

Understanding the picture: the promise and challenges of in-situ imagery data in the study of plankton ecology

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ABSTRACT

Planktons are a fundamental piece of all ocean ecosystems yet, sampling plankton at the high resolution required to understand their dynamics remains a challenge. In-situ imaging tools offer an approach to sample plankton at fine scales. Advances in technology and methodology provide the ability to make in-situ imaging a common tool in plankton ecology. Despite the massive potential of in-situ imaging tools, there are no standard approaches for analyzing the associated data. Consequently, studies are inconsistent in analyzing in-situ imaging data, even for similar questions. This introduces challenges in comparing across studies and sampling devices. In this review, we briefly summarize the increasing use, potential and novel applications of in-situ imaging tools in plankton ecology. Then, we synthesize the common analyses used across these studies. Finally, we address the major statistical challenges associated with the unique sampling mechanisms of in-situ imaging tools and discuss the theoretical uncertainties, which arise from the low-sampling volumes of many in-situ imaging tools. To fully unlock the power of in-situ imaging tools in plankton ecological studies, researchers must carefully consider how to analyze their data. We provide recommendations for processing and analyzing data while also acknowledging a large need for developing new statistical tool.

INTRODUCTION

Planktons represent a fundamental component of all aquatic ecosystems and both zooplankton and phytoplankton are extremely taxonomically and functionally diverse (Litchman and Klausmeier, 2008; Kiørboe *et al.*, 2018). However, understanding plankton abundance and community assemblage remains a major challenge. Planktons are well known to exhibit massive spatiotemporal variation (Haury *et al.*, 1978; Deksheniaks *et al.*, 2001; Cloern and Jassby, 2010; Kuhn *et al.*, 2019). Traditional net-based sampling provides inherently limited spatial and temporal resolutions. Some developments in the 20th century increased net sampling resolution (Longhurst *et al.*, 1966; Hosie *et al.*, 2003; Wiebe and Benfield, 2003). However, nets still face pitfalls like the under-sampling of fragile and gelatinous organisms (Cowen *et al.*, 2013; Whitmore and Ohman, 2021). Researchers have long explored in-situ imaging systems as an alternative approach for plankton sampling (Arnold and Nuttall-Smith, 1974; Ortner *et al.*, 1979; Jaffe, 2015). These instruments can sample at high frequencies. Furthermore, in-situ imagery data provide plankton diversity, abundance and metrics related to traits. In recent years, in-situ imaging tools have greatly developed and seen widespread use (Lombard *et al.*, 2019). Now, researchers are integrating in-situ plankton measurements into standard ocean observing programs (Boss *et al.*, 2018, 2022; Giering *et al.*, 2022).

In-situ imaging offers massive potential to understand plankton dynamics at unprecedented resolution. Despite the promise and increasing use of imagery data, most applications

have focused on particles and there has been limited ecological investigation. One barrier is the massive and complex datasets generated by imaging devices. Considerable work has been devoted to processing and classifying raw images (Irissou *et al.*, 2022). Yet even with taxonomically resolved data, gaining statistically robust insights is not straightforward. In-situ imaging devices vary in sampling volume, frequency and methodology. As a result, each instrument has unique opportunities and limitations with the data it collects. Some analyses are applicable across net-collected data and the various imagery-collected data. However, this is not always the case, and researchers must give consideration to how to process and interpret in-situ imagery data. In this paper, we review applications of in-situ imagery data to study plankton ecology. We provide a brief summary of the major research themes explored with these devices. Then we address the range of analyses used to investigate similar questions. Finally, we discuss the common challenge of the low sampling volumes associated with many in-situ imaging devices.

IN-SITU IMAGING FOR PLANKTON ECOLOGY

For this review paper, we evaluated publications that utilized in-situ imaging in applications of studying plankton ecology. Papers were identified using Google Scholar and Web-of-Science to search for original methods articles describing novel in-situ imaging tools. Then, research articles were identified from those which had cited the original methods papers. Papers were

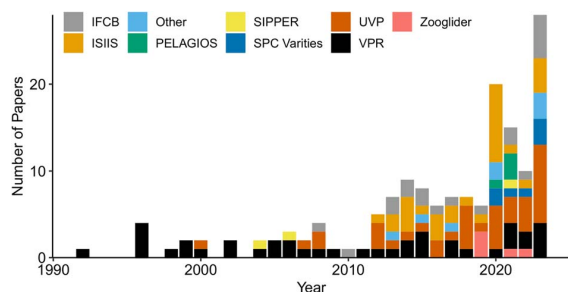


Fig. 1. In-situ imaging studies utilizing major imaging devices since 1992. See Supplemental Table S1 for acronyms and source papers.

