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Review

Mind the gap - The need to integrate novel plankton methods alongside ongoing long-term monitoring

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ABSTRACT

Changes in plankton have important implications for ecosystem services, including supporting fish stocks, carbon sequestration, nutrient cycling, and oxygen production. Standard long-term plankton monitoring relies on light microscopy to identify and count plankton taxa, with methods fully supported by international standards, providing high quality trusted data. Novel methods, including imaging and molecular, offer means of collecting select types of plankton data efficiently, filling targeted knowledge gaps left by standard monitoring and generating a more complete picture of plankton dynamics. Standard and novel monitoring methods present different advantages and costs, positioning their suitability to address different management needs. Standard plankton monitoring time-series are unique in providing the long-term temporal coverage, and thus statistical power, needed to detect and understand climate change impacts. When explored in parallel with standard monitoring, novel methods open doors to observing our seas from complementary perspectives, but further work is necessary before data from standard and novel methods can be integrated to address policy needs. Marine management priorities are shifting, and novel methods are increasingly proposed as possible alternatives to standard monitoring. However, for a long-term taxonomic perspective it is still essential to retain the specialist skills and maintain standard monitoring time-series to inform policy assessments of important changes in pelagic biodiversity. This review aims to inform readers of the value of long-term data, the importance of retaining taxonomic skills and embracing novel methods for marine plankton monitoring to assess pelagic biodiversity. We recommend strategies to maintain long-term monitoring whilst incorporating novel methods.

1. Introduction

Our understanding and management of the natural environment depends on sound monitoring practices to inform assessments of biodiversity. Plankton monitoring time-series have long provided a baseline of information on pelagic biodiversity and have enabled the interpretation of changes in ocean nutrient regulation, climate control, and the food webs that support commercial fish and protected species.

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Plankton monitoring data analysed via microscopy have revealed important large-scale declines in plankton abundance across much of the North-East Atlantic (Edwards et al., 2022; Holland et al., 2023; Schmidt et al., 2020). Here, we introduce the term "standard plankton monitoring" to refer specifically to phyto- and zooplankton collection via net, bottle, bucket, hose, or by underway samplers such as the Continuous Plankton Recorder, to be subsequently identified and counted by trained taxonomists using light microscopy. Standard plankton monitoring time-series have been instrumental for advancing our understanding of marine life, including detecting and identifying Harmful Algal Blooms (HABs) (e.g., Doucette et al., 2018), revealing the diversity, distribution, and feeding habits of zooplankton (e.g., Hélaouët et al., 2016), developing detailed taxonomic classifications for phytoplankton (e.g., Hoppenrath, 2017), and understanding changes in plankton communities over time (e.g., Bedford et al., 2020; Holland et al., 2023), providing valuable information on the impacts of climate change and other human-induced pressures on the marine environment (OSPAR, 2023).

From a management perspective, the data generated via standard plankton monitoring time-series are used to inform regional statutory policy assessments of biodiversity status for OSPAR (the North-East Atlantic regional seas convention), for the European Union (EU) under the Marine Strategy Framework Directive (MSFD), and for the UK under the UK Marine Strategy (UKMS) (McQuatters-Gollop et al., 2019, 2022). Standard plankton monitoring methods are also used to determine the diversity and abundance of toxin producing phytoplankton species in shellfish growing waters as part of the EU Shellfish Hygiene Directive (European Commission, 2019). The Ocean Biodiversity Information System (OBIS), the largest scientific knowledge base on the diversity, distribution and abundance of marine organisms, hosts >150 plankton datasets and is dependent on taxonomically resolved measurements, like those obtained from standard monitoring (Estes et al., 2021). The UN Biodiversity Beyond National Jurisdiction (BBNJ) Agreement, which countries are currently in the process of signing and ratifying, will also require states to measure and conserve biodiversity, including pelagic habitats (Gjerde et al., 2022). This obligation necessitates a comprehensive understanding of changes occurring at the base of the marine food web. While routine marine plankton monitoring is important for informing policy in many jurisdictions globally, we focus here on the North-East Atlantic and North-West European shelf region as a diverse marine ecosystem with well-established plankton monitoring regimes. This article aims to equip those responsible for disseminating scientific insights to government with a comprehensive overview on the importance of maintaining long-term standard monitoring and the associated taxonomic skills and expertise to inform policy decisions, as well as a set of recommendations for how novel methods can supplement our existing monitoring programmes.

The North-East Atlantic and North-West European shelf region is subject to multiple regulations which obligate countries to routinely assess the status of "higher" organisms (e.g., Birds and Habitats Directive (Wils, 2017), Nature Restoration Regulation (Hering et al., 2023)) and protect human health (e.g., EU Shellfish Hygiene Directive (CEC, 2006)). National governments fund monitoring programmes to provide the necessary data to conduct these assessments. However, there is less policy pressure for monitoring and assessing plankton, despite their foundational role in supporting marine food webs. Where we routinely assess multiple criteria for higher organisms (e.g., breeding success, bycatch, abundance, distribution, and habitat quality), there is just one overarching MSFD criterion (i.e., D1C6; Magliozzi et al., 2021) to describe the health of pelagic habitats. The lack of attention paid to pelagic habitats is also highlighted by the limited specificity and late development of the EU reporting guidelines for this criterion (European Commission, 2022). The number of legal obligations we have towards understanding changes in plankton does not reflect their relevance for the marine ecosystem, especially considering the current and anticipated changes in climate and human use of the seas (e.g. wind farms, marine carbon dioxide removal) which may impact on plankton (e.g., Daewel et al., 2022).

The Continuous Plankton Recorder (CPR) Survey is the most widely applied standard plankton monitoring time-series, and forms an important part of the UK and OSPAR biodiversity monitoring networks (Fig. 1a and b). The CPR Survey is the most geographically extensive multi-regional-scale plankton time-series, globally. The CPR dataset now contains over 7 million nautical miles of tows across the North Atlantic, North Pacific, Australia, and the Southern Ocean over 90+ years, routinely counting 650+ taxa (Batten et al., 2019). The CPR Survey collects plankton samples in offshore waters using specialised towed instruments deployed routinely from commercial ships and ferries as they travel their regular routes. The duration, regularity and broad spatial coverage of the CPR Survey enable scientists to study and analyse variation in plankton communities across space and time, detecting important changes in biodiversity and providing crucial insights into the dynamics of marine ecosystems. In the UK and European Union, the CPR Survey forms a part of a larger monitoring network collecting long-term data on plankton communities. This includes regulatory monitoring programmes that have been collecting data in inshore and offshore waters to address requirements of the UK environmental directives (Devlin et al., 2007; Graves et al., 2023) and OSPAR (Holland et al., 2023; McQuatters-Gollop et al., 2019).

The International Council for the Exploration of the Sea (ICES) is an intergovernmental organisation which provides scientific advice for the sustainable use of marine resources in the North Atlantic and hosts much of the data used for statutory OSPAR assessments. There are 115 and 124 phyto- and zooplankton fixed-point monitoring stations, respectively, within ICES jurisdiction (International Group for Marine Ecological Time Series, 2024); almost all are near-coastal, capturing a diverse range of aquatic habitats with terrestrial influence and complementing CPR Survey data (Fig. 1a and b). These stations also monitor a variety of biological and physico-chemical variables from static platforms or by research vessels that repeatedly visit and sample the same set of coordinates. The North-East Atlantic contains the greatest concentration of fixed-point station plankton monitoring time-series globally (O'Brien, 2017), contributing essential data with broad coverage of space and time (Fig. 1c and d) to support OSPAR as well as to inform other European national assessments (e.g., MSFD, UKMS).

A major advantage of fixed-point station monitoring is that it facilitates a high temporal frequency of sampling, as often as weekly (e.g., McEvoy et al., 2023) or even daily (e.g., Wiltshire et al., 2015). Such high sampling frequencies can support studies of dynamic short-term processes (e.g., phytoplankton bloom formation; Mieruch et al., 2010). Many of these sites also have over 30 years of data and therefore collectively provide an overview of large-scale changes in plankton dynamics and their drivers (e.g., water temperature; O'Brien et al., 2012). Such sentinel sites include the UK's Western Channel Observatory (Plymouth Marine Laboratory; McEvoy et al., 2023) and Scottish Coastal Observatory (Marine Directorate of the Scottish Government; Bresnan et al., 2016), the RADIALES programme in Northern Spain (Spanish Institute of Oceanography; Valdés et al., 2021), the Helgoland Roads time-series in Germany (Alfred Wegener Institute; Dummermuth et al., 2023), the French Phytoplankton Observation Network (PhytOBS; Lemoine and Claquin, 2021), and the Naples long-term ecological research site, MareChiara (Stazione Zoologica Anton Dohrn; Russo et al., 2024) (Fig. 2).

Alternate novel approaches for monitoring plankton include imaging, acoustics, and molecular methods. We use the term, "novel" to refer to these newer techniques, while acknowledging many have been in existence for over 40 years (e.g., see Bucklin and Kann (1991) for a molecular method example, or Herman (1992), Gorsky et al. (1992) and Smith and Baker (1982) for optical imaging examples), but may only recently been gaining widespread use. At present, novel technologies have reached a stage of development where the scientific community is investigating ways to implement them to complement, and in some cases substitute, standard monitoring of phyto- and zooplankton (Scott et al.,

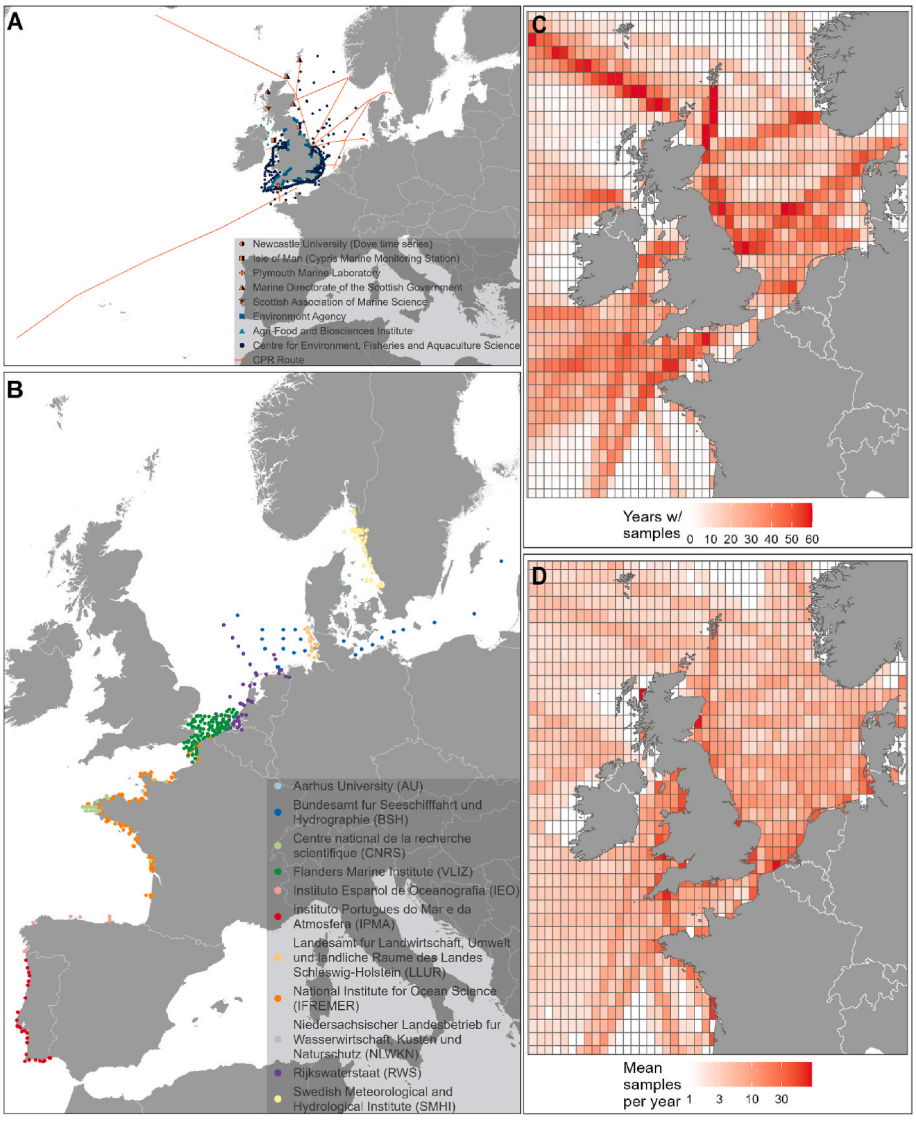

Fig. 1. Standard plankton monitoring routes and stations from the UK monitoring network, including the Continuous Plankton Recorder (CPR) Survey (A) and other fixed-point stations monitored by the European countries within the OSPAR Maritime Area (B). For (A) and (B), points are coloured according to the institution responsible for sampling. Data from the CPR Survey and fixed-point stations were also pooled and intersected with a 0.5° grid to summarise the number of years of samples collected (C) and the mean number of samples per year (D) for each cell in the 0.5° grid. Note that the colour scale for (D) has been log-transformed. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2021; Suter et al., 2021; Vezzulli et al., 2022; Zahir et al., 2024).

