marine snow by swimming macrozooplankton:
834 A new process impacting carbon cycling in the sea. *Deep Sea Research Part I: Oceanographic*
835 *Research Papers*, 47(7), 1227–1245. [https://doi.org/10.1016/S0967-0637\(99\)00105-3](https://doi.org/10.1016/S0967-0637(99)00105-3)

836 Durkin, C. A., Estapa, M. L., & Buesseler, K. O. (2015). Observations of carbon export by small sinking
837 particles in the upper mesopelagic. *Marine Chemistry*, 175, 72–81.
838 <https://doi.org/10.1016/j.marchem.2015.02.011>

839 Evans, N., Boles, E., Kwiecinski, J. V., Mullen, S., Wolf, M., Devol, A. H., et al. (2020). The role of
840 water masses in shaping the distribution of redox active compounds in the Eastern Tropical North
841 Pacific oxygen deficient zone and influencing low oxygen concentrations in the eastern Pacific
842 Ocean. *Limnology and Oceanography*, 65(8), 1688–1705. <https://doi.org/10.1002/lno.11412>

843 Francois, R., Honjo, S., Krishfield, R., & Manganini, S. (2002). Factors controlling the flux of organic
844 carbon to the bathypelagic zone of the ocean. *Global Biogeochemical Cycles*, 16(4), 34-1-34–20.
845 <https://doi.org/10.1029/2001GB001722>

846 Fuchsman, C. A., Devol, A. H., Saunders, J. K., McKay, C., & Rocap, G. (2017). Niche Partitioning of
847 the N Cycling Microbial Community of an Offshore Oxygen Deficient Zone. *Frontiers in*
848 *Microbiology*, 8. <https://doi.org/10.3389/fmicb.2017.02384>

849 Fuchsman, C. A., Palevsky, H. I., Widner, B., Duffy, M., Carlson, M. C. G., Neibauer, J. A., et al. (2019).
850 Cyanobacteria and cyanophage contributions to carbon and nitrogen cycling in an oligotrophic
851 oxygen-deficient zone. *The ISME Journal*, 1. <https://doi.org/10.1038/s41396-019-0452-6>

852 Garcia-Robledo, E., Padilla, C. C., Aldunate, M., Stewart, F. J., Ulloa, O., Paulmier, A., et al. (2017).
853 Cryptic oxygen cycling in anoxic marine zones. *Proceedings of the National Academy of*
854 *Sciences*, 114(31), 8319–8324. <https://doi.org/10.1073/pnas.1619844114>

855 Goldthwait, S. A., Carlson, C. A., Henderson, G. K., & Alldredge, A. L. (2005). Effects of physical
856 fragmentation on remineralization of marine snow. *Marine Ecology Progress Series*, 305, 59–65.

857 Guidi, L., Jackson, G. A., Stemmann, L., Miquel, J. C., Picheral, M., & Gorsky, G. (2008). Relationship
858 between particle size distribution and flux in the mesopelagic zone. *Deep Sea Research Part I:*
859 *Oceanographic Research Papers*, 55(10), 1364–1374. <https://doi.org/10.1016/j.dsr.2008.05.014>

860 Hannides, C. C. S., Landry, M. R., Benitez-Nelson, C. R., Styles, R. M., Montoya, J. P., & Karl, D. M.
861 (2009). Export stoichiometry and migrant-mediated flux of phosphorus in the North Pacific
862 Subtropical Gyre. *Deep Sea Research Part I: Oceanographic Research Papers*, 56(1), 73–88.
863 <https://doi.org/10.1016/j.dsr.2008.08.003>

864 Hartnett, H. E., & Devol, A. H. (2003). Role of a strong oxygen-deficient zone in the preservation and
865 degradation of organic matter: a carbon budget for the continental margins of northwest Mexico
866 and Washington State. *Geochimica et Cosmochimica Acta*, 67(2), 247–264.
867 [https://doi.org/10.1016/S0016-7037\(02\)01076-1](https://doi.org/10.1016/S0016-7037(02)01076-1)

868 Hays, G. C. (2003). A review of the adaptive significance and ecosystem consequences of zooplankton
869 diel vertical migrations. In M. B. Jones, A. Ingólfsson, E. Ólafsson, G. V. Helgason, K.
870 Gunnarsson, & J. Svavarsson (Eds.), *Migrations and Dispersal of Marine Organisms* (pp. 163–
871 170). Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-94-017-2276-6_18

872 Herrera, I., Yebra, L., Antezana, T., Giraldo, A., Färber-Lorda, J., & Hernández-León, S. (2019). Vertical
873 variability of *Euphausia distinguenda* metabolic rates during diel migration into the oxygen

874 minimum zone of the Eastern Tropical Pacific off Mexico. *Journal of Plankton Research*, 41(2),
875 165–176. <https://doi.org/10.1093/plankt/fbz004>

876 Heywood, K. J. (1996). Diel vertical migration of zooplankton in the Northeast Atlantic. *Journal of*
877 *Plankton Research*, 18(2), 163–184. <https://doi.org/10.1093/plankt/18.2.163>

878 Hidalgo, P., Escribano, R., & Morales, C. E. (2005). Ontogenetic vertical distribution and diel migration
879 of the copepod *Eucalanus inermis* in the oxygen minimum zone off northern Chile (20–21° S).
880 *Journal of Plankton Research*, 27(6), 519–529. <https://doi.org/10.1093/plankt/fbi025>

881 Homoky, W. B., Conway, T. M., John, S. G., König, D., Deng, F., Tagliabue, A., & Mills, R. A. (2021).
882 Iron colloids dominate sedimentary supply to the ocean interior. *Proceedings of the National*
883 *Academy of Sciences*, 118(13), e2016078118. <https://doi.org/10.1073/pnas.2016078118>

884 Horak, R. E. A., Ruef, W., Ward, B. B., & Devol, A. H. (2016). Expansion of denitrification and anoxia
885 in the eastern tropical North Pacific from 1972 to 2012. *Geophysical Research Letters*, 43(10),
886 2016GL068871. <https://doi.org/10.1002/2016GL068871>

887 Inthorn, M. (2005). Lateral particle transport in nepheloid layers - a key factor for organic matter
888 distribution and quality in the Benguela high-productivity area. Retrieved from
889 <https://media.suub.uni-bremen.de/handle/elib/2212>

890 Ito, T., Minobe, S., Long, M. C., & Deutsch, C. (2017). Upper ocean O₂ trends: 1958-2015. *Geophysical*
891 *Research Letters*, 44(9), 4214–4223. <https://doi.org/10.1002/2017GL073613>

892 Jackson, G. A., & Burd, A. B. (2001). A model for the distribution of particle flux in the mid-water
893 column controlled by subsurface biotic interactions. *Deep Sea Research Part II: Topical Studies*
894 *in Oceanography*, 49(1), 193–217. [https://doi.org/10.1016/S0967-0645\(01\)00100-X](https://doi.org/10.1016/S0967-0645(01)00100-X)

895 Jiang, S., Dickey, T. D., Steinberg, D. K., & Madin, L. P. (2007). Temporal variability of zooplankton
896 biomass from ADCP backscatter time series data at the Bermuda Testbed Mooring site. *Deep Sea*
897 *Research Part I: Oceanographic Research Papers*, 54(4), 608–636.
898 <https://doi.org/10.1016/j.dsr.2006.12.011>

- 899 Kaartvedt, S., Klevjer, T. A., Torgersen, T., Sørnes, T. A., & Røstad, A. (2007). Diel vertical migration of
900 individual jellyfish (*Periphylla periphylla*). *Limnology and Oceanography*, 52(3), 975–983.
901 <https://doi.org/10.4319/lo.2007.52.3.0975>
- 902 Keil, R. G., Neibauer, J. A., & Devol, A. H. (2016). A multiproxy approach to understanding the
903 “enhanced” flux of organic matter through the oxygen-deficient waters of the Arabian Sea.
904 *Biogeosciences*, 13(7), 2077–2092. <http://dx.doi.org/10.5194/bg-13-2077-2016>
- 905 Kiko, R., Biastoch, A., Brandt, P., Cravatte, S., Hauss, H., Hummels, R., et al. (2017). Biological and
906 physical influences on marine snowfall at the equator. *Nature Geoscience*, 10(11), 852–858.
907 <https://doi.org/10.1038/ngeo3042>
- 908 Kiko, R., Brandt, P., Christiansen, S., Faustmann, J., Kriest, I., Rodrigues, E., et al. (2020). Zooplankton-
909 Mediated Fluxes in the Eastern Tropical North Atlantic. *Frontiers in Marine Science*, 7.
910 <https://doi.org/10.3389/fmars.2020.00358>
- 911 Kwon, E. Y., & Primeau, F. (2008). Optimization and sensitivity of a global biogeochemistry ocean
912 model using combined in situ DIC, alkalinity, and phosphate data. *Journal of Geophysical*
913 *Research: Oceans*, 113(C8), C08011. <https://doi.org/10.1029/2007JC004520>
- 914 Lam, P., & Kuypers, M. M. M. (2011). Microbial Nitrogen Cycling Processes in Oxygen Minimum
915 Zones. *Annual Review of Marine Science*, 3(1), 317–345. <https://doi.org/10.1146/annurev-marine-120709-142814>
- 916
- 917 Lam, P. J., & Marchal, O. (2015). Insights into Particle Cycling from Thorium and Particle Data. *Annual*
918 *Review of Marine Science*, 7(1), 159–184. <https://doi.org/10.1146/annurev-marine-010814-015623>
- 919
- 920 Lam, P. J., Doney, S. C., & Bishop, J. K. B. (2011). The dynamic ocean biological pump: Insights from a
921 global compilation of particulate organic carbon, CaCO₃, and opal concentration profiles from
922 the mesopelagic. *Global Biogeochemical Cycles*, 25(3), n/a-n/a.
923 <https://doi.org/10.1029/2010GB003868>