also found by searching for keywords “in-situ imaging” and “plankton.” There were many in-situ imaging systems that have been described in the literature, but many of these devices are still primarily engineering projects or not yet widely adopted by plankton ecologists (Supplemental Table S1). Furthermore, many imaging systems are also used for studying non-living particles. Other instruments, such as the Imaging Flow CytoBot (IFCB), work for in-situ and bench-top applications. Here, we only focused on studies that utilized in-situ collection of plankton data. With this focus, we included 156 papers in this review from 14 instruments published from 1992 to July 2023 (Fig. 1). Among the reviewed studies, the in-situ imaging tools utilize a range of technology including optical microscopy, shadowgraphy (Greer, 2018) or holography (Nayak et al., 2021). Deployment methodology of imaging instruments included towed systems, profiling/cast approaches and autonomous systems.

The earliest studies published studies of in-situ plankton ecology used the video plankton recorder (VPR) (Davis et al., 1992a, b). However, it was not until the 2010s when in-situ imaging data began to see more widespread use. This increase largely corresponds with the commercial availability of the In-Situ Ichthyoplankton Imaging System (ISIIS) (Cowen and Guigand, 2008) and Underwater Vision Profiler (UVP) (Picheral et al., 2010; Picheral et al., 2022). Additionally, the IFCB has been used for on-going phytoplankton monitoring programs in Martha’s Vineyard (Olson and Sosik, 2007) and the Gulf of Mexico (Anglès et al., 2015). More recently, the Scripps Plankton Camera (Orenstein et al., 2020) and similar variations (Campbell et al., 2020; Merz et al., 2021) have been increasingly used in recent years. These devices are deployed at fixed stations, which can provide extremely high-frequency temporal dynamics.

Interestingly, there were a large number of papers published in 2020, then a slight decrease in 2021 and 2022. This pattern can be attributed to the coronavirus disease 2019 pandemic, where more writing was done in 2020, yet delayed data collection as many oceanographic expeditions were canceled in 2020 and 2021.

Ecological applications of in-situ imaging

In-situ imaging tools have been utilized to study plankton ecology at a wide range of temporal and spatial scales. At the smallest scale, in-situ imagery data is particularly useful for

describing traits and behavior of individuals (Ohman, 2019). Copepod morphology has been linked to changes in spatial distribution (Vilgrain et al., 2021) and behavior (Barth et al., 2023). Additionally, individual behavior, such as vertical orientation, was described to be related to light conditions (Benfield et al., 2000). Several imaging studies have also revealed morphological defenses such as spines (Ohman, 2019) or increased phytoplankton chain sizes (Gallager et al., 1996; Norrbin et al., 1996; Greer et al., 2020a, b). Another key advantage of imaging tools is the ability to describe previously unobserved taxa (Campbell et al., 2010; Henrichs et al., 2013; Christiansen et al., 2018; Hoving et al., 2019) or traits (Gaskell et al., 2019; Greer et al., 2019). Imagery data also can resolve features such as parasite attachment (Peacock et al., 2014).

Resolving spatial patterns

As most plankton range in size from a couple microns to a few millimeters, the majority of interactions in planktonic life are on the micro-scale (mm to cm) (Kjørboe and Saiz, 1995; Kjørboe, 2007a; Kjørboe, 2011). In-situ images have been used to resolve many fine-scale behaviors and interactions. With radiolarians, both symbiotic (Dennett et al., 2002) and predatory behavior have been described (Mars Brisbin et al., 2020). Crustacean associations and foraging are also well documented from imaging studies (Möller et al., 2012; Nishibe et al., 2015; Greer et al., 2017). Due to the exact spatial recording of imaging data, micro-scale patterns can also be inferred, such as swimming behavior to maintain monogenic patches (Davis et al., 1992a, b) or associations with particle fields (Whitmore et al., 2019). Shadowgraph systems can detect micro-scale turbulent layers or fluid deformations (Greer, 2018; Ohman, 2019), which may have influences on zooplankton behavior, yet this has not been investigated with these data types.

Fine-scale (meters to tens of meters) patchiness and vertical structure are a common scale of variability in plankton communities. Despite the ubiquity of such features, fine-scale plankton structures are still relatively understudied. While some net systems offer vertically resolved sampling (e.g. MOCNESS, Multinet), in-situ imagery data offer unparalleled information for resolving fine-scale features. Several studies have utilized these tools for resolving fine-scale vertical structure in zooplankton (Gorsky et al., 2000; Davis et al., 2005; Haëntjens et al., 2020) and phytoplankton (Villareal et al., 1999; Smith et al., 2017). Within Rhizarian taxa, UVP5 data have shown distinct depth-niche partitioning (Biard and Ohman, 2020). Imagery data also can allow for the measurement of fine scale overlap between plankton and potential food sources (Möller et al., 2012; Axler et al., 2020a; Rogge et al., 2023). Walsh et al. (2006) observed that *Trichodesmium* spp. had a distinct vertical structure that matched the distribution of *Karenia brevis*. Such studies provide critical insight to planktonic trophic transfer and nutrient cycling. Phytoplankton thin-layers are also well studied using imaging tools. Studies have investigated thin-layer formation (Greer et al., 2014; Sevadjian et al., 2014) and zooplankton associations in them (Greer et al., 2013; Greer et al., 2020a, b; Grassian et al., 2023).

