Biased measurements by stationary turbidity-fluorescence instruments due to phototactic zooplankton behavior

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Abstract

Submersible fluorescence and turbidity sensors are widely used in studies of oceans and lakes. To reduce the instrument size, an overlapping interrogation volume is commonly used for the two sensors. Fluorescence sensors emit blue light for excitation and measure the red light emitted by excited chlorophyll pigments. However, during the night, many phototactic zooplankters are attracted to the blue light. If the instrument is fixed in place (e.g., on a mooring), the aggregation of the attracted animals may bias both the fluorescence and turbidity readings. To examine this potential bias, we carried out experiments with natural assemblages of zooplankton and Artemia nauplii in tanks equipped with a commercially available fluorescence-turbidity sensor. Our findings indicate that zooplankters were attracted by the blue light emitted from a fluorometer during the dark, biasing the reading of both sensors. The bias in fluorescence was likely due to phytoplankton in the guts of the aggregated zooplankton. The induction of turbulence in the tank greatly reduced the bias, likely due to the inability of the zooplankton to counteract the resulting flow and swim toward the light. Field observations carried out with a similar instrument in a coastal station off Japan were consistent with the laboratory experiments. Our findings indicate a need to redesign coupled fluorescence-turbidity sensors and to reevaluate the results of past studies where they had been used with stationary observing systems.

Optical characteristics of the water, such as transparency, scattering, polarization, and color, serve as key attributes of water bodies in oceanography (Jerlov 1976; Pickard and Emery 2016) and limnology (Wetzel 2001; Cole and Weihe 2016). Methodologies for their quantification have been developed for over 150 years, starting with the Secchi disk, proposed in the mid-19th century (Watson and Zielinski 2013). More sophisticated instruments, such as underwater nephelometers and fluorometers, were developed in the mid-20th century (Strickland and Parsons 1972), followed by miniaturized instruments to simultaneously measure fluorescence and turbidity (McCave 2010; Yagi et al. 2015; Gorokhovich 2016; Zamyadi et al. 2016; Jafar-Sidik et al. 2017; Kakehi et al. 2017).

The first submersible sensor for in situ measurement of turbidity and fluorescence was proposed by Lorenzen (1966) and Stephens (1967) as a derivative of a laboratory fluorometer. This classical device pumps up water into an interior chamber where an optical sensor located. Modern turbidity sensors emit light in the red (610–800 nm) or infrared (> 800 nm) ranges into the free field and measure the scatter from suspended particles there. The intensity of the scatter depends on both the quality, size, and shape of particles and their abundance (Strickland and Parsons 1972). Underwater fluorometers illuminate the water with blue light (435–480 nm) and measure the red fluorescence emitted from chlorophyll pigments contained in phytoplankton and other organisms.

With the further miniaturization of underwater instruments, many now employ a shared interrogation volume for the fluorometer and turbidity readings where the two sensors are assembled side by side, forming a single instrument package (Moore 2010; Zamyadi et al. 2016).
Photoreception is common in marine organisms, including zooplankton and fish (Ringelberg 2010). Typical spectrum range of perception by zooplankton is 350 to 600 nm (Stearns and Forward 1984; Buskey and Swift 1985; Cohen and Forward 2002), that is, including range of wavelengths emitted by fluorometers. The structure of zooplankton sensory organs allows them to distinguish the direction of a light source (Ringelberg 2010). Given the ubiquitous attraction of zooplankton to artificial light during the night (Martynova and Gordeeva 2010), we experimentally assessed the extent to which such behavior affects measurements from combined fluorometer-turbidity instruments when these are used in stationary mode.

**Materials and methods**

**Fluorescence and turbidity sensors**

To test for the aforementioned bias, we used a submersible fluorescence-turbidity sensor manufactured by JFE Advantech (Japan) (Fig. 1a). The fluorescence sensor emits two blue LED beams, peaked at 470 nm, whereas the turbidity sensor uses an infrared LED beam (880 nm). While exact volume for sampling has not been quantified by the manufacturer, a shared receiving window senses a wavelength band ranging from 650 to 1000 nm to cover fluorescent emission by chlorophyll $a$ and scattered infrared light. The sensors are installed on a compact CTD profiler, RINKO-Profiler (Fig. 1a). The sensor design, that is, emitting measurement light beams into a shared interrogation volume in the free field (“open-path” style), is common among other sensors/profilers, such as Water Quality Monitor and HydroCAT-EP by Sea-Bird Scientific, Submersible Fluorometer series and Cyclops series by Turner Designs, Turbidity Meter and Chlorophyll Fluorometer by Seapoint Sensors, and Water Quality Sonde by YSI. Almost all commercially available fluorescence-turbidity sensors use the same design concept.