Automated imaging uses electro-optic or holographic technology to image plankton. The hardware technology couples with data analysis and software systems to collect, discriminate, identify, measure, and count plankton (Sieracki et al., 2010). Various image analysis systems are available for analysing plankton across a range of size spectra in both field- (*in situ*) and lab-based (*ex situ*) applications (e.g., Lombard et al., 2019). Molecular methods use differences within one or more DNA or RNA markers to identify and/or quantify plankton types, sometimes down to species level (Suter et al., 2021). Satellite remote sensing is also a powerful tool for long-term, large-scale observations of phytoplankton biomass, with improving algorithms to move beyond bulk chlorophyll indices (Ruddick et al., 2003). Recent advances in multispectral satellite imaging technology and processing algorithms have improved accuracy in identifying phytoplankton taxa through applications of machine learning and artificial intelligence (Zhang et al., 2024), and allow for the rapid analysis of large datasets and the identification of complex patterns in phytoplankton distribution and dynamics. Satellite remote sensing is also being explored as a key tool to provide early warnings of harmful algal bloom events in some regions (Khan et al., 2021). However, the purpose of this paper is to exclusively discuss and compare the various physical *in situ* sampling methods that can provide detailed taxonomic information, and we refer the reader to recent reviews (e.g., Cetinić et al., 2024; Khan et al., 2021) for a more in-depth appraisal of developments in plankton remote sensing.

The information that novel technologies can provide on the dynamics of the plankton community, such as termination of phytoplankton blooms (Brosnahan et al., 2017), understanding species and strain delineation within genera (Fraga et al., 2015; Gaonkar et al., 2020; John et al., 2014), species level identification (Clayton et al., 2022), toxin production of harmful species (Pearson et al., 2021), as well as revealing diversity and dynamics of fragile plankton (e.g., gelatinous zooplankton) that are poorly sampled by standard methods (Hosia et al., 2017), and the bacterioplankton and viral communities (McQuatters-Gollop et al., 2024) will be transformative in how we understand the marine ecosystem. However, with the exception of satellite remote sensing, there are very few long-term plankton time-series using novel technologies in this study region. While there are objectives to

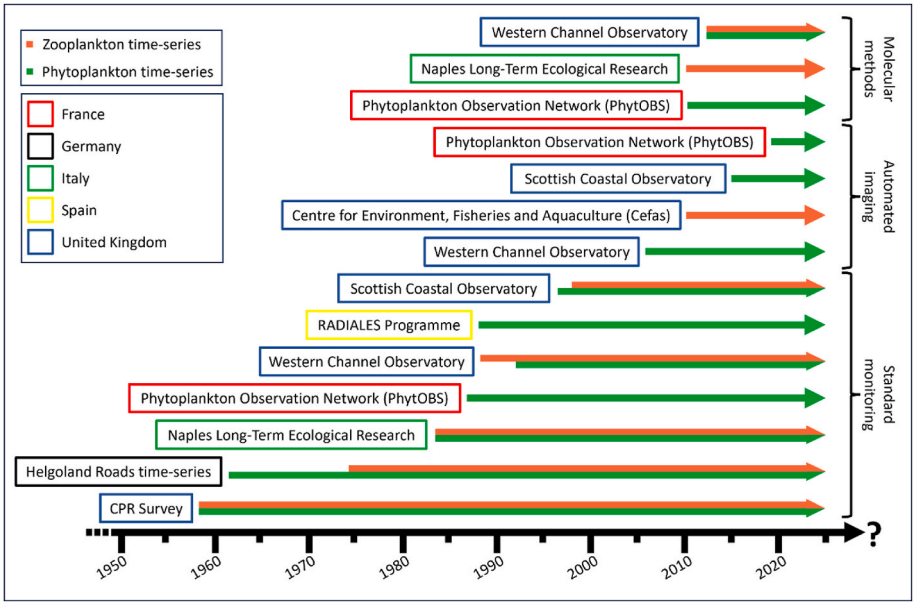

Fig. 2. An example selection of some of the longer European plankton monitoring programmes available for each method. This figure includes monitoring programmes which continue to the date this article was written, and that collect and process samples at monthly or finer intervals, without large gaps in sampling. Monitoring programmes are separated into standard monitoring, automated imaging, and molecular methods. Arrows are coloured according to whether they indicate observations of phyto- or zooplankton. Countries of the institutions responsible for each sampling programme are also indicated by the colour of the text boxes. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

integrate novel technologies into routine plankton monitoring, there are currently significant limitations to how data collected via novel technologies can be used in comparisons between datasets from different sampling programmes or integrated into existing time-series. As these technologies are still rapidly developing, they also lack the long-term consistent record of data required to support assessments of pelagic habitat biodiversity and to detect and understand climate change impacts (Fig. 2).

We argue that we should continue to explore these novel technologies, but it is essential that we do so alongside continued support for standard long-term plankton monitoring programmes and associated taxonomic skills and expertise, since they provide the baseline for environmental assessments and remain essential for gauging the state of the pelagic ecosystem, its biodiversity, and the health of its food web. In addition, the taxonomic and ecological expertise critical for standard monitoring needs to be maintained in order to validate novel methods. To promote their integration into routine monitoring, novel technologies should be explored in parallel (e.g., simultaneous use intercomparison; Ostle and Hélaouët, 2023) with standard monitoring to better understand how the data they generate compare to the detailed taxonomic data obtained from standard monitoring. Advanced taxonomic skills need to be developed to derive the classifications generated by these new methods, and to support the generation of reference image libraries and genetic sequence data to support automated imaging and molecular methods, respectively.

2. Standard monitoring

Standard plankton monitoring involves collecting samples directly from the ocean and subsequently preserving them so they can be later analysed via light microscopy. Plankton are typically collected with bottles, buckets, nets or hoses. In the case of the CPR Survey, a mechanical device automatically collects and preserves samples on a continuously rolling silk net-like mesh. Nets of various mesh sizes and designs are used to collect various fractions of zooplankton, usually dictated by body size. The size of "holes" in the filter material introduces biases to the range of organisms retained in the sample (Riccardi, 2010), requires some extrapolation to define true abundances, and also damages the individual organisms to a greater or lesser extent (Skjoldal et al., 2013). Due to their small size, marine phytoplankton are often collected via bottle or bucket sampling, or using nets with mesh size <50 μm (McQuatters-Gollop et al., 2015), and subsequently concentrated into a smaller volume. For chlorophyll extraction, the sample is drawn through a glass fiber filter (<1 μm) by a mechanical pump and the sample is retained by the filter (Qin et al., 2013). For taxonomic analysis, this concentration step often uses the Utermöhl technique (Edler and Elbrächter, 2010), which uses gravity to allow phytoplankton cells to settle on the bottom of a counting chamber from a column of water of known volume (Edler and Elbrächter, 2010). Some instruments, such as the CPR, can effectively sample both zooplankton as well as larger phytoplankton, although not without instrument-specific biases, since the larger mesh size (270 μm) allows many smaller phytoplankton to escape (McQuatters-Gollop et al., 2015).

Most plankton samples are preserved in formalin or Lugol's iodine for storage and later identification, since identification and counting are time-consuming and often cannot take place in the field. Most sampling is carried out from static platforms, or research vessels visiting fixed-point observatory locations (i.e., stations). The latter can be costly to maintain because they require regular vessel time. By contrast the CPR Survey, and the more recent FerryBox programme (Petersen et al., 2007), respectively, use instruments towed behind or mounted on commercial ships and ferries as they travel their regular routes. In terms of standard monitoring programmes, the CPR Survey and FerryBox programme are unusual cases because they do not require dedicated research vessel time, therefore operational costs can be kept to a much lower level versus research vessel-based sampling. As mentioned previously, the data collected via fixed-point sampling and the large-scale geospatial sampling of the CPR Survey inform different aspects of our understanding of the marine ecosystem.

In the lab, trained taxonomists identify and count organisms in the samples under a light microscope, following a set of consistent and documented methods. Depending on the institute-specific procedure and density of organisms, processing time can take several hours to days per sample (First and Drake, 2012; Zohary et al., 2016). This approach

provides a high level of taxonomic detail, with semi-quantitative to quantitative categories of taxa abundance (Harris, 2010; Holland et al., 2023; Lundsør et al., 2022). The standard approach also allows a very rapid check for unusual results or new taxa. This highly skilled method of plankton identification and enumeration is, understandably, labour intensive.

The high-quality and consistency of data collected in this manner facilitates comparisons over long (multi-decadal) time periods and among laboratories. The North-East Atlantic Marine Biological Analytical Quality Control (NMBAQC) scheme provides a source of external Quality Assurance (QA) for laboratories engaged in the production of such plankton data. Through the NMBAQC scheme, European laboratories engage in regular (at least biennial) intercomparisons to ensure the zooplankton data they generate are comparable to other laboratories and over time. The Canary Islands Harmful Algal Observatory (OCHABs) from the University of Las Palmas de Gran Canaria (ULPGC; Spain), supported by the Intergovernmental Oceanographic Commission (IOC) of UNESCO Centre for Science and Communication of Harmful Algae (Denmark), operate the International Phytoplankton Intercomparison each year on the abundance and composition of marine phytoplankton in water samples. In some instances (e.g., for the identification of shellfish toxin producing phytoplankton species in Europe), laboratories working with statutory monitoring for the EU Shellfish Hygiene Directive have achieved ISO 17025 accreditation for this work (Botana, 2014).

3. Novel methods

Many major funding bodies have shifted towards new research priorities, which has been a key driver for technological advances in marine monitoring technology and has supported the development of more efficient, cost-effective and low-carbon methods to gather plankton data (Borja et al., 2024; Danovaro et al., 2016). For example, the UK Department for Environment, Food & Rural Affairs (Defra) now requires marine and fisheries R&D submission to include novel methods, and their Marine Natural Capital and Ecosystem Assessment (mNCEA) programme aims to deliver: "*innovation in evidence collection by testing the potential for earth observation, autonomous vehicles, new modelling techniques and collaboration with non-governmental organisations*" (Department for Environment Food & Rural Affairs, 2022). Currently there is an array of novel technologies available to identify and/or estimate the abundance or biomass of plankton, including automated imaging (Pitois et al., 2018) and molecular methods (Yates et al., 2019). These techniques take advantage of the latest imaging, sorting, genetic sequencing, and instrumentation technologies, and can provide far greater throughput of samples than could ever be achieved via standard monitoring methods (Lombard et al., 2019).