Mesoscale variability is fairly well studied with net-systems. However, due to the ease of attaching in-situ imaging tools to

standard oceanographic profiling equipment, many imaging studies have focused on describing regional variation. Such studies are unique as they can provide estimates of mesoscale biomass variation (Forest *et al.*, 2013) or patterns of gelatinous and fragile organisms (Sandel *et al.*, 2015; Smith *et al.*, 2017; Dupouy *et al.*, 2018). Another advantage of in-situ imaging is the ability to describe mesoscale variability of fine and micro-scale features. Gleiber *et al.* (2020b) documented fine-scale variation in larval fish-copepod overlap throughout the Florida straight. Imaging also has shown the vertical structure of mesozooplankton groups varies with mesoscale hydrographic variability in the Arctic (Ashjian *et al.*, 2005a, b) and Antarctic (Ashjian *et al.*, 2008).

Fewer imaging studies have focused on macro-scale or biogeographic patterns. However, some instruments have been widely deployed in enough systems to characterize taxa at global scales. The UVP has been used to describe global variation in mesozooplankton taxa (Stemmann *et al.*, 2008a, b; Drago *et al.*, 2022) and Rhizaria (Biard *et al.*, 2016). The ISIIS has also been used to describe global distribution patterns of doliolids (Greer *et al.*, 2023). As in-situ imaging tools become more prevalent on oceanographic expeditions, the collected data will provide massive potential to better resolve large-scale plankton patterns.

Spatiotemporal patterns

Many marine properties which affect plankton exhibit variation in both space and time. Studying such features can be challenging as sampling typically requires following a water mass. As in-situ imaging tools can quickly collect data, they offer improved sampling of such structures. Imagery data have been used to study plankton populations within eddies (Martin *et al.*, 2013; Christiansen *et al.*, 2018; Schmid *et al.*, 2020) and along upwelling fronts (Luo *et al.*, 2014). In the Gulf of Mexico, the Mississippi river plume has been shown with imaging tools to have distinct effects on zooplankton (Axler *et al.*, 2020a), larval fish feeding dynamics (Axler *et al.*, 2020b) and phytoplankton (Dzwonkowski *et al.*, 2017). In the Arctic, Vilgrain *et al.* (2021) used a trait-based, imaging approach to describe how copepod morphology varies along an ice-melt gradient. As the phytoplankton bloom of ice-melts ends, other imaging studies have shown that copepods track the sinking marine snow layer (Toullec *et al.*, 2021).

Diel vertical migration (DVM) is a widespread phenomenon of spatiotemporal change throughout the water column. Many imaging studies have documented DVM (Pan *et al.*, 2018; Melle *et al.*, 2020). In-situ imagery data have described DVM in many gelatinous zooplankton (Treible *et al.*, 2022; Steinberg *et al.*, 2023). Additionally direct observations of individuals can reveal swimming patterns consistent with DVM (Greer *et al.*, 2018; Parra *et al.*, 2019). Greer *et al.* (2013) used ISIIS data to suggest that copepods decreased diel migrations to avoid gelatinous predators. Phytoplanktons, including HAB taxa, have also been shown to display DVM (Walsh *et al.*, 2006; Brosnahan *et al.*, 2017). In areas with low oxygen subsurface regions, imaging studies have revealed mixed migration strategies to avoid or enter oxygen deplete areas (Haus *et al.*, 2016; Hoving *et al.*, 2020). Moored imaging devices can also detect DVM by describing the frequency of observations of certain taxa (Merz *et al.*, 2021).

Temporal and population variability

Due to their immobility, planktons are subject to rapid changes in water quality accompanied by stochastic events like storms and heatwaves. In-situ imaging allows for repeated, low-effort sampling through these events, fully capturing plankton responses. Briseño-Avena *et al.* (2020a, b) described a shift of community composition during the 2016 warm blob in the California Current. Moored imaging systems offer high-temporal frequency and have documented plankton responses to rain events (Grossmann *et al.*, 2015; Anglès *et al.*, 2019; Fiorendino *et al.*, 2023; Thompson *et al.*, 2023). Such high-frequency sampling also can be used to describe population dynamics. Foraminifera in the California Current have been linked to lunar cycles and vertical variability using imaging tools (Gaskell *et al.*, 2019). In-situ, continued observations of plankton populations have facilitated discovery of parasitism influences on both diatoms (Catlett *et al.*, 2023) and copepods (Orenstein *et al.*, 2022a, b). Moored imaging systems have also illuminated bloom dynamics of HAB phytoplankton (Brosnahan *et al.*, 2015, Brosnahan *et al.*, 2017; Kenitz *et al.*, 2023). Imaging tools are now used in monitoring programs as the automated detection of HAB-taxa can be more rapid than traditional monitoring programs (Campbell *et al.*, 2013; Song *et al.*, 2020).