- 924 Lam, P. J., Heller, M. I., Lerner, P. E., Moffett, J. W., & Buck, K. N. (2020). Unexpected Source and
925 Transport of Iron from the Deep Peru Margin. *ACS Earth and Space Chemistry*, 4(7), 977–992.
926 <https://doi.org/10.1021/acsearthspacechem.0c00066>
- 927 Lampitt, R. S., Noji, T., & von Bodungen, B. (1990). What happens to zooplankton faecal pellets?
928 Implications for material flux. *Marine Biology*, 104(1), 15–23.
929 <https://doi.org/10.1007/BF01313152>
- 930 Lee, W.-J., Staneva, V., Mayorga, E., Nguyen, K., Satiawan, L., & Majeed, I. (2021). Echopype:
931 Enhancing the interoperability and scalability of ocean sonar data processing. *The Journal of the*
932 *Acoustical Society of America*, 149(4), A63–A63. <https://doi.org/10.1121/10.0004522>
- 933 Maas, A. E., Frazar, S. L., Outram, D. M., Seibel, B. A., & Wishner, K. F. (2014). Fine-scale vertical
934 distribution of macroplankton and micronekton in the Eastern Tropical North Pacific in
935 association with an oxygen minimum zone. *Journal of Plankton Research*, 36(6), 1557–1575.
936 <https://doi.org/10.1093/plankt/fbu077>
- 937 McDonnell, A. M. P., & Buesseler, K. O. (2010). Variability in the average sinking velocity of marine
938 particles. *Limnology and Oceanography*, 55(5), 2085–2096.
939 <https://doi.org/10.4319/lo.2010.55.5.2085>
- 940 McDonnell, A. M. P., & Buesseler, K. O. (2012). A new method for the estimation of sinking particle
941 fluxes from measurements of the particle size distribution, average sinking velocity, and carbon
942 content. *Limnology and Oceanography: Methods*, 10(5), 329–346.
943 <https://doi.org/10.4319/lom.2012.10.329>
- 944 Neuer, S., Iversen, M., & Fischer, G. (2014). The Ocean’s Biological Carbon pump as part of the global
945 Carbon Cycle. *Limnology and Oceanography E-Lectures*, 4(4), 1–51.
946 <https://doi.org/10.4319/lo.2014.sneuer.miversen.gfischer.9>
- 947 Noji, T. T., Estep, K. W., Macintyre, F., & Norrbin, F. (1991). Image Analysis of Faecal Material Grazed
948 Upon by Three Species Of Copepods: Evidence For Coprorhexy, Coprophagy and Coprochaly.

949 *Journal of the Marine Biological Association of the United Kingdom*, 71(2), 465–480.
950 <https://doi.org/10.1017/S0025315400051717>

951 Ooi, H. (2013, August 8). Where does the offset go in Poisson/negative binomial regression? Retrieved
952 May 2, 2021, from [https://stats.stackexchange.com/questions/66791/where-does-the-offset-go-in-](https://stats.stackexchange.com/questions/66791/where-does-the-offset-go-in-poisson-negative-binomial-regression)
953 [poisson-negative-binomial-regression](https://stats.stackexchange.com/questions/66791/where-does-the-offset-go-in-poisson-negative-binomial-regression)

954 Parris, D. J., Ganesh, S., Edgcomb, V. P., DeLong, E. F., & Stewart, F. J. (2014). Microbial eukaryote
955 diversity in the marine oxygen minimum zone off northern Chile. *Frontiers in Microbiology*, 5.
956 <https://doi.org/10.3389/fmicb.2014.00543>

957 Passow, U., & Carlson, C. (2012). The biological pump in a high CO₂ world. *Marine Ecology Progress*
958 *Series*, 470, 249–271. <https://doi.org/10.3354/meps09985>

959 Pavia, F. J., Anderson, R. F., Lam, P. J., Cael, B. B., Vivancos, S. M., Fleisher, M. Q., et al. (2019).
960 Shallow particulate organic carbon regeneration in the South Pacific Ocean. *Proceedings of the*
961 *National Academy of Sciences*, 116(20), 9753–9758. <https://doi.org/10.1073/pnas.1901863116>

962 Pennington, J. T., Mahoney, K. L., Kuwahara, V. S., Kolber, D. D., Calienes, R., & Chavez, F. P. (2006).
963 Primary production in the eastern tropical Pacific: A review. *Progress in Oceanography*, 69(2–4),
964 285–317. <https://doi.org/10.1016/j.pocean.2006.03.012>

965 Peterson, M. L., Wakeham, S. G., Lee, C., Askea, M. A., & Miquel, J. C. (2005). Novel techniques for
966 collection of sinking particles in the ocean and determining their settling rates. *Limnology and*
967 *Oceanography: Methods*, 3(12), 520–532. <https://doi.org/10.4319/lom.2005.3.520>

968 Picheral, M., Guidi, L., Stemann, L., Karl, D. M., Iddaoud, G., & Gorsky, G. (2010). The Underwater
969 Vision Profiler 5: An advanced instrument for high spatial resolution studies of particle size
970 spectra and zooplankton. *Limnology and Oceanography: Methods*, 8(9), 462–473.
971 <https://doi.org/10.4319/lom.2010.8.462>

972 Picheral, M., Colin, S., & Irisson, J.-O. (2017). *EcoTaxa, a tool for the taxonomic classification of*
973 *images*. Retrieved from <http://ecotaxa.obs-vlfr.fr>

974 Poulsen, L., & Kiørboe, T. (2005). Coprophagy and coprorhexy in the copepods *Acartia tonsa* and
975 *Temora longicornis*: clearance rates and feeding behaviour. *Marine Ecology Progress Series*, 299,
976 217–227. <https://doi.org/10.3354/meps299217>

977 Rabindranath, A., Daase, M., Falk-Petersen, S., Wold, A., Wallace, M. I., Berge, J., & Brierley, A. S.
978 (2011). Seasonal and diel vertical migration of zooplankton in the High Arctic during the autumn
979 midnight sun of 2008. *Marine Biodiversity*, 41(3), 365–382. [https://doi.org/10.1007/s12526-010-](https://doi.org/10.1007/s12526-010-0067-7)
980 0067-7

981 Raven, M. R., Keil, R. G., & Webb, S. M. (2021). Microbial sulfate reduction and organic sulfur
982 formation in sinking marine particles. *Science*, 371(6525), 178–181.
983 <https://doi.org/10.1126/science.abc6035>

984 Ressler, P. H. (2002). Acoustic backscatter measurements with a 153kHz ADCP in the northeastern Gulf
985 of Mexico: determination of dominant zooplankton and micronekton scatterers. *Deep Sea*
986 *Research Part I: Oceanographic Research Papers*, 49(11), 2035–2051.
987 [https://doi.org/10.1016/S0967-0637\(02\)00117-6](https://doi.org/10.1016/S0967-0637(02)00117-6)

988 Riquelme-Bugueño, R., Pérez-Santos, I., Alegría, N., Vargas, C. A., Urbina, M. A., & Escribano, R.
989 (2020). Diel vertical migration into anoxic and high- p CO₂ waters: acoustic and net-based krill
990 observations in the Humboldt Current. *Scientific Reports*, 10(1), 17181.
991 <https://doi.org/10.1038/s41598-020-73702-z>