3.1. Automated imaging

Automated imaging describes the automatic collection, and storage of images. These images are usually subsequently processed using machine learning algorithms which attempt to classify them automatically. The process of image classification is sometimes referred to as "machine vision" or "computer vision" (Ciranni et al., 2024). Images can be collected from a diverse range of instruments (Fig. 3) mounted on research vessels, such as the Plankton Imager (Pi-10, Plankton Analytics), or from static (e.g., buoys), towed (e.g., towed vehicles), remotely operated (e.g., ROVs), or autonomous (e.g., AUVs, ocean gliders) platforms, as described in Lombard et al. (2019). Instruments such as the Imaging FlowCytobot (IFCB, McLane Labs) combine flow cytometry, video technology, and artificial intelligence to rapidly analyse phytoplankton samples (Olson et al., 2017) and can be deployed on moorings to provide high frequency (hours/minutes) time-series data, or on ships for sampling and identifications over wider areas. Automated imaging is also conducted *ex situ* from preserved net or bottle samples pumped through flow-through systems, such as the FlowCam (FlowCam, Yokogawa Fluid Imaging Technologies) (Owen et al., 2022), or poured onto plankton scanners, such as the ZooSCAN (Fig. 3) (ZooSCAN, Hydroptic) (Grandremy et al., 2023; Grosjean et al., 2004).

Fig. 3. Four examples of instruments currently used for automated imaging methods in plankton monitoring. The Plankton Imager (A) (Pi-10; Plankton Analytics), consists of a high-speed camera that images all passing particles in a flow of pumped seawater. Images are identified in real-time and uploaded via satellite. The ZooSCAN (B) (Hydroptic) uses a flatbed scanner with specialised lighting and a watertight scanning chamber to record high-resolution images of zooplankton samples. The Imaging FlowCytobot (C) (McLane Labs) is an automated submersible imaging flow cytometer that captures high-resolution images of a single-file flow of particles (triggered by fluorescence) *in situ*. FlowCam (D) is a flow imaging microscope that captures high-resolution images of microscopic particles as they pass through a flow chamber.

Plankton vary in size from the picometre range (i.e., picoplankton) up to metres for larger gelatinous zooplankton and exhibit extremely diverse behaviours, such as daily and seasonal vertical migration, feeding, reproductive, survival and escape strategies. As a result, no single instrument (either standard or novel) can effectively measure the entire plankton community. Since imaging instruments do not require filtration of a physical sample (e.g., unlike bottles or nets), phyto- and zooplankton are not measured as separate entities, but as a plankton fraction defined by size range. For example, the Imaging FlowCytobot, which operates by rapidly capturing images of individual cells as they flow in single file, is best suited to measuring particles <10–150 μm and is thus primarily suited for measuring phytoplankton. Other imaging instruments, like the Pi-10, are designed to accommodate larger particles within the 200 μm to 3.5 cm size range and are thus much better suited for measuring zooplankton. Others, such as FlowCam, cover the size range 2 μm to 1 mm, therefore, bridging both phyto- and zooplankton.

Automated imaging has received a high level of interest over the past decade and its use is rapidly shifting from experimental towards routine use (Kraft et al., 2022). A major advantage of automated imaging instruments is their ability to provide rapid and unbiased data that can be stored digitally and quickly made available for use (Giering et al., 2022), and without the need for preservatives, since samples can be analysed live. As access to high processing power is becoming more affordable,

real-time imaging, including classification and visualisation, is also becoming a real possibility with Edge computing (Schmid et al., 2023). Because imaging instruments enumerate delicate or gelatinous organisms which may be damaged or under-represented in nets, they allow powerful and complementary insights into pelagic food web structure (Lombard et al., 2019), and crucially, if multiple instruments are used they can bridge the size span between large protists and small metazoa that gets missed in the gap between bottle and net sampling (Atkinson et al., 2021). The ability of imaging instruments to measure size and other characteristics at very high spatiotemporal resolution also allow new insights into processes at the interface of ecology and biogeochemistry, and responses to short-term extreme events such as storms (Rühl and Möller, 2024). Many imaging instruments also have the advantage that they can operate autonomously from static platforms (Agarwal et al., 2023) or research vessels (Scott et al., 2021) as they conduct their regular operations, thus incurring no additional costs for vessel time. However, the benefits of such novel technologies do not come without costs. The rapid data collection at high resolution results in large quantities of images being collected (e.g., one terabyte of image data acquired from a one-month continuous survey; Scott et al., 2023) which may involve high performance computing and data storage costs. Potential cost savings are extremely system-specific and likely to change quickly in the near future.

While allowing for increased spatial and temporal resolution, automated imaging methods still rely on human experts to correctly label image training libraries containing thousands of images per class to support accurate classifications. These libraries take time to generate and are often location specific. Further, image classification algorithms can encounter difficulties in identifying specimens to genus or species level due to the often-subtle morphological differences between closely related taxa (Wilson et al., 2015), which in some cases require physical manipulation by technicians for accurate identification (Skreslet et al., 2000). During regular operation, classification algorithms will classify some images with a low confidence score, requiring manual validation from a trained taxonomic expert. Classification algorithms also still struggle to accurately enumerate single cells in a chain. However, capabilities continue to expand as new techniques emerge and the quality and quantity of training data improve.

3.2. Molecular methods

The development of molecular methods now used to identify plankton began in the 1970s (Woese and Fox, 1977). The simplest and oldest method uses the Polymerase Chain Reaction (PCR) to amplify a DNA marker; typically, the ribosomal DNA (rDNA) gene is used, but the cytochrome oxidase I (COI) gene is also commonly used for classifying animal species. COI and a variety of other markers are used for microbial species (Pawlowski et al., 2012). The PCR generates sequences, which can be compared against a reference library containing millions of other related sequences, with differences primarily reflecting the taxonomic relationships among them. Today there is an array of DNA detection methods currently available (reviewed by Goodwin et al., 2016); Here we specifically discuss those that are relevant or useful for marine plankton monitoring. Next generation metabarcoding or amplicon sequencing is now commonly used to identify all traces of plankton from the DNA contained within water or net samples (known as environmental DNA or eDNA). The power of metabarcoding is in its scalability: millions of DNA "reads" can be converted to amplicon sequence variants (ASVs), corresponding to specific taxa and improving our ability to detect historically poorly recorded or challenging species (Govindarajan et al., 2021; Scorzetti et al., 2009). Quantitative PCR (qPCR), also known as real-time PCR, can also be used to amplify a DNA sequence target and provide a concentration measurement for the gene target in a sample. This technique is used routinely to quantify a selection of target species (e.g., specific harmful algae taxa) at the species level (Pearson et al., 2021).

There is enormous potential in the use of molecular tools for plankton identification most recently by metabarcoding (Bucklin et al., 2022; Burki et al., 2021; Vernette et al., 2022) and for water quality monitoring (Yang et al., 2017). Molecular based surveys using universal single gene markers, like the 18S rDNA gene, tend to identify a different set of plankton taxa versus surveys that rely on microscopy based visual identification. One of the greatest advantages of molecular methods is that they can discover "hidden" diversity, since they can detect taxa that are rare, not obviously present (e.g. parasites), or morphologically identical (Lindeque et al., 2013). Where suitable DNA reference libraries exist, metabarcode sequencing can be useful for identifying rare, economically important, or invasive taxa, even at very low abundances. This is relevant for marine policy and management, because it can serve as an effective early warning tool for non-indigenous species or harmful algae (Govindarajan et al., 2021).

DNA-based metabarcoding and qPCR methods, almost universally used for taxa diversity/abundance surveys, cannot normally detect life stage or reproductive status. It is also currently not possible to determine body condition unless tracking a specific expressed gene. In addition, metabarcoding is not currently capable of quantitative accuracy, owing to non-linear intrinsic factors and methodological specificities (Yates et al., 2019). For the moment, molecular methods are better suited for the provision of presence/absence data. Yet, abundance and biomass data are much more informative for assessing plankton communities. Some studies of aquatic plankton have demonstrated promising relationships between abundance and gene copy number, for example, estimating zooplankton cell biovolume from eDNA (Song and Liang, 2023) and using 18S rDNA gene copy number to estimate biomass of common microbial eukaryotic taxa (Martin et al., 2022; Pitsch et al., 2019). Studies relating gene copy numbers to cell abundance and novel high-throughput methods to directly detect gene copy numbers, even within individual cells (Yarimizu et al., 2021), hold promise for the identification and quantification of taxa within plankton samples using molecular methods.

A central aim for many plankton taxonomists is to create "voucher" specimens with corresponding image and DNA sequence information to improve identification of microscopic organisms (Pawlowski et al., 2012). To achieve this, curated and accurate reference databases, standardised, accessible methodologies, and online collaborative computational tools are required, but not yet fully available. Jerney et al. (2023) estimated the cost of adding all phytoplankton species in the Baltic Sea to reference libraries to be over €1M. Fortunately, these issues have been acknowledged by the scientific community and the standardisation of DNA-based plankton monitoring is now progressing (Goodwin et al., 2016; Jerney et al., 2023; Medlin and Orozco, 2017; U. S. Integrated Ocean Observing System, 2017). Some monitoring programmes, including the CPR Survey, are now reanalysing archival plankton samples with molecular methods to assess changes in harmful algae (reviewed in Vezzulli et al., 2022). Several programmes also now monitor eDNA in parallel with ongoing standard monitoring (Fig. 2) in an attempt to harmonise methods and increase data diversity and quality. However, despite many marine monitoring stations now collecting eDNA samples alongside standard monitoring, eDNA-derived data have not yet been routinely used in assessments to inform marine policy, mostly due to not fitting current management requirements for standardised and validated quantitative taxonomic information.

In addition to issues with reference data libraries, the selection of PCR primer to generate metabarcode datasets can also greatly influence the level of insight available from molecular data. Unfortunately, there is no one-size-fits-all solution to molecular plankton monitoring, with zooplankton DNA metabarcoding lagging behind (Bucklin et al., 2022). In terms of accuracy, the commonly used rDNA marker performs satisfactorily across all taxa, but at the expense of species-specific detection. More specific markers can provide remarkably accurate surveys, but only for a limited set of taxa. These types or studies are less common due to the reduced availability of suitable reference libraries. Capabilities

are continuing to improve as new PacBio (Rhoads and Au, 2015) and Oxford Nanopore (Lu et al., 2016) sequencing technologies (Fig. 4) support longer sequences for breadth of taxa at the highest level of taxonomic detail (Santoferrara, 2019). In the case of metabarcoding approaches, it is widely recognised that intercomparison studies are needed (Bucklin et al., 2022). Caution in sample analysis is also required, including controls for false positives (e.g., detection of plankton from digested remains, lab-based contaminants), and community composition ratios.

In most cases molecular methods require the collection of physical samples prior to laboratory analysis (Song and Liang, 2023; Yates et al., 2019). However, miniaturised biosensors can detect and quantify a larger fixed set of species and their relative abundances (Medlin et al., 2020). These biosensors have been demonstrated from *in situ* platforms, such as the Environmental Sample Processor (Scholin et al., 2017), however, remote operation still requires significant resources. Development of automated nucleic acid samplers (e.g., the Robotic Cartridge Sampling Instrument (RoCSI; McLane Labs), the SEABER YUCO-eDNA (Aquatic Sensors) or Ascension eDNA sampling device (Ocean Diagnostics)) is anticipated to decrease the need for ship-based sampling (Mowlem et al., 2023). Similar to automated imaging, cost is extremely system-specific and likely to change quickly in the near future.