ANALYSES FOR IN-SITU IMAGERY DATA

Most of the focus on data processing of in-situ imaging tools has been on classifying images (Irisson *et al.*, 2022) and describing and inferring traits (Vilgrain *et al.*, 2021; Orenstein *et al.*, 2022a, b). Yet, there is no common framework for drawing statistical inferences from in-situ imagery data. Many studies simply describe abundance patterns; however, some use the novel data type to make ecological inferences. Given the wide range of instruments and deployment methods, there is a range of statistical tools utilized in these studies. From these studies, we review common research themes and evaluate analysis approaches.

Comparisons across space and time

For standard comparisons of plankton abundance across regions, common statistical tools utilizing comparisons of means/medians are applicable (Luo *et al.*, 2014; Haus *et al.*, 2016; Gleiber *et al.*, 2020b). A major benefit of in-situ imaging tools is the ability to describe fine-scale patterns, yet this requires analyses which are not commonly applied with net-collected data. Kolmogorov-Smirnov tests (KS tests) have been used to compare vertical distributions (Basedow *et al.*, 2013; Christiansen *et al.*, 2018). A KS test provides a *P* value for evaluating two populations' distribution differences; however, they do not provide a clear effect size to compare the magnitude of difference. Thus, the KS test simply tells that data are significantly different but not by how much with limited interpretation beyond the context of a single study.

Weighted mean depth (WMD) is a common metric for measuring the vertical structure of plankton (Ohman and Romagnan, 2016; Aarflot *et al.*, 2019). Calculating WMD from in-situ imaging data is not always straight-forward. If sampling is consistent throughout the water column, it can be calculated directly (Neitzel *et al.*, 2021; Whitmore and Ohman, 2021; Mooney *et al.*, 2023). However, many datasets from in-situ

imaging devices have uneven sampling efforts. [Barth et al. \(2023\)](#) used a modified bootstrap approach to account for this issue. More broadly, re-sampling methods have many applications for generating statistics with in-situ imaging data. [Stemmann et al. \(2008a, b\)](#) used a Monte-Carlo approach to construct day/night profiles which were compared using a KS test.

Relating plankton to environmental parameters

Across all studies investigated, the most common analyses involved identifying physical drivers of plankton abundance. In-situ imaging data are collected as similar frequency to environmental sensing systems which facilitates the ability to draw novel insights. Many studies placed their in-situ plankton observations in TS (temperature-salinity) plots ([Ashjian et al., 2005a, b](#); [Ashjian et al., 2008](#)). TS diagrams can provide a clear visual for the environmental range of different taxa ([Bi et al., 2013](#); [Beroujon et al., 2022](#)). However, TS diagrams alone do not provide any statistical inference. [Treible et al. \(2022\)](#) expanded TS diagrams by also providing a single parameter quotient for each environmental variable with a bootstrapping approach.

Correlations, linear and additive models are common tools. In most cases, concentrations of plankton must first be calculated from the imagery data by binning observations over a semi-arbitrary sampling space. The selection of a bin-size is a challenge discussed later in this paper and in [Barth and Stone \(2022\)](#). Once concentrations are calculated in a bin, they can be related to environmental conditions. Correlations are often used as a quick metric to show which environmental parameters relate to plankton concentrations ([Donoso et al., 2017](#); [Axler et al., 2020b](#); [Pan et al., 2021](#)). Researchers should note that plankton concentrations are often non-linear with respect to environmental conditions, limiting the applicability of Pearson's correlation coefficient. Additionally, many biological relationships are non-monotonic, limiting Spearman's correlation coefficient.

Generalized Linear Models (GLMs) are a standard approach ([Davis and McGillicuddy, 2006](#); [Norrbin et al., 2009](#); [Song et al., 2020](#)). GLMs can be fit to several distributions and include non-linear relationships (polynomials). However, most studies try to get a normal distribution, despite the inherent non-normality of in-situ imaging data. Transformations to a skewed dataset may force a normal distribution, yet this approach is often flawed ([Feng et al., 2014](#)). Researchers using GLMs should consider using a Poisson link function ([Greer et al., 2013](#)). Alternatively, binary patterns in data such as population peaks ([Bi et al., 2022](#)) or presence/absence ([Greer et al., 2015](#)) can be extracted. With this information, logistic regressions can be used, which circumvent many issues related to non-normality. Generalized Additive Models (GAMs) are increasingly common with ecological data analysis. Several studies used GAMs to relate imaged plankton data to environmental features ([Bi et al., 2013](#); [Sainmont et al., 2014](#); [Biard and Ohman, 2020](#)). However, researchers utilizing GAMs ought to carefully consider the nature of their data and over-fitting during model selection.