992 Rocap, G., Keil, R., Devol, A., & Deutsch, C. (2017). *Water temperature, salinity, and other data from*
993 *CTD taken from the RV Sikuliaq in the Pacific Ocean between San Diego, California and*
994 *Manzanillo, Mexico from 2016-12-21 to 2017-01-13 (NCEI Accession 0164968)*. [Temperature,
995 Salinity, Oxygen, Beam Attenuation, Fluorescence, PAR]. NOAA National Centers for
996 Environmental Information. Retrieved from <https://accession.nodc.noaa.gov/0164968>

997 Roullier, F., Berline, L., Guidi, L., Durrieu De Madron, X., Picheral, M., Sciandra, A., et al. (2014).
998 Particle size distribution and estimated carbon flux across the Arabian Sea oxygen minimum
999 zone. *Biogeosciences*, 11(16), 4541–4557. <https://doi.org/10.5194/bg-11-4541-2014>

1000 Sainmont, J., Gislason, A., Heuschele, J., Webster, C. N., Sylvander, P., Wang, M., & Varpe, Ø. (2014).
1001 Inter- and intra-specific diurnal habitat selection of zooplankton during the spring bloom
1002 observed by Video Plankton Recorder. *Marine Biology*, 161(8), 1931–1941.
1003 <https://doi.org/10.1007/s00227-014-2475-x>

1004 Saltzman, J., & Wishner, K. F. (1997). Zooplankton ecology in the eastern tropical Pacific oxygen
1005 minimum zone above a seamount: 2. Vertical distribution of copepods. *Deep Sea Research Part*
1006 *I: Oceanographic Research Papers*, 44(6), 931–954. [https://doi.org/10.1016/S0967-](https://doi.org/10.1016/S0967-0637(97)00006-X)
1007 [0637\(97\)00006-X](https://doi.org/10.1016/S0967-0637(97)00006-X)

1008 Saunders, J. K., Fuchsman, C. A., McKay, C., & Rocap, G. (2019). Complete arsenic-based respiratory
1009 cycle in the marine microbial communities of pelagic oxygen-deficient zones. *Proceedings of the*
1010 *National Academy of Sciences*, 116(20), 9925–9930. <https://doi.org/10.1073/pnas.1818349116>

1011 Schmidtko, S., Stramma, L., & Visbeck, M. (2017). Decline in global oceanic oxygen content during the
1012 past five decades. *Nature*, 542(7641), 335–341. <https://doi.org/10.1038/nature21399>

1013 Seibel, B. A. (2011). Critical oxygen levels and metabolic suppression in oceanic oxygen minimum
1014 zones. *Journal of Experimental Biology*, 214(2), 326–336. <https://doi.org/10.1242/jeb.049171>

1015 Sheldon, R. W., Prakash, A., & Sutcliffe Jr., W. H. (1972). The Size Distribution of Particles in the
1016 Ocean. *Limnology and Oceanography*, 17(3), 327–340. <https://doi.org/10.4319/lo.1972.17.3.0327>

1017 Siegel, D. A., Buesseler, K. O., Behrenfeld, M. J., Benitez-Nelson, C. R., Boss, E., Brzezinski, M. A., et
1018 al. (2016). Prediction of the Export and Fate of Global Ocean Net Primary Production: The
1019 EXPORTS Science Plan. *Frontiers in Marine Science*, 3.
1020 <https://doi.org/10.3389/fmars.2016.00022>

1021 Simon, M., Grossart, H., Schweitzer, B., & Ploug, H. (2002). Microbial ecology of organic aggregates in
1022 aquatic ecosystems. *Aquatic Microbial Ecology*, 28(2), 175–211.
1023 <https://doi.org/10.3354/ame028175>

1024 Steinberg, D. K., & Landry, M. R. (2017). Zooplankton and the Ocean Carbon Cycle. *Annual Review of*
1025 *Marine Science*, 9, 413–444. <https://doi.org/10.1146/annurev-marine-010814-015924>

1026 Steinberg, D. K., Carlson, C. A., Bates, N. R., Goldthwait, S. A., Madin, L. P., & Michaels, A. F. (2000).
1027 Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon
1028 in the Sargasso Sea. *Deep Sea Research Part I: Oceanographic Research Papers*, 47(1), 137–
1029 158. [https://doi.org/10.1016/S0967-0637\(99\)00052-7](https://doi.org/10.1016/S0967-0637(99)00052-7)

1030 Stramma, L., Johnson, G. C., Sprintall, J., & Mohrholz, V. (2008). Expanding Oxygen-Minimum Zones
1031 in the Tropical Oceans. *Science*, 320(5876), 655–658. <https://doi.org/10.1126/science.1153847>

1032 Stukel, M. R., Décima, M., Landry, M. R., & Selph, K. E. (2018). Nitrogen and Isotope Flows Through
1033 the Costa Rica Dome Upwelling Ecosystem: The Crucial Mesozooplankton Role in Export Flux.
1034 *Global Biogeochemical Cycles*, 32(12), 1815–1832. <https://doi.org/10.1029/2018GB005968>

1035 Stukel, M. R., Ohman, M. D., Kelly, T. B., & Biard, T. (2019). The Roles of Suspension-Feeding and
1036 Flux-Feeding Zooplankton as Gatekeepers of Particle Flux Into the Mesopelagic Ocean in the
1037 Northeast Pacific. *Frontiers in Marine Science*, 6. <https://doi.org/10.3389/fmars.2019.00397>

1038 Tiano, L., Garcia-Robledo, E., Dalsgaard, T., Devol, A. H., Ward, B. B., Ulloa, O., et al. (2014). Oxygen
1039 distribution and aerobic respiration in the north and south eastern tropical Pacific oxygen
1040 minimum zones. *Deep Sea Research Part I: Oceanographic Research Papers*, 94, 173–183.
1041 <https://doi.org/10.1016/j.dsr.2014.10.001>

1042 Turner, J. T. (2015). Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological
1043 pump. *Progress in Oceanography*, 130, 205–248. <https://doi.org/10.1016/j.pocean.2014.08.005>

1044 Van Mooy, B. A. S., Keil, R. G., & Devol, A. H. (2002). Impact of suboxia on sinking particulate organic
1045 carbon: Enhanced carbon flux and preferential degradation of amino acids via denitrification.
1046 *Geochimica et Cosmochimica Acta*, 66(3), 457–465. [https://doi.org/10.1016/S0016-](https://doi.org/10.1016/S0016-7037(01)00787-6)
1047 [7037\(01\)00787-6](https://doi.org/10.1016/S0016-7037(01)00787-6)

1048 Weber, T., & Bianchi, D. (2020). Efficient Particle Transfer to Depth in Oxygen Minimum Zones of the
1049 Pacific and Indian Oceans. *Frontiers in Earth Science*, 8.
1050 <https://doi.org/10.3389/feart.2020.00376>

1051 Widner, B., Fuchsman, C. A., Chang, B. X., Rocap, G., & Mulholland, M. R. (2018). Utilization of urea
1052 and cyanate in waters overlying and within the eastern tropical north Pacific oxygen deficient
1053 zone. *FEMS Microbiology Ecology*, *94*(10). <https://doi.org/10.1093/femsec/fiy138>

1054 Wilson, S. E., Steinberg, D. K., & Buesseler, K. O. (2008). Changes in fecal pellet characteristics with
1055 depth as indicators of zooplankton repackaging of particles in the mesopelagic zone of the
1056 subtropical and subarctic North Pacific Ocean. *Deep Sea Research Part II: Topical Studies in*
1057 *Oceanography*, *55*(14–15), 1636–1647. <https://doi.org/10.1016/j.dsr2.2008.04.019>

1058 Wishner, K. F., Ashjian, C. J., Gelfman, C., Gowing, M. M., Kann, L., Levin, L. A., et al. (1995). Pelagic
1059 and benthic ecology of the lower interface of the Eastern Tropical Pacific oxygen minimum zone.
1060 *Deep Sea Research Part I: Oceanographic Research Papers*, *42*(1), 93–115.
1061 [https://doi.org/10.1016/0967-0637\(94\)00021-J](https://doi.org/10.1016/0967-0637(94)00021-J)

1062 Wishner, K. F., Outram, D. M., Seibel, B. A., Daly, K. L., & Williams, R. L. (2013). Zooplankton in the
1063 eastern tropical north Pacific: Boundary effects of oxygen minimum zone expansion. *Deep Sea*
1064 *Research Part I: Oceanographic Research Papers*, *79*, 122–140.
1065 <https://doi.org/10.1016/j.dsr.2013.05.012>

1066 Wishner, K. F., Seibel, B. A., Roman, C., Deutsch, C., Outram, D., Shaw, C. T., et al. (2018). Ocean
1067 deoxygenation and zooplankton: Very small oxygen differences matter. *Science Advances*, *4*(12),
1068 eaau5180. <https://doi.org/10.1126/sciadv.aau5180>