Turbidity has several units, such as Nephelometric Turbidity Units (e.g., Doxaran et al. 2009) and Formazin Nephelometric Units (e.g., Saraceno et al. 2017). The US Geological Survey offers the definitions for different turbidity units. As the RINKO-Profiler measures the infrared light backscattered from particles (30 ± 15° to incident beam), the Formazin Backscatter Unit (FBU) is used in this study.

**Tank experiments**

Two types of laboratory experiments were conducted. The first (hereinafter **Experiment A**) examined the effect of zooplankton phototactic behavior on turbidity and fluorescence measurements using a natural assembly of marine zooplankton. The second, **Experiment B**, examined the effects of water motion on the possible bias using nauplii of cultured *Artemia salina*.

For **Experiment A** we collected zooplankton in shallow water (5 m depth) off Ubatuba, Brazil, in July 2018 (austral winter) and February 2019 (summer) by oblique tows of a plankton net (100 μm mesh) containing a solid cod end. Samples were brought to the laboratory and processed within 30 min upon collection. Microscopic sorting of the collected zooplankton indicated typical taxonomic composition dominated by a calanoid copepod *Acartia lilljeborgi* during winter and marine cladocerans *Pseudovadne tergestina* and *Penilia avirostris* and the calanoid *Temora turbinata* during summer (Lopes 1994; Melo Júnior 2016). In a dark room, a RINKO-Profiler was positioned on top of a 7.8-L glass tank filled with GF/F-filtered seawater from the sampling location, assuring that the optical path of the fluorescence-turbidity sensor was entirely submerged (Fig. 1b). The winter experiment used high animal densities of 430, 870, and 1300 individuals L$^{-1}$ which are among the highest densities naturally occurring in the ocean (Hamner and Carleton 1979). The summer experiment employed lower animal densities of 2.5, 25, and 50 individuals L$^{-1}$, a typical range in the sampling site. During the measurements, the room lights were turned on and off to produce consecutive light–dark intervals lasting 3 min each, during a trial of

![Fig. 1.](image) **Fig. 1.** (a) RINKO-profiler (JFE Advantech) which carries the combined fluorescence and turbidity sensor. Blue LED beams are designed for fluorescence measurements (white arrow). (b) Experimental setup for the Experiments A and B. Natural zooplankton communities mainly composed of copepod and cladoceran species collected off Ubatuba, Brazil, were used for Experiment A, and cultured *Artemia salina* (nauplius larvae) for Experiment B.
15 min in total. The sensors’ measurement frequency was set to 10 Hz.

For Experiment B, nauplii of *A. salina* were hatched and kept until the onset of the experiment, < 24 h after hatching. The fluorescence-turbidity sensor was installed in a beaker (~ 1 L) filled with artificial seawater (Fig. 1b). The water temperature was set to 28.5°C, and the abundance of *A. salina* nauplii was ~1850 individuals L⁻¹. A tube was installed to generate turbulent flow in the beaker by aeration (Fig. 1b). The end of the tube was located at a bottom corner to generate a circulation without contaminating data by air bubbles. The experiment was carried out under dark condition, and the aeration was started occasionally to imitate strong levels of turbulence in the ocean. The sampling frequency for the probe was set to 10 Hz as in Experiment A.

Videos taken by a smartphone camera were used to estimate 2D RMS turbulent velocity, based on a cross-correlation method (Catton et al. 2011). The calculation region was 100 × 100 pixels, where the center was 1 cm below the fluorescence-turbidity sensor. The maximum lag was set to 50 pixels. Given the pixel resolution (0.05 mm pix⁻¹) and frame rate (30 Hz), the minimum and maximum detectable velocities are 0.15 and 10.6 cm s⁻¹, respectively. Noise velocities from trajectories of swimming individuals were manually removed. Additionally, swimming speeds of individual nauplii were estimated by frame-by-frame playback.