There are multivariate analyses that can also be applied to environmental-plankton modeling. Dimension reduction can create composite explanatory variables for regressions ([Song et al., 2020](#)). While other researchers have directly assessed all variables (environmental and plankton abundance) in

redundancy analyses ([Gislason et al., 2016](#)) or canonical analyses ([Greer et al., 2015](#)). Machine learning analyses have also been explored such as regression trees ([Luo et al., 2014](#); [Schmid et al., 2020](#); [Drago et al., 2022](#)) and random forest algorithms ([Kenitz et al., 2023](#); [Schmid et al., 2023](#)). Similar to a GAM, this suite of analyses can offer a way to get large explanatory power yet require careful model selection and fitting.

Co-occurrence

Many analyses focus on quantifying the overlap or separation of different taxa. This can include investigations of niche-partitioning, community composition or predator-prey interactions. Taxonomic assemblages can be distinguished with dimension reduction ([Stemmann et al., 2008a, b](#); [Anglès et al., 2015](#); [Hoving et al., 2020](#)) or unsupervised clustering methods ([Luo et al., 2014](#); [Gaskell et al., 2019](#); [Briseño-Avena et al., 2020a, b](#)). With time-series data and consistent sampling, the co-occurrence of two populations can be directly assessed. [Orenstein et al. \(2022a, b\)](#) used convergent cross mapping to identify a causal impact of a parasite on copepod population dynamics. As moored-imaging datasets become more common, further applications of causal impact analyses should be explored.

Several studies used a version of an overlapping index to assess if two taxa co-occur at fine spatial scales. One approach to measure the co-occurrence of two species is to use the Local Index of Collocation, originally described by [Pianka \(1973\)](#):

$$LIOC = \frac{\sum_i^n (P_{A_i} P_{B_i})}{\sqrt{\sum_i^n (P_{A_i})^2 \sum_i^n (P_{B_i})^2}}$$

where P_A and P_B correspond to the proportion of species A and B at each i bin for all n bins. The LIOC traditionally uses proportions of biomass but could be used with taxa concentration as well. [Whitmore and Ohman \(2021\)](#) used LIOC to assess predator/prey overlap in micro-scale bins. A similar overlap metric, O , is also used in zooplankton studies ([Williamson and Stoeckel, 1990](#)). Note that at times the LIOC is referred to as Pianka's O , yet we distinguish O as a separate metric. O measures the vertical overlap between two species:

$$O = \frac{\sum_i^n (A_i B_i) n}{\sum_i^n A_i \sum_i^n B_i}$$

where A and B are the concentration of each species measured for each i observation of all n bins sampled. Imaging studies have used O to infer predator-prey overlap as well ([Möller et al., 2012](#); [Greer et al., 2013](#)). O and LIOC can generate very similar inferences despite slightly different calculations. Given the similarity of these metrics, LIOC is likely more appropriate in most cases. LIOC is more common in general ecology ([Carroll et al., 2019](#)) and not sensitive to bin number or resolution (n). The AB ratio is also a metric applicable to in-situ imaging data ([Greer and Woodson, 2016](#)). While the reviewed studies used overlapping metrics for vertical bins, the approach is applicable to temporal or spatial bins. A comprehensive review of overlapping metrics is available by [Carroll et al. \(2019\)](#). Due to the nature of

in-situ imaging data, overlapping metrics offer large potential for addressing questions in plankton ecology.

Describing plankton patchiness

A common metric to describe patchiness is Lloyd's patchiness index, P (Lloyd, 1967):

$$P = 1 + \frac{\sigma^2 - m}{m^2}$$

where m is the mean count across all bins (referred to as quadrats by Lloyd's original work) and σ^2 is the variance. Thus, if the $m = \sigma^2$ (Poisson distribution), planktons are evenly spaced and $P = 1$. A value of $P > 1$ indicates that planktons are aggregated at some point throughout the water column. Thus, P is a single description of the entire system. Several in-situ imaging studies have used P (Greer *et al.*, 2013, 2014, 2018). In all these cases, the bin size was set at a consistent 1 m^3 . Consequentially, the counts of plankton are not different from the densities. However, in many in-situ imaging applications, planktons are binned over scales with variable sampling volumes. In these cases, P is no longer applicable because it is not compatible with density data (Bez, 2000).