1069 Wishner, K. F., Seibel, B., & Outram, D. (2020). Ocean deoxygenation and copepods: coping with
1070 oxygen minimum zone variability. *Biogeosciences*, *17*(8), 2315–2339. [https://doi.org/10.5194/bg-](https://doi.org/10.5194/bg-17-2315-2020)
1071 [17-2315-2020](https://doi.org/10.5194/bg-17-2315-2020)

1072 Yang, C., Xu, D., Chen, Z., Wang, J., Xu, M., Yuan, Y., & Zhou, M. (2019). Diel vertical migration of
1073 zooplankton and micronekton on the northern slope of the South China Sea observed by a moored
1074 ADCP. *Deep Sea Research Part II: Topical Studies in Oceanography*, *167*, 93–104.
1075 <https://doi.org/10.1016/j.dsr2.2019.04.012>

1076

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

6 Jacob A. Cram¹, Clara A. Fuchsman¹, Megan E. Duffy², Jessica L. Pretty³, Rachel M.
7 Lekanoff³, Jacquelyn A Neibauer², Shirley W. Leung², Klaus B. Huebert¹, Thomas S.
8 Weber⁴, Daniele Bianchi⁵, Natalya Evans⁶, Allan H. Devol², Richard G. Keil², Andrew
9 M.P. McDonnell³

10

11 ¹Horn Point Laboratory, University of Maryland Center for Environmental Science,
12 Cambridge, MD, USA.

13 ²School of Oceanography, University of Washington Seattle, Seattle, WA, USA.

14 ³College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks,
15 AK, USA.

16 ⁴School of Arts and Sciences, University of Rochester, Rochester, NY, USA.

17 ⁵Department of Atmospheric and Oceanic Sciences, University of California Los
18 Angeles, Los Angeles, CA, USA.

19 ⁶Department of Biological Sciences, University of Southern California, Los Angeles, CA,
20 USA.

21

22 Contents of this file

23

24 Figures S1 to S12

25 Caption for Text S1

26

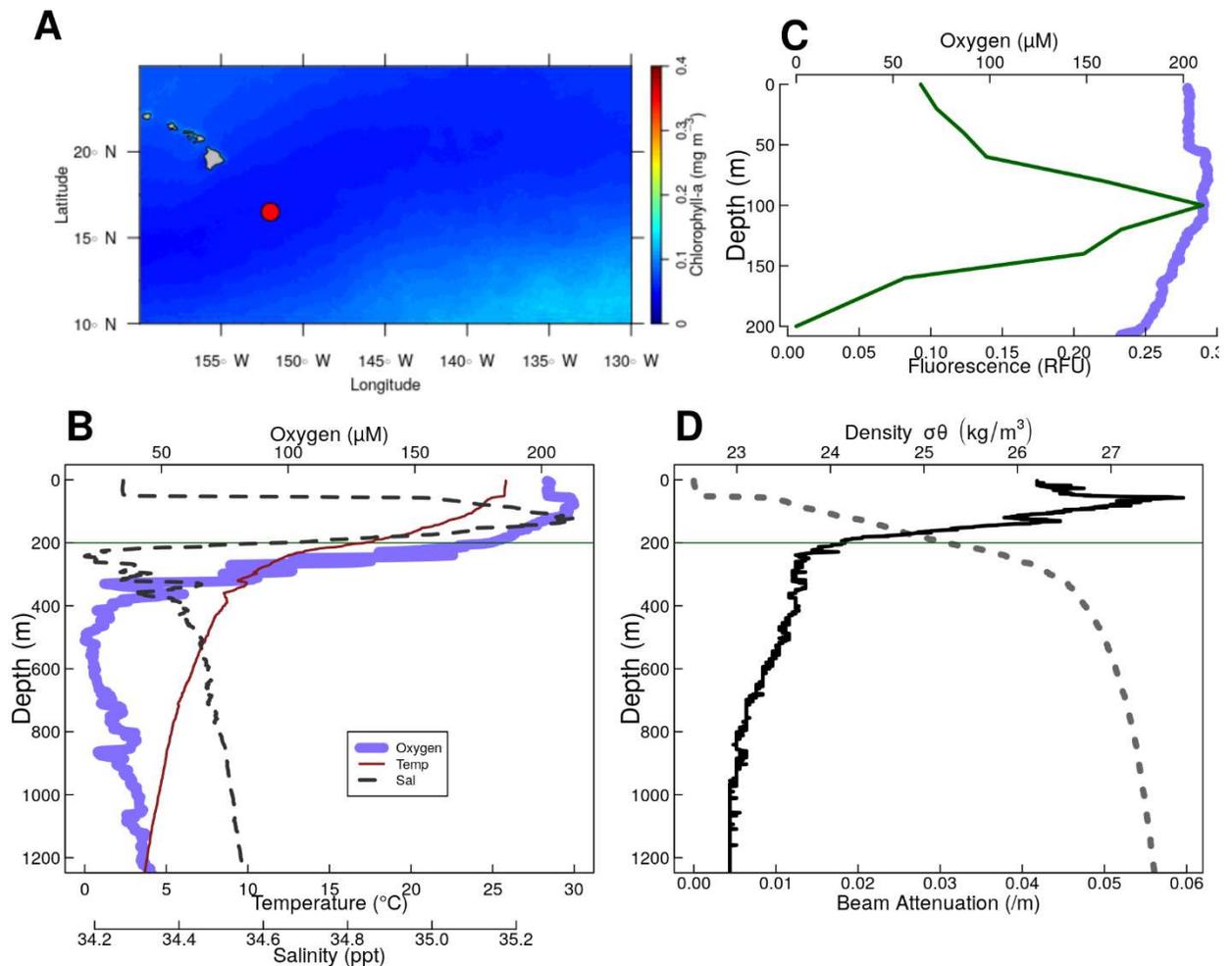
27 Additional Supporting Information (Files uploaded separately)

28

29 Text S1

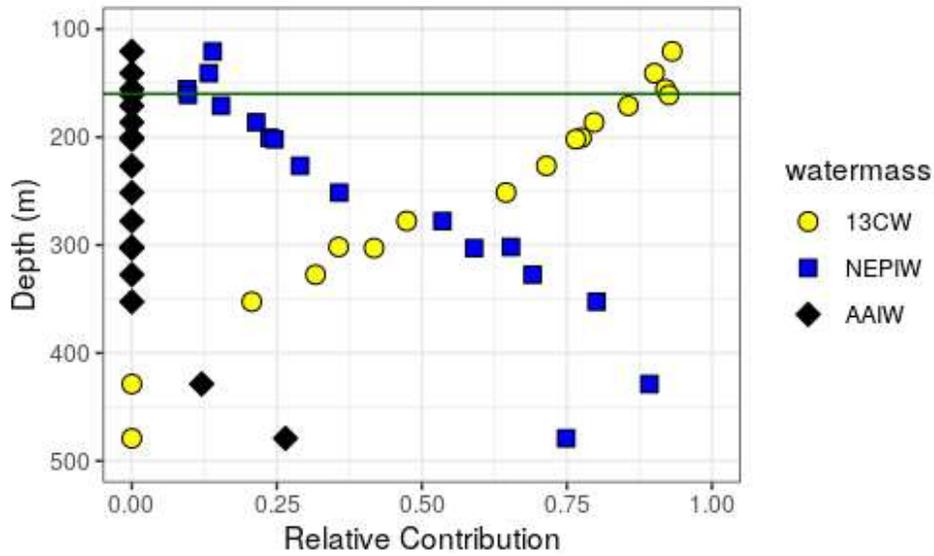
30 Introduction

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.