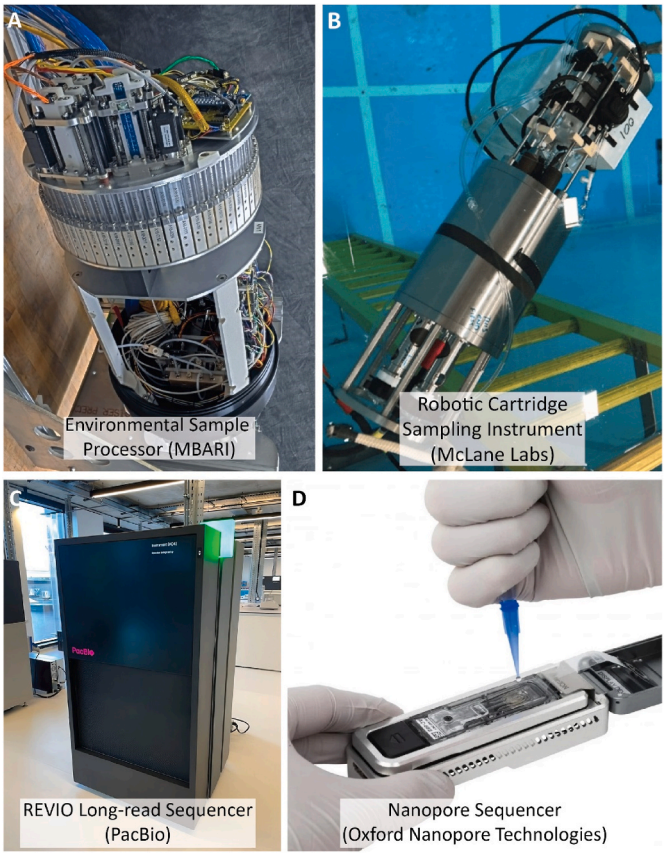

Fig. 4. Four examples of instruments currently used for molecular methods in plankton monitoring. The Environmental Sample Porcessor (A) (ESP; Monterey Bay Aquarium Research Institute) autonomously collects and filters water samples to be preserved or directly analysed with molecular methods in near real-time. The Robotic Cartridge Sampling Instrument (B) (RoCSI eDNA Sampler) is an *in situ* autonomous sampling instrument that collects and preserves water samples for later eDNA analysis. The Revio Long-read Sequencer (C) (PacBio) generates long, accurate DNA reads by observing the rate at which fluorescently labeled nucleotides are incorporated into the synthesis of new DNA strands. The Nanopore Sequencer (D) (Oxford Nanopore Technologies) enables real-time sequencing of long DNA fragments by measuring the variation in electrical current as these fragments pass individually through a tiny pore (2–3 nm).

4. Standard and novel methods operate at different scales

The different spatial and temporal scales at which standard and novel methods typically operate means that fundamentally different areas of science can be explored. Standard monitoring is usually conducted at weekly to monthly temporal resolution, and spatially at single stations, such as the Scottish Coastal Observatory monitoring sites, station clusters, such as in the Gulf of Finland (Uusitalo et al., 2013), or 10-nautical mile transects in the case of the CPR Survey (Richardson et al., 2006). Automated imaging approaches are operated at meters vertically and horizontally, or over minutes to hours, providing the fine resolution needed to address questions related to fine scale processes, such as plankton patchiness and distribution in the water column. However, most novel technologies have not been in routine use for long enough to build time-series with sufficient statistical power to resolve change at climate change-relevant scales (Ratnarajah et al., 2023). Moreover, the difference in scale at which standard and novel technologies operate makes intercalibration highly challenging. This fine level of spatial-temporal resolution is also generally not necessary for addressing current policy needs, though policy will likely shift in response to the level of detail available from future monitoring programmes.

Standard monitoring, automated imaging, and molecular methods differ in terms of spatial and temporal resolution, taxonomic specificity, and scalability. To maintain costs at reasonable levels, standard monitoring is typically restricted to routine sampling of large water volumes at a limited number of stations, or integrated over large distances (e.g., 10 nautical miles for the CPR Survey; Richardson et al., 2006). Costs also limit the frequency with which a site can be sampled, with most station time-series collecting samples at weekly or monthly resolution, although there are some exceptions (e.g., Helgoland Roads time-series; Dummermuth et al., 2023). The level of detail available from standard monitoring to resolve variation across short distances or time scales is therefore often limited. Molecular methods are subject to many of these same limitations, since molecular methods usually involve physical sample collection and subsequent land-based laboratory analysis. By contrast, probably the greatest fundamental advantage of automated imaging is the ability to rapidly collect large amounts of quantitative data that are highly resolved in both space and time (MacNeil et al., 2021).

With the exception of morphologically identical taxa, taxonomic specificity in standard monitoring is mainly limited by the quality of the preserved sample, the skills of the technicians responsible for processing samples and the time available for processing. Standard monitoring relies solely on morphological differences to differentiate related taxa, however, unlike other methods samples can often be physically manipulated by the technician to more clearly observe key identifying features (Skreslet et al., 2000). Physical manipulation is not typically available from automated imaging, and image classification algorithms still lag behind the best taxonomic technicians. Acquiring the skills to accurately classify samples often involves years of supervised training (Clayton et al., 2022). Taxonomic specificity of automated imaging is likely to improve with the development of more extensive image libraries and advancement of classification algorithms, considering the exponential pace of development in data analytics and artificial intelligence. Molecular methods can also deliver a very high taxonomic specificity, although this is dependent on the quality of available reference libraries.

In terms of initiating and scaling a plankton monitoring programme, automated methods requiring limited human intervention are likely to become more popular in the future (Borja et al., 2024; Danovaro et al., 2016), as technologies and methods are further refined. Instruments and technologies that can process and analyse samples *in situ* (e.g., FerryBox, ESP) or collect samples for downstream land-based processing (e.g., CPR

Survey, RoCSI), can offer significant cost-savings over dedicated ship-based surveys. In some cases, imaging and molecular instruments can be deployed without the need for experts on board. The initial cost of instruments and ongoing materials costs make novel methods less scalable than standard monitoring in their current form. This is likely to change in future as uptake increases and costs come down. At present, deployment of automated imaging systems may have a reduced carbon footprint compared to manned research vessel based surveys, but there is a downstream carbon footprint from data storage and real-time delivery to users – these aspects are likely to be part of ongoing discussions aimed at moving marine research towards net zero.

5. The risks associated with losing standard plankton monitoring time-series

As highlighted, standard and novel monitoring approaches present different advantages and costs, which positions their suitability to addressing different management needs (Fig. 5). One approach cannot replace the other. The higher capacity and finer scales of identifying and/or enumerating plankton associated with novel methods make them powerful tools for assessing biodiversity knowledge gaps and for understanding short-term responses to longer-term processes. This information complements standard monitoring methods and serves to improve our ability to understand biological responses to anthropogenic pressures and helps with planning mitigation actions. However, there are significant hurdles involved with operationalising any novel method into long-term practical routine monitoring with validation effort and investment being significant. These challenges need to be overcome before novel methods can demonstrate the consistent high-quality and comparable results of the standard monitoring methods which have been in use for the past century. Standard monitoring also remains the most accessible globally due to the relatively lower startup costs and training to start a monitoring programme and so remains the only option in many countries. Capacity development (training and technology itself) in the case of developing countries is a much bigger challenge for novel and often expensive technologies which will also delay their adoption. Novel methods operate on hardware and software technologies that will continue to be upgraded as improvements are made (e.g., faster processing, more efficient image capture, more accurate identifications). Upgrades in novel methods pose a challenge for maintaining a consistency of methods in long-term monitoring. These are aspects that need to be considered as novel methods become integrated into monitoring practices. Currently, most automated imaging and molecular methods have high initial outlays and maintenance costs, with significant resource and skills required to perform proper validation, which in some instances may take years. However, this is compensated for by a higher throughput of samples, albeit currently with a much higher cost for consumables.

One of the biggest challenges of long-term environmental research is maintaining adequate funding to continue operating (Vucetich et al., 2020). During the 1980s, 40% of the long-term oceanographic monitoring programmes initiated after World War II globally were terminated because administrators mistook them for poor science (Duarte and Cebrián, 1992; Richardson et al., 2006). In the 1980s the CPR Survey was almost lost due to funding constraints at a time when the North Sea was undergoing a regime shift that was first detected in the plankton (Beaugrand, 2009; Reid et al., 2016). Several CPR routes off the US east coast were also suspended. In the 2010s, again due to funding cuts, several CPR routes in the North-East Atlantic were cut, and around 25% of CPR taxonomists were lost in a restructure. Similarly in the US, funding was lost for two CPR routes, and the US CPR program was effectively shut down after many decades. Recent funding by the US has allowed these routes to restart. If the CPR Survey had not been saved, our current understanding of climate change and its impacts on marine biodiversity would be severely hampered (Beaugrand et al., 2019; Holland et al., 2023; McQuatters-Gollop et al., 2019). Several CPR routes have been temporarily reinstated through the UK Marine Natural Capital and Ecosystem Assessment (mNCEA) programme, however, future funding remains uncertain.

Multiple fixed-point stations are currently also in a precarious status. This includes all long-term zooplankton monitoring sites in the UK, through funding reductions or loss of taxonomic expertise; and an uncertain future for the time-series in the Dutch EEZ that were reported to OSPAR for the 2023 Quality Status Report (OSPAR, 2023). The Dutch time-series was established as part of OSPAR's eutrophication assessment concerning harmful algae blooms, which has now been discontinued as part of the suite of OSPAR eutrophication indicators. Currently, monitoring is limited to three Dutch coastal sites. While standard plankton monitoring in Dutch waters has been eroded, significant funding has been made available for exploration of novel techniques in the "Nature Strengthening and Species Protection Monitoring Survey" (MONS) programme under the Dutch North Sea Agreement (Overlegorgaan Fysieke Leefomgeving, 2020).

Many of the current plankton monitoring programmes throughout the North-East Atlantic and North-West European shelf waters have been ongoing since the 1970s to early 2000s, with the CPR commencing much earlier in 1931 (Stern et al., 2018). Similar to the international practice of standardising methods across fish trawl surveys conducted by different nations, the international plankton monitoring community also recognises the importance of intra-survey consistency in methods. Most programmes have employed the same sampling equipment and methods since they were initiated to maintain comparability along their time-series. Due to the highly variable and patchy distribution of plankton in both space and time, long-term monitoring is mandatory for detecting important changes. Hydrological processes, such as the Atlantic Multidecadal Oscillation (AMO) (Edwards et al., 2013) and

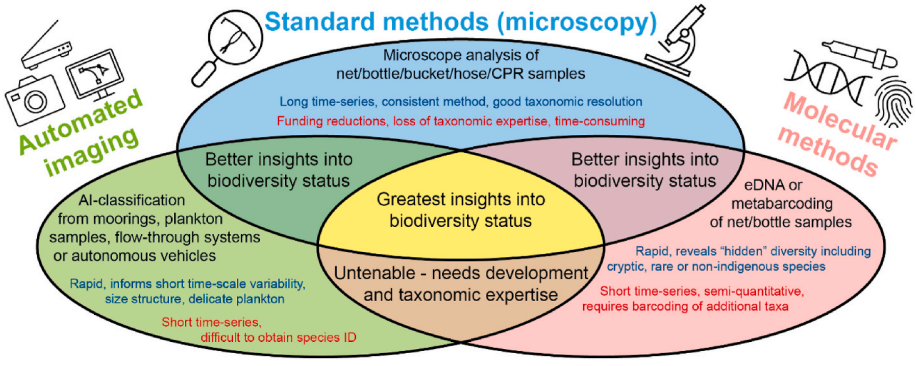

Fig. 5. Venn diagram summarising the scientific advantages (blue text) and limitations (red text) of the three methods described in this paper. Intersections describe the current issues and potential insights that can be gained through combinations of these methods. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

North Atlantic Oscillation (NAO) (Zhai et al., 2013) and associated changes to the sub-polar gyre index (Johnson et al., 2013), generate pressures on plankton communities lasting several decades. Changes in plankton communities resulting from direct human impacts can often be overshadowed by the variability attributed to these natural cyclical processes (Harris et al., 2014). Thus, long-term continuous data are necessary for detecting the effects of climate change, such as ocean acidification, shifting circulation patterns, and rising sea levels, to support sustainable use of marine resources. We also need to continuously maintain long-term time-series to understand ecological change since we can only detect change by comparing current conditions to previous conditions. Therefore, the value of a time-series for addressing ecological questions is inextricably linked to its consistency and duration (Edwards et al., 2010).