To measure patchiness across a survey area, a point-process method can be used as described by Gallager *et al.* (1996):

$$Ag = \frac{\sum_i (N_i/N)}{2(N-1)/L}$$

Note the term aggregation index, Ag was set by Gallager *et al.* (2004). Fundamentally, Ag assess the distribution of individuals in bins by measuring the proportion of observations in subunits of each bin. L is the size of the bin. Then within each bin, i subunits are determined of equal length so N_i refers to the count of individuals in an i^{th} subunit and N refers to the total number of individual in the bin. This method produces a value of Ag for each bin across a survey area. This method was applied to VPR tow data (Gallager *et al.*, 1996, 2004). In both cases, Gallager calculated the significance of aggregation across the survey area by bootstrapping confidence intervals from the array of Ag values. This point-process is theoretically robust to variations in sampling volume and can provide unique insight.

Plankton patchiness can also be described by measuring neighbors. Bez (2000) suggested a density-friendly modification of Lloyd's mean crowding to calculate the average number of neighbors. This approach, while applicable to in-situ imaging, has not yet been applied. Directly calculating the distance between individuals can be used to estimate the scale of interaction between plankters (Ashjian *et al.*, 2005a, b). Because imaging reveals the exact coordinates of a plankter, distance to nearest neighbor/encounter values can be calculated (Greer *et al.*, 2016a, b). This is possible with a range of instruments and could be expanded with instruments which record 3D positioning (Nayak *et al.*, 2021). Better describing patchiness is a major frontier in plankton ecology facilitated by in-situ imaging. Future studies will benefit from investigations into

robust methods to quantify patchiness across instruments and sampling schemes.

THE BIG CHALLENGE OF SMALL SAMPLING VOLUMES

The challenge of accurately measuring plankton counts has been considered both in the context of traditional microscopy (Postel *et al.*, 2000) and bench-top imaging systems (Álvarez *et al.*, 2011). However, in-situ imaging offers a unique challenge in that researchers are not often concerned with how much to count but rather how much to measure. A common challenge for imaging devices is the extremely small sampling volumes relative to nets. Multiple studies noted that small sampling volumes limit the ability to get reliable estimates of plankton abundance (Villareal *et al.*, 1999; Gorsky *et al.*, 2000; Ashjian *et al.*, 2008; Basedow *et al.*, 2013). Towed devices, such as the ISIS, can sample large volumes so that abundance estimates are on-par with net-based systems (Cowen *et al.*, 2013). However, imaging instruments deployed on CTD rosettes, AUVs or moorings inherently have smaller sampling volumes (tens of liters per profile). Calculating abundances with small sampling volumes can result in extreme variability of estimates between profiles (surveys, casts, tows, etc.) (Norrbin *et al.*, 1996; Nocera *et al.*, 2021; Barth and Stone, 2022). Some researchers suggested pooling multiple profiles over a similar area to increase sampling volume (Stemmann *et al.*, 2008a, b; Lombard *et al.*, 2019). While effective, this approach reduces the primary benefit of high sampling resolution.

Ideally, researchers can have the highest resolution possible with accurate concentration estimates. Thus, researchers must make choices on how to process and present their imagery data. However, in many studies, these choices are not clearly reported. Many papers reported analyzing data in depth-strata in less than 10 m. At this fine of scale, the estimates of a single taxon's abundance can be a function of detection/non-detection if their concentration is low. Furthermore, most papers do not readily report the sampling volume, which is critical to proper interpretation. This lack of clarity across papers is a result of a lack of a clear method for selecting bin sizes and reporting uncertainty in concentration estimates.

One approach to gain reliable insights from in-situ imaging data is to set a minimum observation threshold. Benfield *et al.* (1996) first set a non-detection threshold using a the first-order Poisson Process term $P(n=0) = e^{-\lambda v}$, where n is the number of individuals observed in a bin with v volume sampled. By setting the threshold, $P(n=0) < 0.05$, and the average v in a bin, the minimum concentration, λ could be calculated. Some studies used the same approach with less stringent thresholds (Broughton and Lough, 2006), yet largely in-situ imaging studies do not apply a quantitative threshold.