### Cabled observatory

Data from a cabled observatory system (Oshima Coastal Environmental data Acquisition Network System, OCEANS - Izu-Oshima Island, Japan; Fig. 2) allowed for in situ evaluation of the bias detected during laboratory experiments. The island is about 30 km away from mainland Japan, and the waters around the island are oligotrophic (Takahashi et al. 1980). The cabled observatory was deployed near the southeastern tip of the island at 20 m depth. An Infinity-CLW (JFE Advantech), that is, a stationary data logger which carries the same fluorescence-turbidity sensor as in the RINKO-Profiler, was mounted to the cabled observatory. The sampling frequency was set to 1 Hz, and the observation period was between 12 August and 30 November 2014.

To investigate the zooplankton community, an in situ plankton camera (Continuous Plankton Imaging and Classification System, CPICS) was installed on the cabled observatory (Yamazaki et al. 2016). In-focus zooplankton images were automatically detected by the computer, and the smallest detectable size was 200 pix² in area. The detected zooplanktons were manually classified during the observation period.

To evaluate the effects of flow and turbulence on the aforementioned bias, a representative velocity scale was quantified as maximum orbital velocity of surface gravity waves based on the linear wave theory. For the calculation, significant wave height was estimated from pressure data recorded at a frequency of 1 Hz by a pressure sensor mounted on the cabled observatory (Goda and Kudaka 2007). By solving the dispersion relation, wavenumber was estimated from wave period which was originally derived from a peak frequency of surface elevations (Soulsby 2006).

### Statistical analyses

Two-way ANOVA was used to test the effects of light vs. dark and animal densities on measurements of turbidity and fluorescence in Experiment A. Separate tests were performed for each zooplankton assemblage: the three levels of low densities in the summer experiment and the three levels of high densities in the winter experiment.

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**Fig. 2.** Observation site and cabled observatory. (a) Regional map around the observation site. (b) Izu-Oshima Island showing the location (34°41.0′N, 139°26.7′E) of the site of the cabled observatory off the southern end of the island (arrow). (c) Underwater photograph of the cabled observatory.
One-way Kruskal-Wallis test was used to test the effect of time on changes in turbidity readings in Experiment A, starting 2 min prior to the onset of dark conditions through 3 min afterward, divided into 15 intervals, each 20 s long. For this test, turbidity readings were normalized by the mean of the top 5% for each dark section and then grouped into the 20 s intervals. This test allowed us to examine the occurrence of gradual intensification of the bias in turbidity readings due to a gradual accumulation of zooplankton in the volume after the light was turned off. Dwass-Steel-Critchlow-Fligner test for pairwise comparisons was used to test for differences between pairs of those intervals during the light and dark periods.

One-way Kruskal-Wallis test was also used to test the effect of current speed on the magnitude of the bias in the turbidity and fluorescence readings measured during nighttime at the OCEANS site. For this test, turbidity and fluorescence anomalies from the overall averages of those readings were grouped in six velocity intervals in the range of 0 to 0.6 m s\(^{-1}\).

All statistical tests were performed using SYSTAT (V. 13).

**Results**

**Experiment A (natural assembly of zooplankton)**

The effects of illumination (light vs. dark) and levels of zooplankton density on the readings of turbidity and fluorescence were highly significant (two-way ANOVA, \( p < 0.00001 \); Table 1), showing a substantial increase in turbidity readings during the dark and under higher zooplankton densities, with less substantial, nevertheless significant effects on fluorescence (Figs. 3a–d and 4). In all cases, the interaction between illumination and zooplankton abundance was highly significant (\( p < 0.00001 \); Table 1). Local peaks in turbidity and fluorescence appeared during the dark periods (3–6 and 9–12 min in Fig. 3a–d), caused by the zooplankton accumulating in the sensor’s sampling volume (Fig. 3e,f). Emergences of the peaks for two signals (turbidity and fluorescence) were not necessarily concurrent (Fig. 3a–d).