Research funding follows technological advances in automation and digitalisation, so funding is increasingly allocated to exploring novel and innovative methods and technologies, whilst there are decreasing routes to fund long-term initiatives (Vucetich et al., 2020). During the early 2000s, US National Science Foundation (NSF) funding for short-term ecological research increased by around 70%, while their funding for long-term research was reduced by approximately 60% (Vucetich et al., 2020). The UK Natural Environment Research Council (NERC) has declared a priority to reduce net emissions from climate-related science, including ocean observing, to help meet net zero goals (National Oceanography Centre, 2021; UK Research and Innovation, 2023). One of the ways they aim to achieve this is through promoting the use of uncrewed surface vehicles, which can monitor the ocean autonomously (Parker, 2021). The NERC Digital Strategy 2021–2030 prioritises the use of data from new technologies, including autonomous platforms, genomics, and eDNA incorporated into sensors; benthic crawlers; and animal borne sensors (National Oceanography Centre, 2023). Novel methods and associated monitoring datasets may also seem a preferred option to standard monitoring programmes due to limited funding, however, there are also significant hidden costs associated with the implementation, validation, and maintenance of novel methodology, as well as with the long-term storage and delivery of data acquired with novel methods.

The erosion of monitoring programme funding has also contributed to reducing taxonomic and ecological capability within the plankton research community (Rogers et al., 2022; Science and Technology Committee, 2008). With the current inability to recruit junior taxonomists, often driven by a lack of resources, those who remain have little time to develop their skill set to focus on emerging species of concern. Critical skills are also lost when experienced taxonomists leave their work area or retire (see McQuatters-Gollop et al., 2017). Although recent definitive data on the age of taxonomists are lacking, in the UK taxonomic experts are retiring and are not being replaced (Science and Technology Committee, 2008). Research roles of the future including those driving the development of novel techniques will require taxonomic skills just as much as previously; for example, to train artificial intelligence classification models, validate and interpret genetic databases, and perform validation between standard and novel methods. There needs to be a stronger recognition of the essential role that long-term time-series and taxonomic skills play in the development and incorporation of new technologies into biodiversity assessments. Maintaining standard long-term monitoring programmes will provide opportunities and incentives to promote training in taxonomy and will foster accelerated development of novel technology.

6. How novel technologies can complement standard monitoring

While imaging (Ostle and Hélaouët, 2023) and molecular (Suter et al., 2021) technologies lack the duration of use (Fig. 2) compared to standard plankton monitoring (Stern et al., 2018), some parallel datasets, such as Plymouth Marine Laboratory's Western Channel Observatory flow cytometry time-series, commencing in 2007, and eDNA time series starting in 2012 (McEvoy et al., 2023) are significantly longer, and can now support meaningful comparative and harmonisation efforts to complement standard approaches (Lombard et al., 2019; Ratnarajah et al., 2023). However, due to plankton's diverse range of sizes and patterns of distribution, there is no single universal method that can effectively sample the full plankton community, leading researchers to select the most appropriate method to fulfil particular research or policy aims (McQuatters-Gollop et al., 2024; Owens et al., 2013; Skjoldal et al., 2013; Suter et al., 2021). In some cases, novel technologies can provide efficient alternatives for addressing questions related to plankton distribution in space and time (Scott et al., 2021), targeted detection of harmful algal bloom species (Medlin and Orozco, 2017), new migrants or alien species (Créach et al., 2021), and identification of cryptic species which cannot be readily identified via standard methods (Goetze, 2003). Automated imaging also holds potential for sampling the currently under-surveyed large open ocean areas outside of national jurisdictions due to their ability to operate continuously from autonomous platforms (e.g., ocean gliders, buoys) (Ratnarajah et al., 2023). However, standard methods and associated skills remain critical to obtaining a detailed taxonomic accounting of the plankton community and validating novel methods. Most importantly, only standard methods have decades of associated historical data required to detect long-term ecological changes.

It is essential that we continue to optimise existing monitoring programmes, and this may mean pairing novel methods while maintaining the value of historical data and ensuring the continuity of valuable long-term time-series and retention of taxonomic skills (Benway et al., 2019). To achieve this, we make five recommendations (Fig. 6).

1. **Gradual integration and intercalibration:** We need to conduct parallel studies which apply novel methods alongside standard plankton monitoring to calibrate, align and verify novel data types against standard microscopy methods to ensure compatibility, consistency, and reliability. These studies need taxonomic experts at their core. Additionally, we need to prioritise combined studies that take advantage of the specific benefits of both standard (e.g., long-term perspective) and novel (e.g., higher temporal- or taxonomic resolution) data types.
2. **Rethink how we value and employ taxonomists:** The need for skilled taxonomists is increasing, rather than declining, since their skills underpin an expanding suite of sampling methods. We need a much wider realisation of this taxonomic need, at all levels spanning from funder to that of individual institutes. Much more resource is needed to invest in training current researchers in both taxonomy and in operating and interpreting data from novel methods and recognition of the value of their skillsets. This will help bridge the gap between traditional taxonomic skills and digital skills to improve the continuity of long-term monitoring.
3. **Incentivise open data practices:** Make data from both standard and novel methods more readily available for public use. The provision of such data needs to be better rewarded, for instance through improved data citation cultures and reward structures that are currently cantered on users rather than producers of data. This should incentivise rather than stipulate that data producers adopt FAIR (Findable, Accessible, Interoperable, Reusable; Wilkinson et al., 2016) principles. Address issues around reproducibility (e.g., container platforms; Perkel, 2019) and use of sensitive data.
4. **Improve communication:** Long-term research is increasingly underfunded and can be forced into competition with funding for new technology. The message that long-term time-series are valuable for climate change research is still not getting through, and we need to better communicate the value of long-term science to policy-makers, funders and the public, as well as establishing a better understanding of the true costs and benefits involved with the various standard and novel methods.

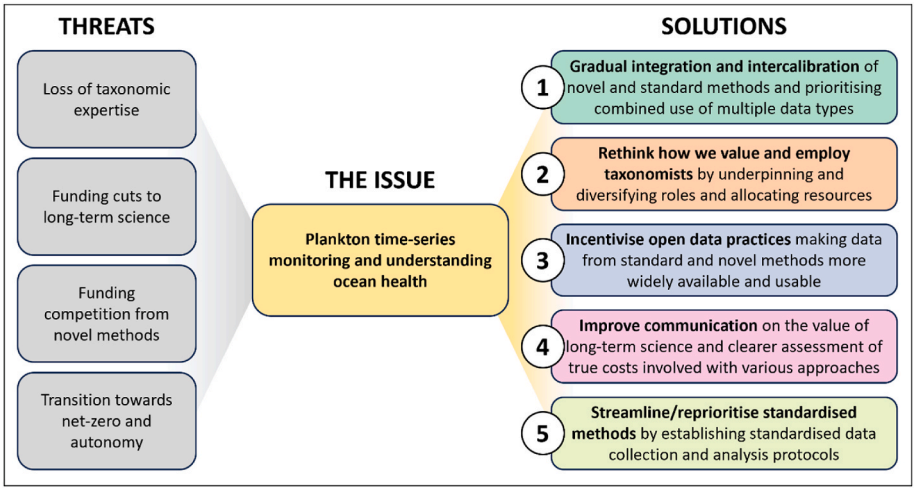

Fig. 6. Schematic outlining current threats to ongoing plankton time-series and our understanding of ocean health, as well as a set of recommendations elaborated in this paper on how to encourage greater adoption of novel methods into monitoring and better integration of these methods with long-term standard monitoring time-series.

5. **Streamline/reprioritise standardised methods:** We need to establish standardised data collection and analysis protocols that integrate standard and novel methods to ensure time-series remain comparable across sites and over time. Communication between laboratories can provide practical efficiency savings at both sample collection and analysis stages. Standardised methods will improve the comparability of novel datasets. This requires international cooperation and cost-benefit analysis to establish a set of best-practices.

In summary, we should continue to embrace novel technology, while also ensuring the continuity of standard monitoring time-series. We cannot simply switch from standard to novel methods since the continuity of long time-series remains critical to supporting biodiversity assessments (McQuatters-Gollop et al., 2019, 2022); however, it is imperative that pathways to incorporate these innovative techniques are soon established. This will require adequate funding, and a recognition of the time and resources needed for a proper validation of these techniques to integrate them into routine monitoring. Not only can novel methods complement conventional monitoring, but conventional monitoring and associated taxonomic expertise remain critical for informing and validating these methods. As technology continues to improve, it is possible in the decades to come that standard plankton monitoring will become less important (Giering et al., 2022), however, until this occurs, we must find ways to apply standard long-term and novel methods in a complementary manner to maintain taxonomic skills, facilitate ongoing scientific progress and inform decision making.

CRediT authorship contribution statement

Matthew M. Holland: Writing – review & editing, Writing – original draft, Project administration, Investigation, Conceptualization. **Luis Felipe Artigas:** Writing – review & editing. **Angus Atkinson:** Writing – review & editing, Writing – original draft, Conceptualization. **Mike Best:** Writing – review & editing, Writing – original draft, Project administration, Funding acquisition, Conceptualization. **Eileen Bresnan:** Writing – review & editing, Writing – original draft, Conceptualization. **Michelle Devlin:** Writing – review & editing, Writing – original draft, Conceptualization. **Dafne Eerkes-Medrano:** Writing – review & editing. **Marie Johansen:** Writing – review & editing. **David G. Johns:** Writing – review & editing, Writing – original draft, Conceptualization. **Margarita Machairopoulou:** Writing – review & editing, Writing – original draft, Conceptualization. **Sophie Pitois:** Writing – review & editing, Writing – original draft, Conceptualization. **James Scott:** Writing – review & editing, Writing – original draft, Conceptualization. **Jos Schilder:** Writing – review & editing. **Rowena Stern:** Writing – review & editing, Writing – original draft, Conceptualization. **Karen Tait:** Writing – review & editing. **Callum Whyte:** Writing – review & editing. **Claire Widdicombe:** Writing – review & editing. **Abigail McQuatters-Gollop:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

References

Agarwal, V., Chávez-Casillas, J., Mouw, C.B., 2023. Sub-monthly prediction of harmful algal blooms based on automated cell imaging. Harmful Algae 122, 102386.
Atkinson, A., Lilley, M.K., Hirst, A.G., McEvoy, A.J., Tarran, G.A., Widdicombe, C., Fileman, E.S., Woodward, E.M.S., Schmidt, K., Smyth, T.J., 2021. Increasing nutrient stress reduces the efficiency of energy transfer through planktonic size spectra. Limnol. Oceanogr. 66 (2), 422–437.
Batten, S.D., Abu-Alhaija, R., Chiba, S., Edwards, M., Graham, G., Jyothibabu, R., Kitchener, J.A., Koubbi, P., McQuatters-Gollop, A., Muxagata, E., 2019. A global plankton diversity monitoring program. Front. Mar. Sci. 6, 321.
Beaugrand, G., 2009. Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. Deep Sea Res. Part II Top. Stud. Oceanogr. 56 (8–10), 656–673.