This approach can be calculated across a range of theoretical values which are realistic scenarios for an in-situ imaging device. We did this through a Poisson process for non-detection, $P(n=0) = e^{-\lambda v}$, across a range of sampling volumes, v , and a true concentration, λ ($\lambda = N/V$ where N is the true number individuals in some larger unmeasurable volume, V) (Fig. 2). We calculated the non-detection probability across sampling volumes from 1 L to 1000 L. Concentrations are shown from 1 m^{-3}

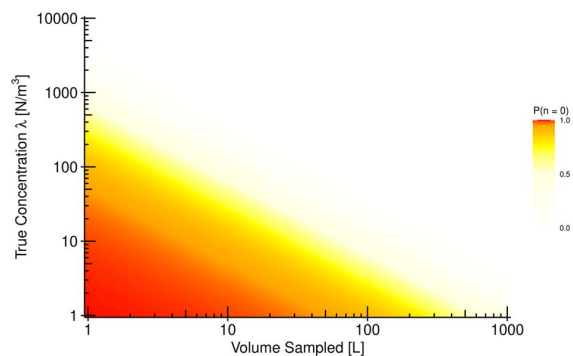


Fig. 2. Theoretical probabilities for non-detection of a plankton given a sampling volume and known true concentration ($\lambda = N \text{ m}^{-3}$). Non-detection probability is calculated as the first-order term of a Poisson process, with a rate parameter and expected value of λ and the sampling volume as observation set. Color scale indicates probability of not detecting any plankton even if those planktons actually are occurring in the system. Note both axes are log-scaled.

to $10\,000 \text{ m}^{-3}$. Across all reviewed papers, the concentration of taxa reported ranged from less than 1 indiv. m^{-3} to 1000 of indiv. m^{-3} , thus this represents a useful range for plankton ecologists.

Clearly, non-detection is fairly high at concentrations $<10 \text{ indiv. m}^{-3}$ (Fig. 2). Similarly, non-detection is likely at low sampling volumes ($<25 \text{ L}$). While some towed instruments have larger sampling volumes, many are restricted to smaller values. Additionally, some taxa, such as phytoplankton, may occur in concentrations well above what are shown here. However, it should be noted that the presented calculations are for one group. If researchers are considering investigations with increased taxonomic resolution, the concentration of each group must be considered individually.

The concept of non-detection can be extended following a Poisson Point Process to better understand theoretical uncertainty in estimating abundances. Poisson statistics are useful in determining uncertainty in counts of plankton (Postel *et al.*, 2000). In the case of in-situ imaging, researchers are interested in not accuracy in their counts but rather estimating concentration from some much larger volume of water (i.e. an ocean basin or lake system). Here, we present a Poisson process to estimate the probability of measuring a given number of individual plankton in an imaging study; $P(n) \sim \text{Poisson}(\lambda v)$. Here, n is the number of imaged plankton in sampling volume v . If the true concentration is λ , with N is number of plankton in the entire area of interest, then for researchers to correctly estimate concentration they would need to observe N/v plankton across their images. Traditionally, 20% accuracy is regarded as acceptable in plankton enumeration (Postel *et al.*, 2000), so the Poisson process can be used to find $P(n = N/v \pm 20\%)$. When done across a range of possible sampling volumes, it is clear that accurate estimation of λ is feasible only at high concentrations and sampling volumes (Supplemental Fig. S1). While this approach is useful for an easy calculation, when generalizing across theoretical scenarios, it produces counterintuitive artifacts. First, because the Poisson distribution only works with integers, the theoretical

probability of a $\pm 20\%$ estimate can make large jumps due to rounding differences (Supplemental Fig. S1; Supplemental Fig. S2). Secondly, the overall concept of measuring the probability of an accurate estimate of the “true” concentration is not reflective of the typical process utilized by plankton researchers. In practice, the “true” concentration is not known, researchers only know the observed plankton and sampling volume. From there, researchers can calculate an estimate of concentration, Therefore, it is more useful to directly model the uncertainty associated with the actual parameter of interest, concentration (λ). This is not directly possible following a traditional Poisson Process, yet utilizing Bayesian statistics can make this approach feasible. Bisson *et al.* (2022) detail a framework for estimating the uncertainty associated with imaging large particles. While the original work was focused on extending the uncertainty to derived carbon flux estimates, the foundational approach is applicable to plankton concentration estimates. Briefly, in Bayesian statistics the parameter (in this case the concentration λ) is modeled as a random variable, whose (posterior) distribution is a function of some prior distribution and observed data. In this case the observed data are the number of imaged plankton, n and the sampling volume, v . A conjugate prior for a Poisson distribution is the Gamma distribution. Assuming a non-informative prior the posterior distribution of the concentration parameter can be modeled as $\lambda \sim \Gamma(n + 0.5, v)$. Note for the sake of brevity, we do not provide the complete formulation of this approach which is available in context (Bisson *et al.*, 2022) and more generally (Kruschke, 2015; Downey, 2022). Using the posterior distribution of λ , the uncertainty in concentration estimates can be expressed as the width of the credible interval.