Such trends in turbidity and fluorescence were found for the entire range of zooplankton densities (2.5 to 1300 individuals L\(^{-1}\)) but were more remarkable for the higher densities (Fig. 3c,d).

| Table 1. Results of two-way ANOVA testing the effects of light vs. dark (denoted as “Illum”) and zooplankton density (“Zoopl”) on the readings of turbidity and fluorescence in the two experiments of Experiment A, using natural assemblies of zooplankton. |
| Parameter | Zoopl range | Source | df | SS | MS | \( F \) | \( p\)-value |
|-----------|-------------|--------|----|----|----|---------|---------|
| Turbidity | Low         | Illum  | 1  | 892.2 | 892.2 | 2813.8 | < 0.00001 |
|           |             | Zoopl  | 2  | 572.6 | 286.3 | 902.9  | < 0.00001 |
|           |             | Illum×Zoopl | 2  | 512.7 | 256.3 | 808.4  | < 0.00001 |
|           | High        | Illum  | 1  | 3599.3 | 3599.3 | 5384.1 | < 0.00001 |
|           |             | Zoopl  | 2  | 850.7 | 425.3 | 636.2  | < 0.00001 |
|           |             | Illum×Zoopl | 2  | 404.8 | 202.4 | 302.8  | < 0.00001 |
| Fluorescence | Low        | Illum  | 1  | 12.3 | 12.3 | 824.6  | < 0.00001 |
|           |             | Zoopl  | 2  | 1.4 | 0.69 | 46     | < 0.00001 |
|           |             | Illum×Zoopl | 2  | 5.8 | 2.9 | 194.1  | < 0.00001 |
|           | High        | Illum  | 1  | 69.1 | 69.1 | 1523.4 | < 0.00001 |
|           |             | Zoopl  | 2  | 29.4 | 14.7 | 323.8  | < 0.00001 |
|           |             | Illum×Zoopl | 2  | 17.1 | 8.6 | 188.7  | < 0.00001 |
Larger increases in turbidity and fluorescence from the light conditions were found for higher zooplankton abundances in each assemblage (Fig. 4). Among the low-density trials (using summer assemblage), a slight increase was found in turbidity with increasing zooplankton abundance from 2.5 to 25 individuals L\(^{-1}\), while a dramatic change was found when the abundance shifted from 25 to 50 individuals L\(^{-1}\) (Fig. 4a). A large difference in turbidity was found between 430 and 870 individuals L\(^{-1}\) for the high-density trials (Fig. 4b). The fluorescence increases from the light conditions were much larger among the high-density cases (Fig. 4d). The bias of higher reading gradually increased after the onset of dark conditions (Fig. 5; Kruskal-Wallis, \(p < 0.0001\)). A pairwise comparison between 20-s long intervals, across the time windows starting 2 min before dark conditions ending 3 min afterward, indicated significant differences (Dwass-Steel-Critchlow-Fligner pairwise test, \(p < 0.03\)) for all intervals but 2 among the 36 possible pairs included in the dark intervals and only 7 of the 13 possible pairs under light conditions. Regardless, the increments of increase were monotonic and much higher during darkness, indicating a gradual aggregation of zooplankters in the volume illuminated by the instrument after the onset of dark conditions (Fig. 5).

**Experiment B (cultured brine shrimp)**

The Artemia nauplii accumulated around the sampling volume as in Experiment A. The turbidity data were about 30 FBU when the packing density in the sampling volume was saturated (e.g., see around 10 s in Fig. 6a). Total area of the detected particles in the still images (including living and nonliving) was highly correlated with turbidity (\(r = 0.98\), \(p < 0.01\)) and fluorescence (\(r = 0.98\), \(p < 0.01\)). While the number of the detected particles was also significantly correlated with turbidity and fluorescence (\(r = 0.94\), \(p < 0.01\) and \(r = 0.94\), \(p < 0.01\), respectively), the correlations were slightly lower than those of their areas. The RMS velocity increased when the air pump started (around 15 and 80 s in Fig. 6c).

**Fig. 4.** Average (a, b) turbidity and (c, d) fluorescence under the dark (full bars) and light (hatched bars) conditions for different densities of zooplankton. Zooplankton in this experiment was sampled in the sea. The effects of illumination and animal density, as well as their interaction, were highly significant (two-way ANOVA, \(p < 0.00001\); Table 1). Panels on the left and right are for trials with low and high density of zooplankton, respectively. Error bars indicate standard deviation.

**Fig. 5.** Turbidity, normalized by the mean of the top 5% for each dark section, averaged over 20-s time bins relative to the beginning of the dark condition, based on the six different levels of ambient zooplankton abundance considered in Experiment A. Error bars denote standard deviation. The effect of time interval on the normalized turbidity was highly significant (Kruskal-Wallis, \(p < 0.00001\); see text).