Beaugrand, G., Edwards, M., Hélaouët, P., 2019. An ecological partition of the Atlantic Ocean and its adjacent seas. Prog. Oceanogr. 173, 86–102.
Bedford, J., Ostle, C., Johns, D.G., Atkinson, A., Best, M., Bresnan, E., Machairopoulou, M., Graves, C.A., Devlin, M., Milligan, A., 2020. Lifeform indicators reveal large-scale shifts in plankton across the North-West European shelf. Global Change Biol. 26 (6), 3482–3497.
Benway, H.M., Lorenzoni, L., White, A.E., Fiedler, B., Levine, N.M., Nicholson, D.P., DeGrandpre, M.D., Sosik, H.M., Church, M.J., O'brien, T.D., 2019. Ocean time series observations of changing marine ecosystems: an era of integration, synthesis, and societal applications. Front. Mar. Sci. 6, 393.
Borja, A., Berg, T., Gundersen, H., Hagen, A.G., Hancke, K., Korpinen, S., Leal, M.C., Luisetti, T., Menchaca, I., Murray, C., 2024. Innovative and practical tools for monitoring and assessing biodiversity status and impacts of multiple human pressures in marine systems. Environ. Monit. Assess. 196 (8), 694.
Botana, L.M., 2014. Guide to phycotoxin monitoring of bivalve mollusk-harvesting areas. Seafood and Freshwater Toxins: Pharmacology, Physiology and Detection, third ed. CRC Press, Taylor and Francis, New York (NY), pp. 39–56.
Bresnan, E., Cook, K., Hindson, J., Hughes, S., Lacaze, J., Walsham, P., Turrell, W., 2016. The scottish coastal observatory 1997–2013: Part 1—executive summary. Scottish Marine and Freshwater Science 7 (16), 1881, 1881.
Brosnahan, M.L., Ralston, D.K., Fischer, A.D., Solow, A.R., Anderson, D.M., 2017. Bloom termination of the toxic dinoflagellate *Alexandrium catenella*: vertical migration behavior, sediment infiltration, and benthic cyst yield. Limnol. Oceanogr. 62 (6), 2829–2849.
Bucklin, A., Batta-Lona, P.G., Questel, J.M., Wiebe, P.H., Richardson, D.E., Copley, N.J., O'Brien, T.D., 2022. COI metabarcoding of zooplankton species diversity for time-series monitoring of the NW atlantic continental shelf. Front. Mar. Sci. 9, 867893.
Bucklin, A., Kann, L., 1991. Mitochondrial DNA variation of copepods: markers of species identity and population differentiation in Calanus. Biol. Bull. 181 (2), 357, 357.
Burki, F., Sandin, M.M., Jamy, M., 2021. Diversity and ecology of protists revealed by metabarcoding. Curr. Biol. 31 (19), R1267–R1280.
CEC, 2006. Council Directive 2006/113/EC of 12 December 2006 on the quality required of shellfish waters (codified version). Off. J. Eur. Union 376, 14–20.
Cetinić, I., Rousseaux, C.S., Carroll, I.T., Chase, A.P., Kramer, S.J., Werdell, P.J., Siegel, D.A., Dierssen, H.M., Catlett, D., Neeley, A., 2024. Phytoplankton composition from sPACE: requirements, opportunities, and challenges. Rem. Sens. Environ. 302, 113964.
Ciranni, M., Murino, V., Odone, F., Pastore, V.P., 2024. Computer vision and deep learning meet plankton: milestones and future directions. Image Vis Comput., 104934
Clayton, S., Gibala-Smith, L., Mogatas, K., Flores-Vargas, C., Marciniak, K., Wigginton, M., Mulholland, M.R., 2022. Imaging technologies build capacity and accessibility in phytoplankton species identification expertise for research and monitoring: lessons learned during the COVID-19 pandemic. Front. Microbiol. 13, 823109.
Créach, V., Derveaux, S., Owen, K.R., Pitois, S., Antajan, E., 2021. Use of environmental DNA in early detection of *Mnemiopsis leidyi* in UK coastal waters. Biol. Invasions 1–10.
Daewel, U., Akhtar, N., Christiansen, N., Schrum, C., 2022. Offshore wind farms are projected to impact primary production and bottom water deoxygenation in the North Sea. Communications Earth & Environment 3 (1), 292.
Danovaro, R., Carugati, L., Berzano, M., Cahill, A.E., Carvalho, S., Chenuil, A., Corinaldesi, C., Cristina, S., David, R., Dell'Anno, A., 2016. Implementing and innovating marine monitoring approaches for assessing marine environmental status. Front. Mar. Sci. 3, 213.
Department for Environment Food & Rural Affairs, 2022. Policy paper, natural capital and ecosystem assessment programme. Updated 5 October 2022. https://www.gov.uk/government/publications/natural-capital-and-ecosystem-assessment-programme/natural-capital-and-ecosystem-assessment-programme.
Devlin, M., Best, M., Coates, D., Bresnan, E., O'Boyle, S., Park, R., Silke, J., Cusack, C., Skeats, J., 2007. Establishing boundary classes for the classification of UK marine waters using phytoplankton communities. Mar. Pollut. Bull. 55 (1–6), 91–103.
Doucette, G.J., Medlin, L.K., McCarron, P., Hess, P., 2018. Detection and surveillance of harmful algal bloom species and toxins. Harmful Algal Blooms: A Compendium Desk Reference 39–114.
Duarte, C.M., Cebrián, J., 1992. Uncertainty of detecting sea change. Nature 356 (6366).
Dummermuth, A., Wiltshire, K.H., Kirstein, I., Brodte, E.-M., Wichels, A., Shama, L., Bergmann, A., Hofmann, C., Fischer, P., Mölter, K., 2023. Marine stations Helgoland and sylt operated by the alfred wegener institute helmholtz Centre for polar and marine research. Journal of large-scale research facilities JLSRF 8 (1).
Edler, L., Elbrächter, M., 2010. The Utermöhl method for quantitative phytoplankton analysis. Microscopic and molecular methods for quantitative phytoplankton analysis 110, 13–20.
Edwards, M., Beaugrand, G., Hays, G.C., Koslow, J.A., Richardson, A.J., 2010. Multi-decadal oceanic ecological datasets and their application in marine policy and management. Trends Ecol. Evol. 25 (10), 602–610.
Edwards, M., Beaugrand, G., Helaouët, P., Alheit, J., Coombs, S., 2013. Marine ecosystem response to the atlantic multidecadal oscillation. PLoS One 8 (2), e57212.
Edwards, M., Beaugrand, G., Kléparski, L., Hélaouët, P., Reid, P.C., 2022. Climate variability and multi-decadal diatom abundance in the Northeast Atlantic. Communications Earth & Environment 3 (1), 1–8.
Estes, M., Muller-Karger, F., Forsberg, K., Leinen, M., Kholeif, S., Turner, W., Cripe, D., Gevorgyan, Y., Fietzek, P., Canonico, G., 2021. Integrating biology into Ocean Observing infrastructure. Oceanography 34 (4), 36–43.
European Commission, 2019. Regulation of the European Commission of 15 March 2019 laying down uniform practical arrangements for the performance of official controls on products of animal origin intended for human consumption in accordance with Regulation (EU) 2017/625 of the European Parliament and of the Council and amending Commission Regulation (EC) No 2074/2005 as regards official controls. Off. J. Eur. Union L 131–151.
European Commission, 2022. MSFD CIS Guidance Document No. 19. *Article 8 MSFD*.
First, M.R., Drake, L.A., 2012. Performance of the human "counting machine": evaluation of manual microscopy for enumerating plankton. J. Plankton Res. 34 (12), 1028–1041.
Fraga, S., Sampedro, N., Larsen, J., Moestrup, Ø., Calado, A.J., 2015. Arguments against the Proposal 2302 by John & Al. To Reject the Name Gonyaulax Catenella (Alexandrium Catenella). Centro Oceanográfico de Vigo.
Gaonkar, C.C., Piredda, R., Sarno, D., Zingone, A., Montresor, M., Kooistra, W.H., 2020. Species detection and delineation in the marine planktonic diatoms Chaetoceros and Bacteriastrum through metabarcoding: making biological sense of haplotype diversity. Environ. Microbiol. 22 (5), 1917–1929.
Giering, S.L., Culverhouse, P.F., Johns, D.G., McQuatters-Gollop, A., Pitois, S.G., 2022. Are plankton nets a thing of the past? An assessment of in situ imaging of zooplankton for large-scale ecosystem assessment and policy decision-making. Front. Mar. Sci. 9, 986206.
Gjerde, K.M., Clark, N.A., Chazot, C., Cremers, K., Harden-Davies, H., Kachelriess, D., Payne, C.R., Rodriguez-Chaves, M., Spadone, A., Thiele, T., 2022. Getting beyond yes: fast-tracking implementation of the United Nations agreement for marine biodiversity beyond national jurisdiction. npj Ocean sustainability 1 (1), 6.
Goetze, E., 2003. Cryptic speciation on the high seas; global phylogenetics of the copepod family Eucalanidae. Proc. Roy. Soc. Lond. B Biol. Sci. 270 (1531), 2321–2331.
Goodwin, S., McPherson, J.D., McCombie, W.R., 2016. Coming of age: ten years of next-generation sequencing technologies. Nat. Rev. Genet. 17 (6), 333–351.
Gorsky, G., Aldorf, C., Kage, M., Picheral, M., Garcia, Y., Favole, J., 1992. Vertical distribution of suspended aggregates determined by a new underwater video profiler: Annales de lInstitut océanographique, vol. 68.
Govindarajan, A.F., Francolini, R.D., Jech, J.M., Lavery, A.C., Llopiz, J.K., Wiebe, P.H., Zhang, W., 2021. Exploring the use of environmental DNA (eDNA) to detect animal taxa in the mesopelagic zone. Frontiers in Ecology and Evolution 9, 574877.
Grandremy, N., Dupuy, C., Petitgas, P., Mestre, S.L., Bourriau, P., Nowaczyk, A., Forest, B., Romagnan, J.B., 2023. The ZooScan and the ZooCAM zooplankton imaging systems are intercomparable: a benchmark on the Bay of Biscay zooplankton. Limnol Oceanogr. Methods 21 (11), 718–733.
Graves, C., Best, M., Atkinson, A., Bear, B., Bresnan, E., Holland, M., Johns, D., Machairopoulou, M., McQuatters-Gollop, A., Mellor, A., 2023. At what scale should we assess the health of pelagic habitats? Trade-offs between small-scale manageable pressures and the need for regional upscaling. Ecol. Indicat. 154, 110571.
Grosjean, P., Picheral, M., Warembourg, C., Gorsky, G., 2004. Enumeration, measurement, and identification of net zooplankton samples using the ZOOSCAN digital imaging system. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 61 (4), 518–525.
Harris, R., 2010. The L4 time-series: the first 20 years. J. Plankton Res. 32 (5), 577–583.
Harris, V., Edwards, M., Olhede, S.C., 2014. Multidecadal Atlantic climate variability and its impact on marine pelagic communities. J. Mar. Syst. 133, 55–69.
Hélaouët, P., Beaugrand, G., Reygondeau, G., 2016. Reliability of spatial and temporal patterns of C. finmarchicus inferred from the CPR survey. J. Mar. Syst. 153, 18–24.
Hering, D., Schürings, C., Wenskus, F., Blackstock, K., Borja, A., Birk, S., Bullock, C., Carvalho, L., Dagher-Kharrat, M.B., Lakner, S., 2023. Securing success for the nature restoration law. Science 382 (6676), 1248–1250.
Herman, A.W., 1992. Design and calibration of a new optical plankton counter capable of sizing small zooplankton. Deep-Sea Res., Part A 39 (3–4), 395–415.
Holland, M.M., Louchart, A., Artigas, L.F., Ostle, C., Atkinson, A., Rombouts, I., Graves, C.A., Devlin, M., Heyden, B., Machairopoulou, M., Bresnan, E., Schilder, J., Jakobsen, H.H., Lloyd-Hartley, H., Tett, P., Best, M., Goberville, E., McQuatters-Gollop, A., 2023. Major declines in NE Atlantic plankton contrast with more stable populations in the rapidly warming North Sea. Sci. Total Environ., 165505 https://doi.org/10.1016/j.scitotenv.2023.165505.
Hoppenrath, M., 2017. Dinoflagellate taxonomy—a review and proposal of a revised classification. Mar. Biodivers. 47 (2), 381–403.
Hosia, A., Falkenhaug, T., Baxter, E.J., Pagès, F., 2017. Abundance, distribution and diversity of gelatinous predators along the northern Mid-Atlantic Ridge: a comparison of different sampling methodologies. PLoS One 12 (11), e0187491.
International Group for Marine Ecological Time Series, 2024. Analysis and Synthesis of Global Marine Ecological Changes as Seen through Biogeochemical and Plankton Time Series. IOC-UNESCO. Retrieved November 2024 from. https://igmets.net/metabase.
Jerney, J., Hällfors, H., Jakobsen, H., Jurgensone, I., Karlson, B., Kremp, A., Lehtinen, S., Majaneva, M., Meissner, K., Norros, V., 2023. DNA Metabarcoding: Guidelines to Monitor Phytoplankton Diversity and Distribution in Marine and Brackish Waters. Nordic Council of Ministers.
John, U., Litaker, W., Montresor, M., Murray, S., Brosnahan, M.L., Anderson, D.M., 2014. (2302) Proposal to reject the name Gonyaulax catenella (Alexandrium catenella) (Dinophyceae). Taxon 63 (4), 932.
Johnson, C., Inall, M., Häkkinen, S., 2013. Declining nutrient concentrations in the northeast Atlantic as a result of a weakening Subpolar Gyre. Deep Sea Res. Oceanogr. Res. Pap. 82, 95–107.
Khan, R.M., Salehi, B., Mahdianpari, M., Mohammadimanesh, F., Mountrakis, G., Quackenbush, L.J., 2021. A meta-analysis on harmful algal bloom (HAB) detection and monitoring: a remote sensing perspective. Rem. Sens. 13 (21), 4347.
Kraft, K., Velhonoja, O., Eerola, T., Suikkanen, S., Tamminen, T., Haraguchi, L., Ylöstalo, P., Kielosto, S., Johansson, M., Lensu, L., 2022. Towards operational