We calculated the credible interval widths for estimation of λ across the range of potential sampling volumes and possible observed data (Fig. 3). Following this approach, a plankton ecologist can calculate the width of the credible interval given their sampling volume (v) and observed concentration (n/v). Again, the credible intervals are for a single group of plankton and as taxonomic resolution increases the calculations should be considered individually for each group. Clearly, to reach the 20% precision threshold a large volume of water must be imaged, or a particularly high concentration must be observed. This is possible with some instruments or taxa, namely towed imaging systems or devices targeting smaller organisms which occur in high concentrations. However, many of the reviewed papers in this study reported concentration estimates from such fine resolution that the uncertainty associated with those estimates is extremely high.

In some contexts, wider credible intervals may be acceptable, yet researchers should be aware of their uncertainty and readily report sampling volume. Furthermore, when selecting aggregation methods for binned-observations researchers should report their methods. It should be noted that bins are often not constructed based on equal sampling volume but some physical factor (depth, time, etc.). Thus, if observations are assumed to follow a Poisson Process, the concentration estimate in each bin comes from a unique Poisson distribution that would lead to a violation of the identical distribution assumption of many statistical models.

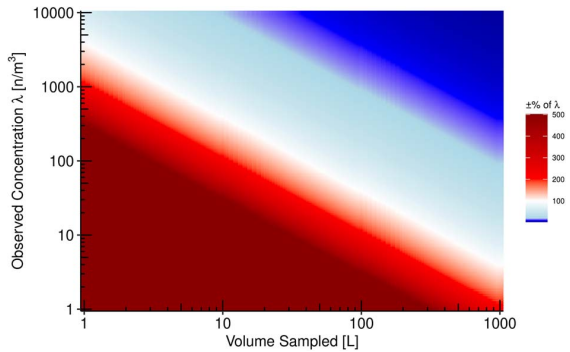


Fig. 3. Credible interval width for posterior probability distribution of observed concentration value ($\lambda =$ number observed/ volume sampled) across a range of possible sampling volumes (v). λ is modelled using a gamma distribution with vague priors. Color scale represents the width of credible interval as a percentage of λ . A wider credible interval signifies a less reliable estimate. Note axes are both log-scaled.

There is a great need for further work to describe statistical methods to handle the uncertainty inherent to plankton imaging data. We argue that the Poisson Process—Gamma framework outlined here provides a clear starting point for establishing credible thresholds. It should be noted that a Poisson distribution assumes observations are homogeneously distributed throughout the set, which is rarely actually the case for plankton. Nonetheless, this is implicitly assumed when calculating concentration, whether from nets or imaging systems. Possibly, measuring deviations from a Poisson distribution can be useful in determining heterogeneity (Postel *et al.*, 2000). Alternatively, statistical models which can incorporate variable sampling effort (Kéry and Schmidt, 2008) may be a promising avenue of research, which has not been explored in the context of plankton studies.

CONCLUSIONS AND FUTURE DIRECTIONS

Overall, in-situ imaging tools offer plankton ecologists immense opportunity to investigate a critical part of our oceans. To date, a variety of instruments have been deployed, revealing insights into plankton traits, gelatinous organisms and fine-scale patterns. As imaging tools become more common, increased datasets will facilitate new lines of investigation. Much of the long-term imaging work has been done with phytoplankton datasets, so there is opportunity for investigation with mesozooplankton as data become available. With the development of smaller (Picheral *et al.*, 2022) or low-cost imaging devices (Lertvilai, 2020), the spatial and temporal resolutions of sampling will greatly increase. This resolution could provide datasets, which can better describe fine-scale features of plankton. Additionally, measuring patchiness and its environmental drivers at a global scale can have large implication for better understanding ocean functioning. Deployment of imaging systems on floats, such as BGC-ARGO systems could provide unique Lagrangian sampling of plankton communities (André *et al.*, 2020). Finally, as a consequence of the changing climate, storms, heatwaves and other extreme events are increasing in frequency across the globe. In-situ imaging may

facilitate studies that provide data to understand how planktons respond to such events.

There is still a need for studies, which benchmark imaging systems and describe best practices (Lombard *et al.*, 2019; Ollevier *et al.*, 2022). While instruments have different scopes and applications, consideration should be given to collecting and analyzing data in ways that are generalizable across systems. Planktons span a wide range of sizes, resulting in many studies only focusing on sub discipline-specific questions. By combining different cameras or instruments, the possibility to sample the whole plankton community may become a more common approach (Romagnan *et al.*, 2015; Lombard *et al.*, 2019). To fully harness the power of in-situ imaging data, researchers must carefully consider their data processing and analysis choices. In order to facilitate future aggregation of research and collaboration, researchers should provide detail for sampling volume and bin-size selection. Future studies investigating the applicability of analyses that can account for variable sampling effort would greatly benefit the field.

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SUPPLEMENTARY DATA

Supplementary data can be found at *Journal of Plankton Research* online.

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