**Fig. 6.** Effects of water motion on zooplankton-induced bias in turbidity and fluorescence measurements in Experiment B. (a) Black and green lines denote turbidity and fluorescence, respectively. (b) Black line denotes total area of the particles, and gray line denotes number of the particles. (c) Image-based 2D RMS velocity of turbulent flow in the calculation region (100 x 100 pixels) located 1 cm below the sampling volume of the fluorescence and turbidity sensor. Horizontal black bars denote periods of induced turbulence.
volume were flushed away as the RMS velocity exceeded their swimming speeds \((0.95 \pm 0.15 \text{ cm s}^{-1}; \text{mean} \pm \text{SD}; n = 10)\), resulting in sudden drops in the readings of turbidity, fluorescence, and the number of particles and their area (Fig. 6).

**In situ measurements**

A total of 15 taxa were identified among the zooplankters recorded by CPICS (Table 2), 9 of them appearing almost exclusively during the night (Table 2). Both turbidity and fluorescence readings during the night exhibited prominent peaks, likely reflecting the passing of a zooplankter within the interrogation volume (Fig. 7). Some turbidity peaks exceeded the instrument’s upper bound (1300 FBU) and were automatically clipped at that level, indicating that our measurements underestimated the magnitude of the bias during the night. The bias in both turbidity and fluorescence during nighttime was most conspicuous when plotted relative to time of day (Fig. 8). However, this bias was substantially reduced during periods of strong currents, usually occurring when high waves associated with storm event generated strong orbital velocities (Fig. 8a). Extreme levels of biased turbidity and fluorescence readings were observed under calm conditions (e.g., during nights in August; Fig. 8b,c). The effect of current speed on the readings of turbidity and fluorescence was highly significant (Kruskal-Wallis, \(p < 0.00001\)), exhibiting a remarkable decrease in the bias as currents were intensified (Fig. 9).

**Discussion**

This study demonstrates a substantial artifact in nocturnal measurements of turbidity and fluorescence by stationary devices with an open-path turbidity-fluorescence sensor. The

**Table 2.** Taxonomic composition of zooplankton groups and their relative occurrence during the nighttime observation windows, as recorded with the CPICS imaging system from the OCEANS cabled observatory, Izu-Oshima Island, Japan.

| Taxa             | Nighttime appearance (%) |
|------------------|--------------------------|
| Chaetognatha     | 100.0                    |
| Decapoda         | 100.0                    |
| Ostracoda        | 100.0                    |
| Mysida           | 99.8                     |
| Monstriloida     | 99.1                     |
| Polychaeta       | 98.9                     |
| Cumacea          | 96.3                     |
| Isopoda          | 95.7                     |
| Amphipoda        | 95.6                     |
| Larvacea         | 79.8                     |
| Harpacticoida    | 75.0                     |
| Poecilostomatoida| 68.3                     |
| Calanoida        | 65.1                     |
| Hydrozoa         | 60.6                     |
| Cyclopoida       | 59.2                     |

![Fig. 7.](image1) The temporal correspondence between (a) turbidity and (b) fluorescence as measured in situ at Izu-Oshima Island, Japan, during a period between 15 and 23 August 2014. Turbidity frequently hit sensor’s upper bound at 1300 FBU.

![Fig. 8.](image2) Time series for orbital velocity (a), and diel variations in turbidity (b), and fluorescence anomalies (c) throughout the observation period. (b, c) Black lines denote time for dawn and dusk. White blanks denote unreliable data due to the small number of samples \((n < 3000)\). Note the lower bias during nighttime in periods of relatively strong orbital velocities (see Fig. 9).
were highly significant (Kruskal-Wallis, p < 0.00001 for each parameter). The effects of current speed on both the turbidity and fluorescence anomalies were highly significant (Karaköylü et al. 2009). Biased measurements by turbidity-fluorescence instruments.

Fig. 9. (a) Turbidity and (b) fluorescence anomalies, relative to the overall averages, during nighttime from the OCEANS site averaged over different levels of orbital velocity. Error bars denote standard deviation. The changes in the magnitude of the bias remains unclear, it suggests the strength of the bias is not linearly proportional to the zooplankton density. Confounding factors include the taxonomic composition of the zooplankton assemblage, in addition to the zooplankton body size and swimming behavior.