phytoplankton recognition with automated high-throughput imaging, near-real-time data processing, and convolutional neural networks. Front. Mar. Sci. 9, 867695.
Lemoine, M., Claquin, P., 2021. PHYTOBS. French National Service of Observation Program for Phytoplankton in Coastal Waters. The 9th EuroGOOS International Conference 2021. 3–5 May 2021, Brussels, Belgium.
Lindeque, P.K., Parry, H.E., Harmer, R.A., Somerfield, P.J., Atkinson, A., 2013. Next generation sequencing reveals the hidden diversity of zooplankton assemblages. PLoS One 8 (11), e81327.
Lombard, F., Boss, E., Waite, A.M., Vogt, M., Uitz, J., Stemmann, L., Sosik, H.M., Schulz, J., Romagnan, J.-B., Picheral, M., 2019. Globally consistent quantitative observations of planktonic ecosystems. Front. Mar. Sci. 6, 196.
Lu, H., Giordano, F., Ning, Z., 2016. Oxford Nanopore MinION sequencing and genome assembly. Dev. Reprod. Biol. 14 (5), 265–279.
Lundsør, E., Eikrem, W., Stige, L.C., Engesmo, A., Stadniczeñko, S.G., Edvardsen, B., 2022. Changes in phytoplankton community structure over a century in relation to environmental factors. J. Plankton Res. 44 (6), 854–871.
MacNeil, L., Missan, S., Luo, J., Trappenberg, T., LaRoche, J., 2021. Plankton classification with high-throughput submersible holographic microscopy and transfer learning. BMC Ecology and Evolution 21 (1), 123.
Magliozzi, C., Druon, J.-N., Palialexis, A., Artigas, L., Boicenco, L., González-Quirós, R., Gorokhova, E., Heyden, B., McQuatters-Gollop, A., Varkitzi, I., 2021. Pelagic Habitats under MSFD D1: Current Approaches and Priorities: an Overview of Approaches towards D1C6 Assessment.
Martin, J.L., Santi, I., Pitta, P., John, U., Gypens, N., 2022. Towards quantitative metabarcoding of eukaryotic plankton: an approach to improve 18S rRNA gene copy number bias. Metabarcoding and Metagenomics, 6, e85794.
McEvoy, A.J., Atkinson, A., Airs, R.L., Brittain, R., Brown, I., Fileman, E.S., Findlay, H.S., McNeill, C.L., Ostle, C., Smyth, T.J., Somerfield, P.J., Tait, K., Tarran, G.A., Thomas, S., Widdicombe, C., Woodward, M., Beesley, A., Conway, D.V.P., Fishwick, J., Widdicombe, S., 2023. The Western Channel Observatory: a century of physical, chemical and biological data compiled from pelagic and benthic habitats in the Western English Channel. Earth Syst. Sci. Data 2023, 1–42.
McQuatters-Gollop, A., Atkinson, A., Aubert, A., Bedford, J., Best, M., Bresnan, E., Cook, K., Devlin, M., Gowen, R., Johns, D.G., 2019. Plankton lifeforms as a biodiversity indicator for regional-scale assessment of pelagic habitats for policy. Ecol. Indicat. 101, 913–925.
McQuatters-Gollop, A., Edwards, M., Helaouët, P., Johns, D.G., Owens, N.J., Raitsos, D. E., Schroeder, D., Skinner, J., Stern, R.F., 2015. The Continuous Plankton Recorder survey: how can long-term phytoplankton datasets contribute to the assessment of Good Environmental Status? Estuar. Coast Shelf Sci. 162, 88–97.
McQuatters-Gollop, A., Guérin, L., Arroyo, N.L., Aubert, A., Artigas, L.F., Bedford, J., Corcoran, E., Dierschke, V., Elliott, S.A.M., Geelhoed, S.C.V., Gilles, A., González-Irusta, J.M., Haelters, J., Johansen, M.F., Lynam, C.P., Niquil, N., Meakins, B., Mitchell, I., Vina-Herbon, C., 2022. Assessing the state of marine biodiversity in the Northeast Atlantic. Ecol. Indicat. 141, 109148. https://doi.org/10.1016/j.ecolind.2022.109148.
McQuatters-Gollop, A., Johns, D.G., Bresnan, E., Skinner, J., Rombouts, I., Stern, R., Aubert, A., Johansen, M., Bedford, J., Knights, A., 2017. From microscope to management: the critical value of plankton taxonomy to marine policy and biodiversity conservation. Mar. Pol. 83, 1–10.
McQuatters-Gollop, A., Stern, R.F., Atkinson, A., Best, M., Bresnan, E., Creach, V., Devlin, M., Holland, M., Ostle, C., Schmidt, K., 2024. The silent majority: pico-and nanoplankton as ecosystem health indicators for marine policy. Ecol. Indicat. 159, 111650.
Medlin, L.K., Gamella, M., Mengs, G., Serafín, V., Campuzano, S., Pingarrón, J.M., 2020. Advances in the detection of toxic algae using electrochemical biosensors. Biosensors 10 (12), 207.
Medlin, L.K., Orozco, J., 2017. Molecular techniques for the detection of organisms in aquatic environments, with emphasis on harmful algal bloom species. Sensors 17 (5), 1184.
Mieruch, S., Freund, J., Feudel, U., Boersma, M., Janisch, S., Wiltshire, K.H., 2010. A new method of describing phytoplankton blooms: examples from Helgoland Roads. J. Mar. Syst. 79 (1–2), 36–43.
Mowlem, M., Carvalho, F., Hanz, R., Abdi, E., Catalano, C., Mougiou, K.H., Abualhaija, R., Evans, S., Hayes, D., Alrefaey, A., 2023. Technologies for Ocean Sensing project developments in imaging and sensing. OCEANS 2023-Limerick, IEEE.
National Oceanography Centre, 2021. NZOC: net zero oceanographic capability summary Report. https://noc.ac.uk/facilities/ships/net-zero-oceanographic-capability.
National Oceanography Centre, 2023. UK sustained scientific observation priorities (SSOOP). https://ocean-observations.uk/sites/oc-obs-rev/files/documents/COMMS1358%20SSOOP%20REPORT%20V13.pdf.
O'Brien, T.D., Li, W.K., Morán, X.A.G., 2012. ICES Phytoplankton and Microbial Plankton Status Report 2009/2010.
O'Brien, T.D., 2017. What Are Marine Ecological Time Series Telling Us about the Ocean? A Status Report.
Olson, R.J., Shalapyonok, A., Kalb, D.J., Graves, S.W., Sosik, H.M., 2017. Imaging FlowCytobot modified for high throughput by in-line acoustic focusing of sample particles. Limnol Oceanogr. Methods 15 (10), 867–874.
OSPAR, 2023. Pelagic Habitat Thematic Assessment (The 2023 Quality Status Report for the Northeast Atlantic. Issue. https://oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023/thematic-assessments/pelagic-habitats/.
Ostle, C., Hélaouët, P., 2023. The Continuous Plankton Recorder as a platform for sensor development. PICES Press 31 (2), 64–65.
Overlegorgaan Fysieke Leefomgeving, 2020. The North Sea Agreement. https://www.noordzeeloket.nl/publish/pages/184533/the_north_sea_agreement.pdf.
Owen, B.M., Hallett, C.S., Cosgrove, J.J., Tweedley, J.R., Moheimani, N.R., 2022. Reporting of methods for automated devices: a systematic review and recommendation for studies using FlowCam for phytoplankton. Limnol Oceanogr. Methods 20 (7), 400–427.
Owens, N., Hosie, G., Batten, S., Edwards, M., Johns, D., Beaugrand, G., 2013. All plankton sampling systems underestimate abundance: response to "Continuous plankton recorder underestimates zooplankton abundance" by JW Dippner and M. Krause. J. Mar. Syst. 128, 240–242.
Parker, J., 2021. The future of the UK national monitoring fleet capability. Cefas Project Report for National Oceanography Centre.
Pawlowski, J., Audic, S., Adl, S., Bass, D., Belbahri, L., Berney, C., Bowser, S.S., Cepicka, I., Decelle, J., Dunthorn, M., 2012. CBOL protist working group: barcoding eukaryotic richness beyond the animal, plant, and fungal kingdoms. PLoS Biol. 10 (11), e1001419.
Pearson, L.A., D'Agostino, P.M., Neilan, B.A., 2021. Recent developments in quantitative PCR for monitoring harmful marine microalgae. Harmful Algae 108, 102096.
Perkel, J.M., 2019. Make code accessible with these cloud services. Nature 575 (7781), 247–249.
Petersen, W., Colijn, F., Hydes, D., Schroeder, F., 2007. FerryBox: from On-Line Oceanographic Observations to Environmental Information. EU Project FerryBox, pp. 2002–2005.
Pitois, S.G., Tilbury, J., Bouch, P., Close, H., Barnett, S., Culverhouse, P.F., 2018. Comparison of a cost-effective integrated plankton sampling and imaging instrument with traditional systems for mesozooplankton sampling in the Celtic Sea. Front. Mar. Sci. 5, 5.
Pitsch, G., Bruni, E.P., Forster, D., Qu, Z., Sonntag, B., Stoeck, T., Posch, T., 2019. Seasonality of planktonic freshwater ciliates: are analyses based on V9 regions of the 18S rRNA gene correlated with morphospecies counts? Front. Microbiol. 10, 248.
Qin, H., Li, S., Li, D., 2013. An improved method for determining phytoplankton chlorophyll a concentration without filtration. Hydrobiologia 707, 81–95.
Ratnarajah, L., Abu-Alhaija, R., Atkinson, A., Batten, S., Bax, N.J., Bernard, K.S., Canonico, G., Cornils, A., Everett, J.D., Grigoratou, M., 2023. Monitoring and modelling marine zooplankton in a changing climate. Nat. Commun. 14 (1), 564.
Reid, P.C., Hari, R.E., Beaugrand, G., Livingstone, D.M., Marty, C., Straile, D., Barichivich, J., Goberville, E., Adrian, R., Aono, Y., 2016. Global impacts of the 1980s regime shift. Global Change Biol. 22 (2), 682–703.
Rhoads, A., Au, K.F., 2015. PacBio sequencing and its applications. Dev. Reprod. Biol. 13 (5), 278–289.
Riccardi, N., 2010. Selectivity of plankton nets over mesozooplankton taxa: implications for abundance, biomass and diversity estimation. J. Limnol. 69 (2), 287.
Richardson, A., Walne, A., John, A., Jonas, T., Lindley, J., Sims, D., Stevens, D., Witt, M., 2006. Using continuous plankton recorder data. Prog. Oceanogr. 68 (1), 27–74.
Rogers, A.D., Appeltans, W., Assis, J., Ballance, L.T., Cury, P., Duarte, C., Favoretto, F., Hynes, L.A., Kumagai, J.A., Lovelock, C.E., 2022. Discovering marine biodiversity in the 21st century. Adv. Mar. Biol. 93, 23–115.
Ruddick, K., Lacroix, G., Park, Y., Rousseau, V., De Cauwer, V., Debruyn, W., Sterckx, S., 2003. Overview of Ocean Colour: Theoretical Background, Sensors and Applicability for the De-tection and Monitoring of Harmful Algae Blooms (Capabilities and Limitations).
Rühl, S., Möller, K.O., 2024. Storm events alter marine snow fluxes in stratified marine environments. Estuar. Coast Shelf Sci. 302, 108767.
Russo, L., Murano, C., D'Alelio, D., 2024. Mapping Topic Evolution across the 40-Year-Old Long-Term Ecological Research MareChiara Site in the Gulf of Naples, Italy. Oceans. MDPI.
Santoferrara, L.F., 2019. Current practice in plankton metabarcoding: optimization and error management. J. Plankton Res. 41 (5), 571–582.
Schmid, M.S., Daprano, D., Damle, M.M., Sullivan, C.M., Sponaugle, S., Cousin, C., Guigand, C., Cowen, R.K., 2023. Edge computing at sea: high-throughput classification of in-situ plankton imagery for adaptive sampling. Front. Mar. Sci. 10, 1187771.
Schmidt, K., Birchill, A.J., Atkinson, A., Brewin, R.J., Clark, J.R., Hickman, A.E., Johns, D.G., Lohan, M.C., Milne, A., Pardo, S., 2020. Increasing picocyanobacteria success in shelf waters contributes to long-term food web degradation. Global Change Biol. 26 (10), 5574–5587.
Scholin, C.A., Birch, J., Jensen, S., Marin III, R., Massion, E., Pargett, D., Preston, C., Roman, B., Ussler, I.I.I.W., 2017. The quest to develop ecogenomic sensors: a 25-year history of the Environmental Sample Processor (ESP) as a case study. Oceanography 30 (4), 100–113.
Science and Technology Committee, 2008. Systematics and taxonomy: follow-up. House of Lords. https://publications.parliament.uk/pa/ld200708/ldselect/ldsctech/162/162.pdf.
Scorzetti, G., Brand, L., Hitchcock, G., Rein, K., Sinigalliano, C., Fell, J., 2009. Multiple simultaneous detection of Harmful Algal Blooms (HABs) through a high throughput bead array technology, with potential use in phytoplankton community analysis. Harmful Algae 8 (2), 196–211.
Scott, J., Pitois, S., Close, H., Almeida, N., Culverhouse, P., Tilbury, J., Malin, G., 2021. In situ automated imaging, using the Plankton Imager, captures temporal variations in mesozooplankton using the Celtic Sea as a case study. J. Plankton Res. 43 (2), 300–313.
Scott, J., Pitois, S., Creach, V., Malin, G., Culverhouse, P., Tilbury, J., 2023. Resolution changes relationships: optimizing sampling design using small scale zooplankton data. Prog. Oceanogr. 210, 102946.