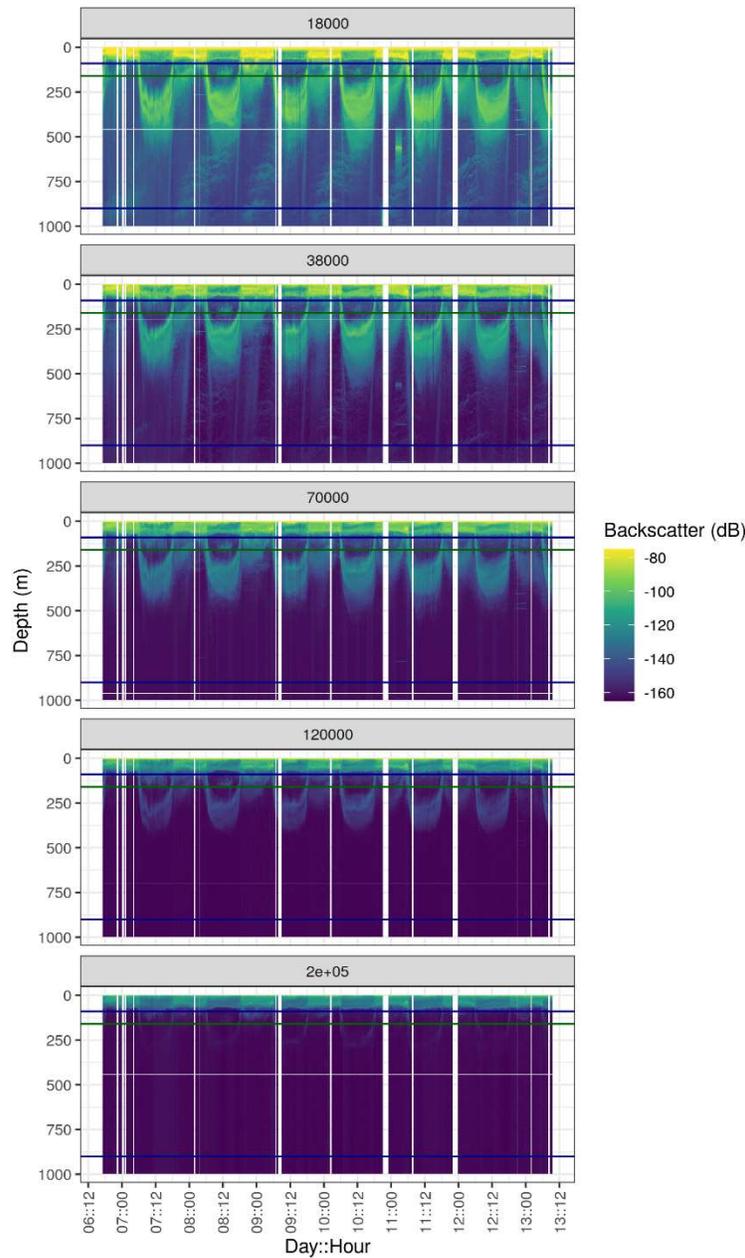


35

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.

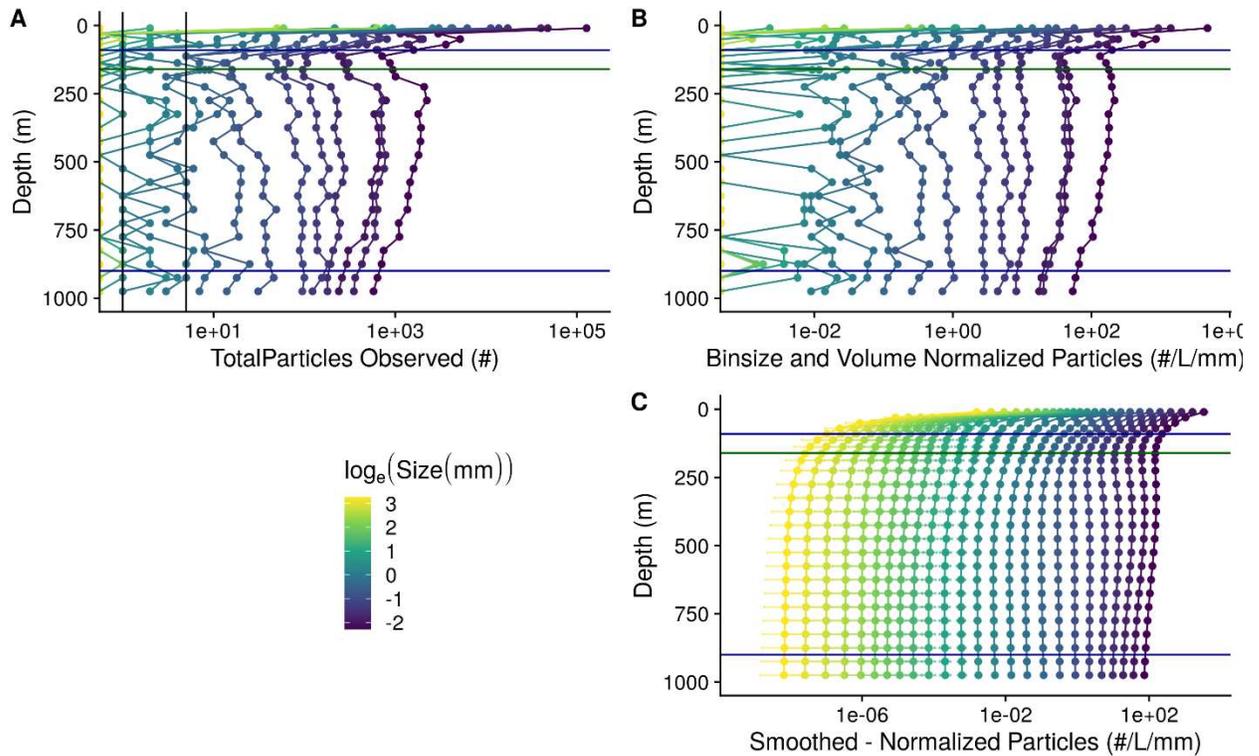


45
 46 Figure S2. Water mass analysis at ETNP Station P2 indicates the relative contributions
 47 proportions of the three primary water masses at this site, **13°C** water (13CW), North
 48 Equatorial Pacific Intermediate Water (NEPIW) and Antarctic Intermediate Water
 49 (AAIW). Values indicate relative 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).



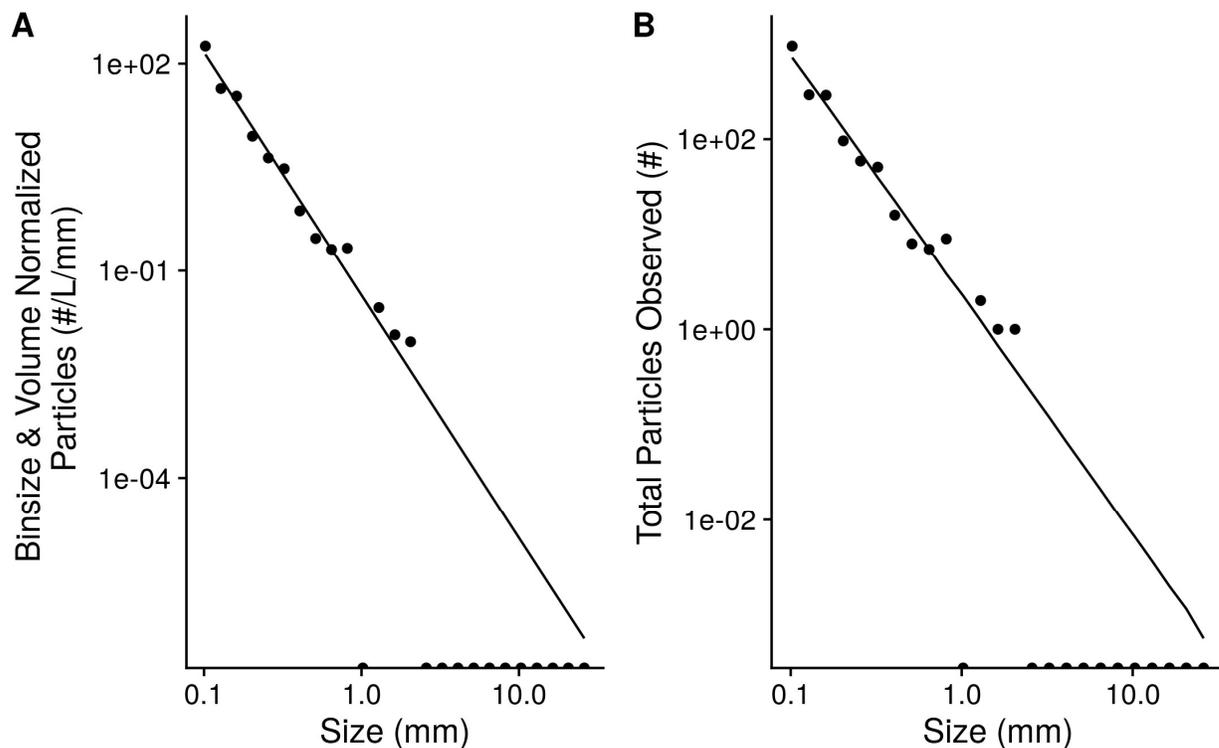
52

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.