Strong currents and turbulence are expected to act against the directional swimming toward the light by phototactic zooplankters, thereby hindering their accumulation in the interrogation volume (Figs. 6, 8, and 9). While marine copepods may reach instantaneous swimming speed of 0.5 m s$^{-1}$ during short (< 0.1 s) escape bouts (Svetlichny et al. 2018), their normal swimming speed is generally < 0.1 m s$^{-1}$ (Buskey and Swift 1985). Under the strong current speeds measured at OCEANS (> 0.5 m s$^{-1}$) (Fig. 8a), even large zooplankters would be unable to maintain an oriented swimming. This is consistent with our results showing that the bias caused by the light beam from a stationary fluorescence probe was stronger under low-turbulence conditions (Figs. 6 and 9). Interestingly, an opposite bias has been reported for a profiling instrument package containing an open-path fluorometer which is a similar device to our sensor, that is, emitting LED blue light into the free field (Benoit-Bird et al. 2010). Nighttime vertical profiles with those optical sensors triggered zooplankton avoidance instead of eliciting positive phototaxis, as observed in our investigation. Benoit-Bird et al. (2010) proposed that the wavelength of the excitation light from the fluorometer (470 nm) is close to the peak wavelength of dinoflagellate bioluminescence, which is known to provide visual clues for zooplankton predators and to cause photophobic responses by copepods. The reason for the apparent contrasting zooplankton responses toward the fluorometer light remains unclear. It could be related to the fact that in our study the fluorometers were stationary, whereas Benoit-Bird et al. (2010) used a moving (profiling) fluorometer. Furthermore, the zooplankton taxa along the coast of California, where Benoit-Bird et al. (2010) performed their observations, were likely different from those we studied. Different zooplankton taxa are known to exhibit distinct phototactic behavior (Martynova and Gordeevo 2010; Zarubin et al. 2012).

Benoit-Bird et al. (2010) have pointed out that zooplankton data from in situ instrument packages carrying fluorometers need to be considered with care. Our data demonstrate that turbidity and chlorophyll fluorescence measurements themselves become biased by swimmers, indicating a two-way impact of such probes. A clear increase of in vivo fluorescence during the night was observed by Marra (1997), who explained it in terms of phytoplankton physiology and growth. However, the possibility that zooplankton attracted to the fluorometer light also contributed to that pattern had not been proposed. Moored instrument packages containing
fluorescence and turbidity sensors have been routinely used in estuarine and coastal regions for several decades (McCave 2010; Moore 2010; Yagi et al. 2015; Gorokhovich 2016; Zamyadi et al. 2016; Jafar-Sidik et al. 2017; Kakehi et al. 2017). Fluorescence and turbidity measurements obtained during the night in such studies should be reevaluated. Additionally, in a clear water like at the OCEANS site, LED beams from fluorometer would transmit far and be visible from a distance. Hence, data from such site also need a careful interpretation.

Fluorescence sensors require a new design to minimize the suite of impacts reported in this study. We agree with Benoit-Bird et al. (2010) that a contained flow-through cell for fluorescence measurements under dark conditions would represent a compromise solution for moored or profiling instrument packages, instead of the open-path approach. Such design is needed to minimize bias in turbidity and chlorophyll fluorescence data, while the pump system has been developed for other purposes; for example, conductivity-temperature measurements. This will prevent a major impact on the quantitative estimation of zooplankton densities when organisms are concurrently recorded by acoustic or imaging devices. However, as pump devices require a high power supply, it should be a challenge to carry out long-term deployments using such system. Additionally, pump suctions generate shear flows inside pipes and lead to breakage of particles there (e.g., aggregates, phytoplankton cells), potentially leading to bias in turbidity and chlorophyll fluorescence readings (Cetinić et al. 2016). A stand-alone turbidity sensor could be free from the bias, as its infrared/red LED beam would not elicit zooplankton phototactic behavior. A simple alternative to minimize the bias is to program turbidity and fluorescence readings with enough interval between each other so that animals attracted by the blue light would disperse before turbidity is recorded. However, since we noticed that fluorescence itself can be affected by the presence of zooplankton, such strategy would not guarantee fully unbiased measurements, particularly at high zooplankton densities. A definitive technical solution for this problem remains unclear, considering the existing technology.

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