Sieracki, M.E., Benfield, M., Hanson, A., Davis, C., Pilskaln, C.H., Checkley, D., Sosik, H. M., Ashjian, C., Culverhouse, P., Cowen, R., 2010. Optical plankton imaging and analysis systems for ocean observation. Proc. Ocean Obs 9, 21–25.
Skjoldal, H.R., Wiebe, P.H., Postel, L., Knutsen, T., Kaartvedt, S., Sameoto, D.D., 2013. Intercomparison of zooplankton (net) sampling systems: results from the ICES/GLOBEC sea-going workshop. Prog. Oceanogr. 108, 1–42.
Skreslet, S., Olsen, K., Mohus, Å., Tande, K., 2000. Stage-specific habitats of *Calanus finmarchicus* and *Calanus helgolandicus* in a stratified northern Norwegian fjord. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 57 (6), 1656–1663.
Smith, R., Baker, K., 1982. Oceanic chlorophyll concentrations as determined by satellite (Nimbus-7 coastal zone color scanner). Mar. Biol. 66, 269–279.
Song, J., Liang, D., 2023. Community structure of zooplankton and its response to aquatic environmental changes based on eDNA metabarcoding. J. Hydrol. 622, 129692.
Stern, R., Kraberg, A., Bresnan, E., Kooistra, W.H., Lovejoy, C., Montresor, M., Morán, X. A.G., Not, F., Salas, R., Siano, R., 2018. Molecular analyses of protists in long-term observation programmes—current status and future perspectives. J. Plankton Res. 40 (5), 519–536.
Suter, L., Polanowski, A.M., Clarke, L.J., Kitchener, J.A., Deagle, B.E., 2021. Capturing open ocean biodiversity: comparing environmental DNA metabarcoding to the continuous plankton recorder. Mol. Ecol. 30 (13), 3140–3157.
U.S. Integrated Ocean Observing System, 2017. *Manual For Real-Time Quality Control of Phytoplankton Data : a Guide to Quality Control and Quality Assurance of Phytoplankton Observations* (Manual for Real-Time Quality Control of Phytoplankton Data: a Guide to Quality Control and Quality Assurance of Phytoplankton Observations, Issue. N. O. a. A. A. U.S. Department of Commerce. National Ocean Service, Integrated Ocean Observing System.
UK Research and Innovation, 2023. NERC achieves standard on action towards net zero. https://www.ukri.org/news/nerc-achieves-standard-on-action-towards-net-zero/.
Uusitalo, L., Fleming-Lehtinen, V., Hällfors, H., Jaanus, A., Hällfors, S., London, L., 2013. A novel approach for estimating phytoplankton biodiversity. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 70 (2), 408–417.
Valdés, L., Bode, A., Latasa, M., Nogueira, E., Somavilla, R., Varela, M.M., González-Pola, C., Casas, G., 2021. Three decades of continuous ocean observations in North Atlantic Spanish waters: the RADIALES time series project, context, achievements and challenges. Prog. Oceanogr. 198, 102671.
Vernette, C., Lecubin, J., Sánchez, P., Sunagawa, S., Delmont, T.O., Acinas, S.G., Pelletier, E., Hingamp, P., Lescot, M., 2022. The Ocean Gene Atlas v2. 0: online exploration of the biogeography and phylogeny of plankton genes. Nucleic Acids Res. 50 (W1), W516–W526.
Vezzulli, L., Martinez-Urtaza, J., Stern, R., 2022. Continuous Plankton Recorder in the omics era: from marine microbiome to global ocean observations. Curr. Opin. Biotechnol. 73, 61–66.
Vucetich, J.A., Nelson, M.P., Bruskotter, J.T., 2020. What drives declining support for long-term ecological research? Bioscience 70 (2), 168–173.
Wilkinson, M.D., Dumontier, M., Aalbersberg, I.J., Appleton, G., Axton, M., Baak, A., Blomberg, N., Boiten, J.-W., da Silva Santos, L.B., Bourne, P.E., 2016. The FAIR Guiding Principles for scientific data management and stewardship. Sci. Data 3 (1), 1–9.
Wils, W.P., 2017. The Birds Directive 15 years later: a survey of the case law and a comparison with the Habitats Directive. In: European Environmental Law. Routledge, pp. 443–466.
Wilson, R.J., Speirs, D.C., Heath, M.R., 2015. On the surprising lack of differences between two congeneric calanoid copepod species, *Calanus finmarchicus* and *C. helgolandicus*. Prog. Oceanogr. 134, 413–431.
Wiltshire, K.H., Boersma, M., Carstens, K., Kraberg, A.C., Peters, S., Scharfe, M., 2015. Control of phytoplankton in a shelf sea: determination of the main drivers based on the Helgoland Roads Time Series. J. Sea Res. 105, 42–52.
Woese, C.R., Fox, G.E., 1977. Phylogenetic structure of the prokaryotic domain: the primary kingdoms. Proc. Natl. Acad. Sci. USA 74 (11), 5088–5090.
Yang, J., Zhang, X., Xie, Y., Song, C., Sun, J., Zhang, Y., Giesy, J.P., Yu, H., 2017. Ecogenomics of zooplankton community reveals ecological threshold of ammonia nitrogen. Environ. Sci. Technol. 51 (5), 3057–3064.
Yarimizu, K., Sildever, S., Hamamoto, Y., Tazawa, S., Oikawa, H., Yamaguchi, H., Basti, L., Mardones, J.I., Paredes-Mella, J., Nagai, S., 2021. Development of an absolute quantification method for ribosomal RNA gene copy numbers per eukaryotic single cell by digital PCR. Harmful Algae 103, 102008.
Yates, M.C., Fraser, D.J., Derry, A.M., 2019. Meta-analysis supports further refinement of eDNA for monitoring aquatic species-specific abundance in nature. Environmental DNA 1 (1), 5–13.
Zahir, M., Su, Y., Shahzad, M.I., Ayub, G., Rehman, S.U., Ijaz, J., 2024. A review on monitoring, forecasting, and early warning of harmful algal bloom. Aquaculture, 741351.
Zhai, L., Platt, T., Tang, C., Sathyendranath, S., Walne, A., 2013. The response of phytoplankton to climate variability associated with the North Atlantic Oscillation. Deep Sea Res. Part II Top. Stud. Oceanogr. 93, 159–168.
Zhang, Y., Shen, F., Zhao, H., Sun, X., Zhu, Q., Li, M., 2024. Optical distinguishability of phytoplankton species and its implications for hyperspectral remote sensing discrimination potential. J. Sea Res. 202, 102540.
Zohary, T., Shneor, M., Hambright, K.D., 2016. PlanktoMetrix–a computerized system to support microscope counts and measurements of plankton. Inland Waters 6 (2), 131–135.