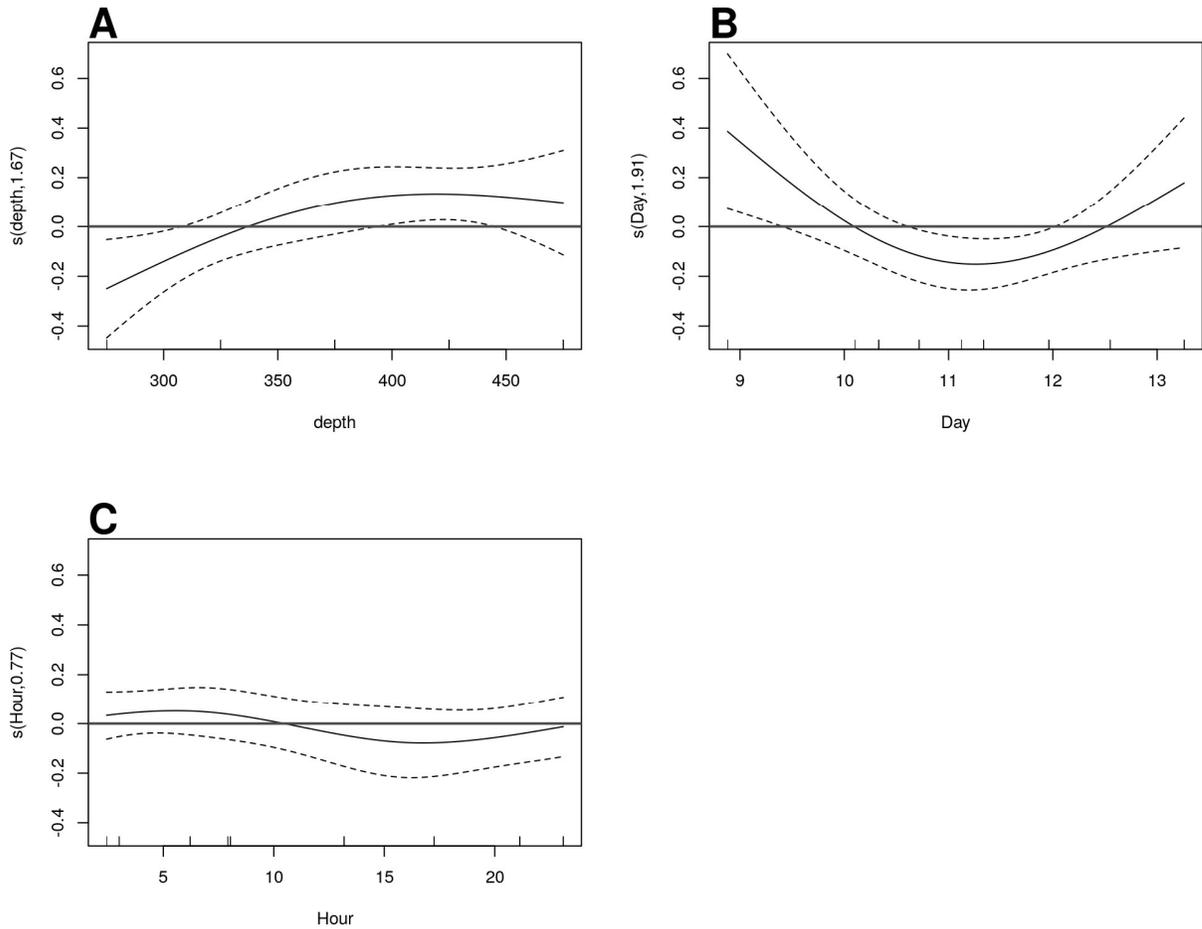
58

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.



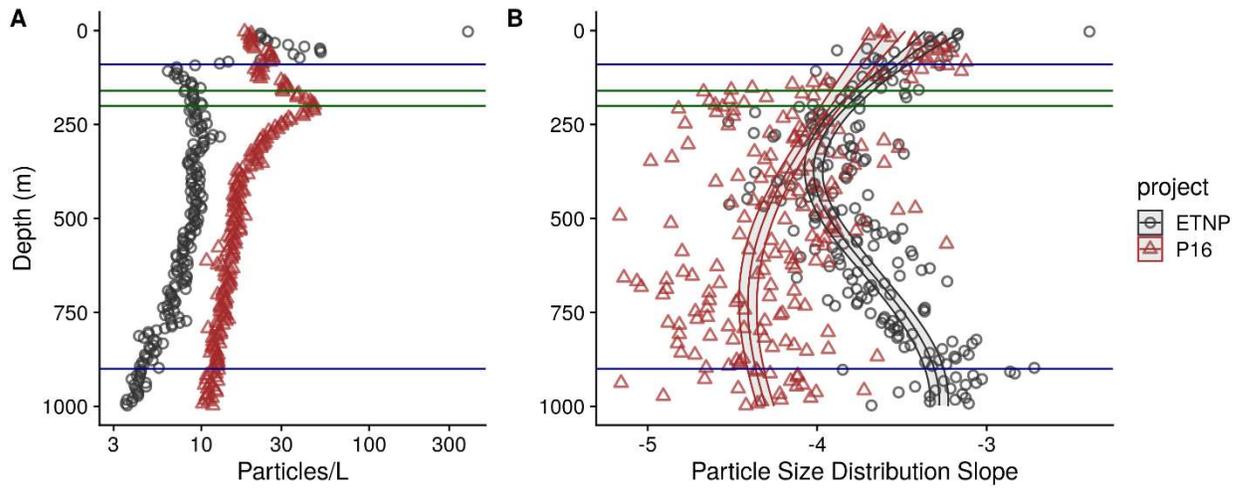
67

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.



78

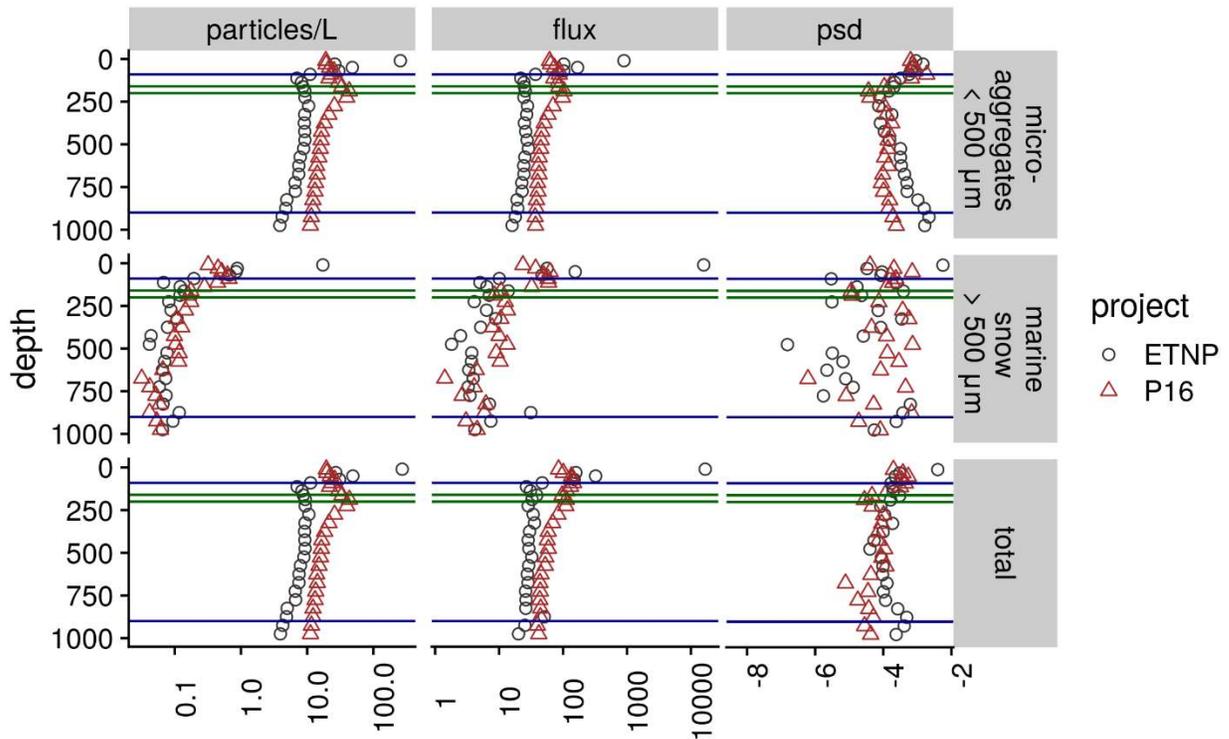
79 Figure S6. GAM predicted effects of A Depth, B Day of the month in January 2017, and
 80 C hour of the day on the fifth-root transformed, depth normalized, rate of change of flux
 81 at ETNP Station P2. Y axis indicates the value of the component smooth functions effect
 82 on Flux. Positive values 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).



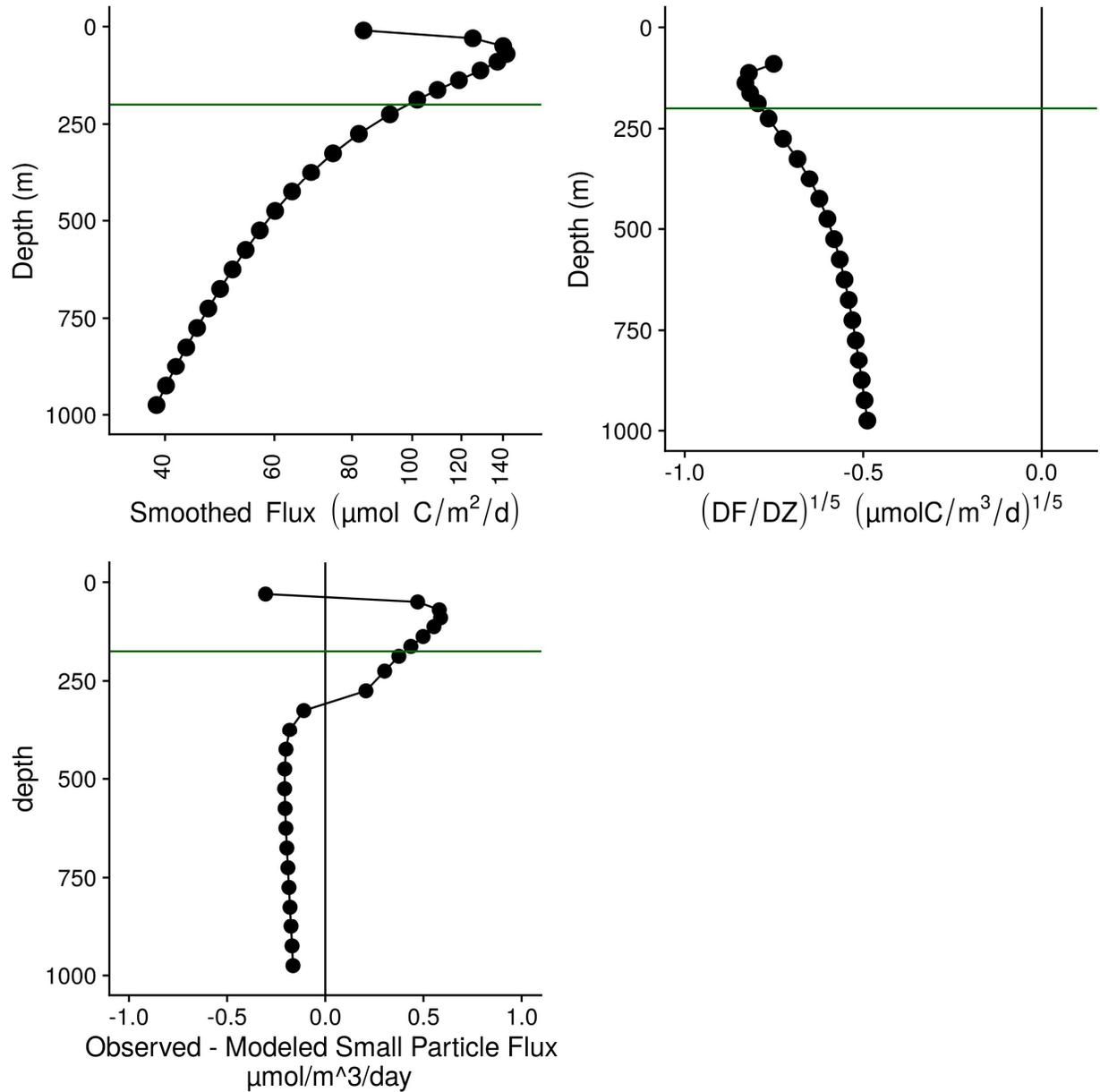
87

88 Figure S7. As above, but for the final cast taken at ETNP station P2 and the only cast
 89 collected from the P16 transect at Station 100. P16 Station 100 was chosen because it is
 90 at a similar latitude to ETNP station P2. (A) Total particle numbers, (B) Particle size
 91 distribution. Horizontal blue lines indicate the surface and bottom of the ODZ at the
 92 ETNP station, while the horizontal green lines indicate the bases of the photic zone at
 93 ETNP Station P2 (160m) and P16 Station 100 (200m).

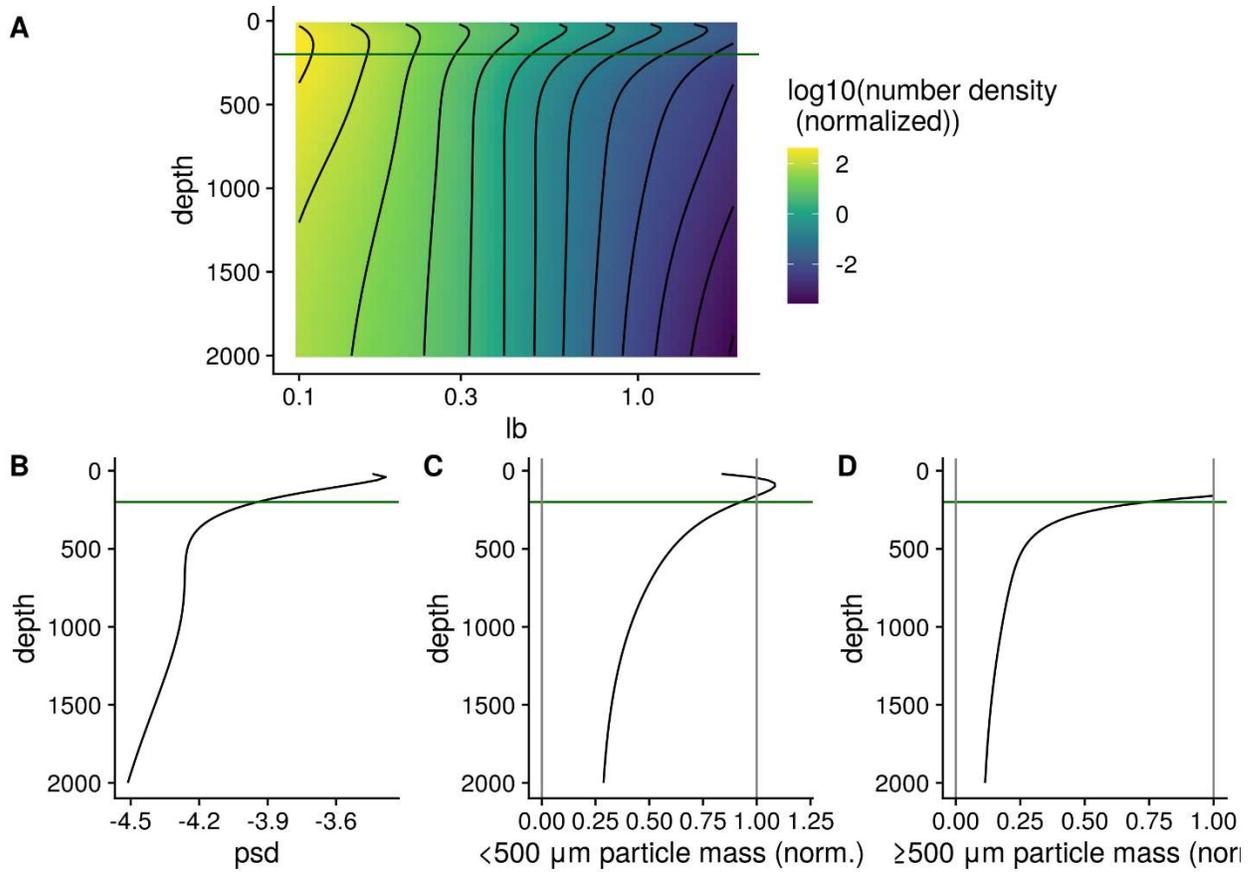
94



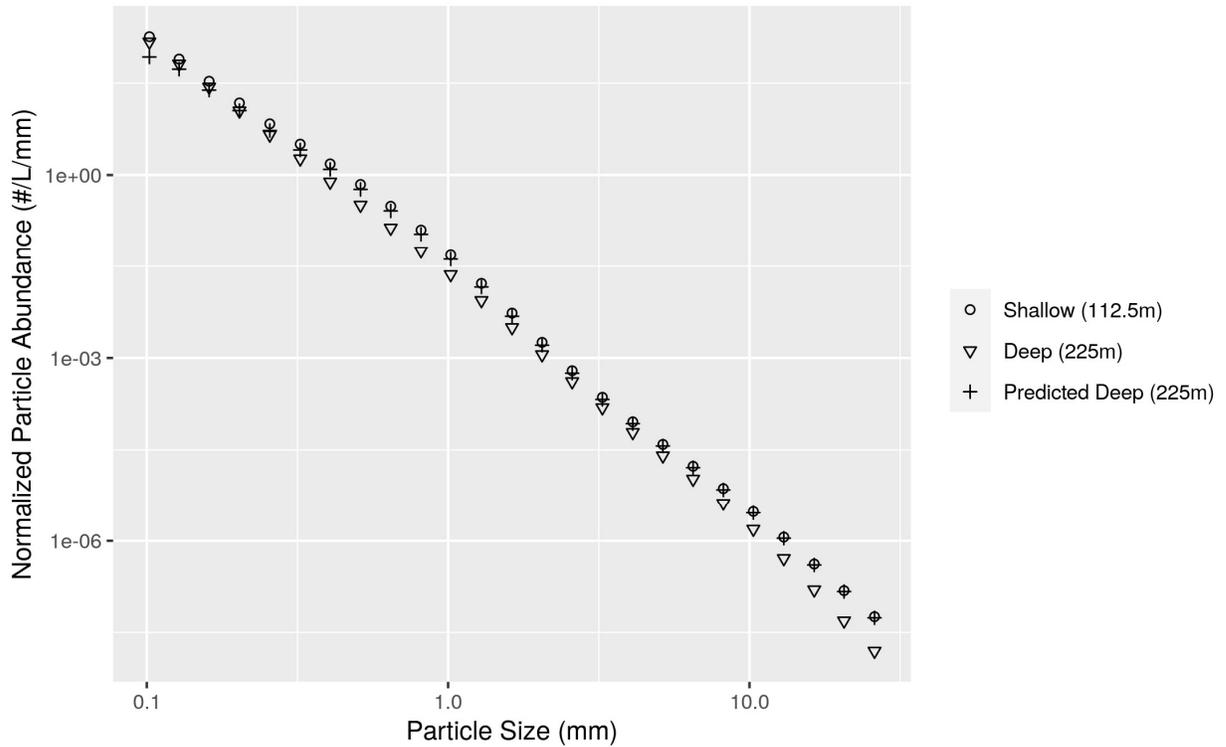
95
 96 Figure S8. Depth binned particle number (volume normalized), particle size slope (PSD),
 97 and flux (estimated as in Fig. 4) for microaggregates ($\leq 500 \mu\text{m}$), marine snow ($>$
 98 $500 \mu\text{m}$) and total particles, at the oxic (P16 Station 100) and anoxic site (ETNP Station
 99 P2). Within each panel, horizontal blue lines indicate the surface and bottom of the ODZ
 100 at the ETNP station, while the horizontal green lines indicate the bases of the photic zone
 101 at ETNP Station P2 (160m) and P16 Station 100 (200m).



102 Figure S9. Flux profiles and flux attenuation at P16 Station 100. (A) Flux profile (B)
 103 Fifth-root transformed depth normalized rate of flux decrease. (C) Difference between
 104 observed and modeled results. Higher values suggest more disaggregation-like processes.
 105 The horizontal green line at 200 m indicates the base of the DCM as estimated by World
 106 Ocean Atlas data for this site.
 107



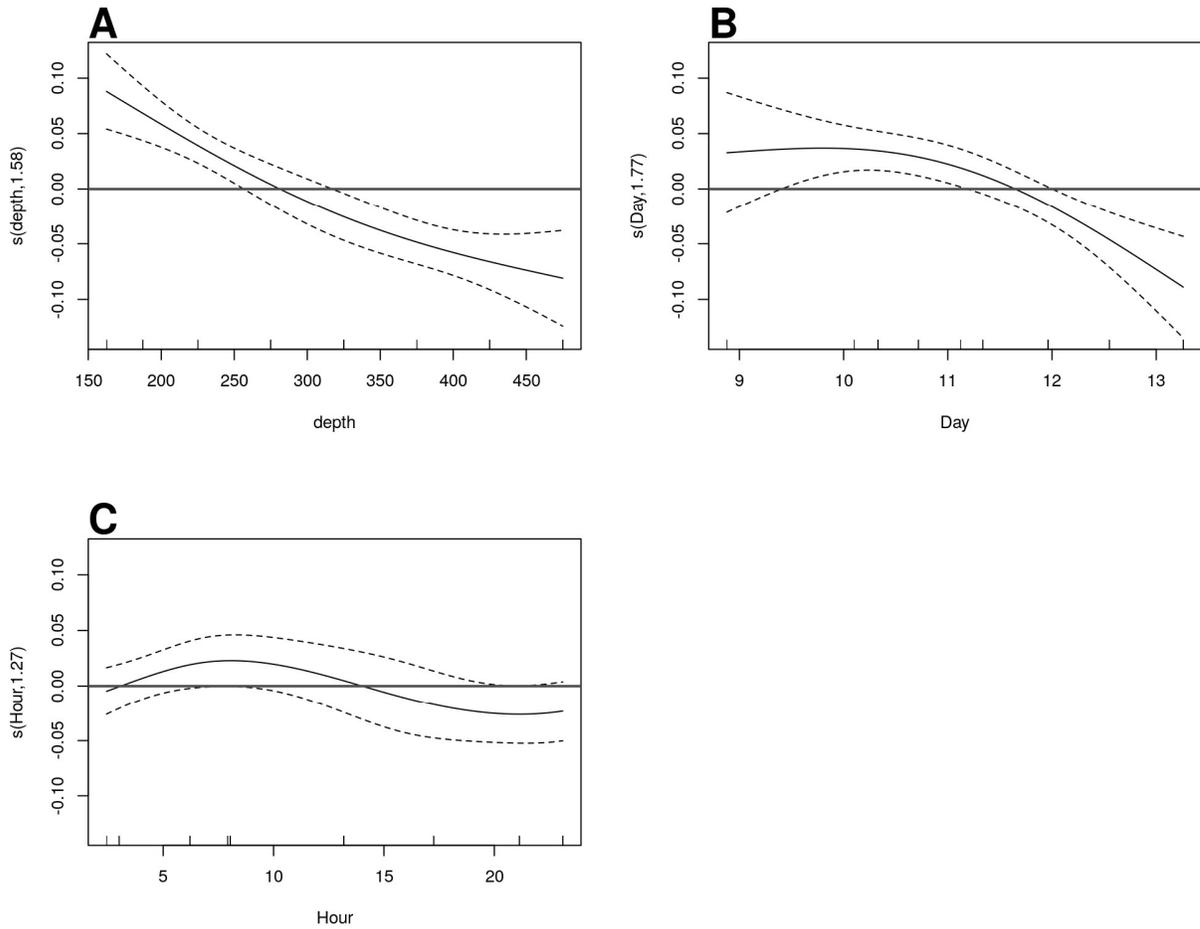
108
 109 Figure S10. The same profiles as shown in Figure 5, but for the oxic site P16 Station
 110 100. (A) GAM smoothed bin-size and volume particle numbers at each particle size class.
 111 (B) Particle size distributions. And estimated biomass of (C) Small and (D) Large
 112 particles. The horizontal green line at 200 m indicates the base of the DCM as estimated
 113 by World Ocean Atlas data for this site.



114

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.



125
 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

Jacob A. Cram

May 21, 2021

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 α . C_m is a constant.

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

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

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

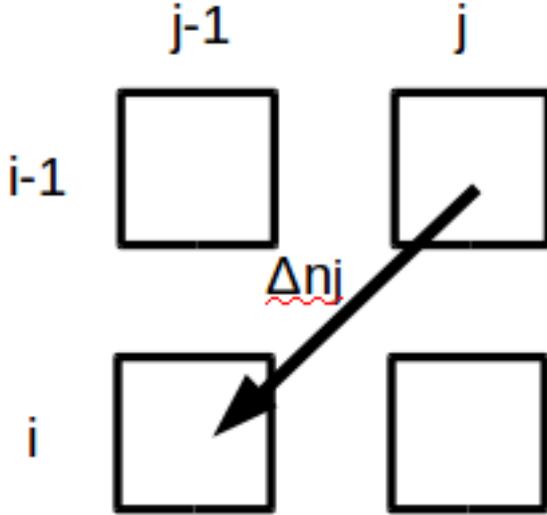


Figure 1: Some number of particles Δn_j of size “j” remineralize to size “j-1” as they sink from depth “i-1” to depth “i”.

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 Φ is a placeholder standing for either side of equation 7, which I will subsequently substitute into things.

Solve for Δn_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 Δf_j is the flux attenuation from bin of size j and Δf_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 Δz 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 Δf_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, Δn_1 is the number of particles leaving bin $j = 1$, but we haven’t solved for that yet.

4 Solving for Δn_j

Recall that Δn_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 Δf_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 Φ 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 Φ

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

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

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

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

5 Solving for C_r

We can calculate ΔF , 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 ΔF

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 Δn_j when $j = 1$ for Δn_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^γ 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 Δn_j . We can thus compute Δn_j for each size class to see how many particles from that bin move to the next bin smaller.