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Pathways for converting zooplankton traits to ecological insights are paved with findable, accessible, interoperable, and reusable (FAIR) data practices

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Abstract

The use of trait-based approaches and trait data in zooplankton ecology is rapidly growing to better understand and predict the patterns of zooplankton distributions and their role in aquatic ecosystems and biogeochemical cycles. Although the number of zooplankton trait-based studies and available trait datasets is increasing, several challenges remain for the findability, accessibility, interoperability, and reusability (FAIR) in trait-based approaches that, if unaddressed, may stifle progress in this research area. Here, we review recent applications of trait-based approaches in zooplankton research and summarize the currently available trait data resources. To realize the potential of trait-based approaches to resolve ecological roles of zooplankton, datasets and approaches must adhere to FAIR principles. We provide recommendations and pathways forward to ensure FAIRness while highlighting the importance of collaborative efforts. These practical and easily implementable strategies will enhance the FAIRness of trait data, ultimately advancing zooplankton ecological research and connecting these findings to aquatic ecosystem functioning.

Keywords: trait; zooplankton; FAIR; trait-based approaches

Introduction

Zooplankton are functionally and biologically diverse components of aquatic ecosystems that link primary producers to higher trophic levels and influence many ecological processes, including energy and matter flows through food webs, biogeochemical cycles, and carbon sequestration (Steinberg and Landry 2017). They span a range of sizes from unicellular microzooplankton to large gelatinous animals and include the early life stages of most aquatic animals. The majority of zooplankton observational studies maximize the resolution of taxonomic identification (i.e. to the genus or species level), which is foundational for documenting biodiversity and describing its biogeography and community associations. However, while taxonomy and community associations can be used to infer ecological interactions, they do not explicitly address ecological processes and functions. Complementing taxonomy with information on traits, which are commonly shared by multiple species, allows for the more direct analysis of ecologically relevant processes. which have the potential of scaling up to ecosystem functioning.

The trait-based approach shifts the focus from the taxonomic identity of individuals to the traits that describe individuals. Various definitions of the term "trait" have been put forward, from narrow and study specific to broader, with the latter approach including the widest swath of trait-based information that can be gleaned from different approaches and sampling devices. In alignment with common usage in trait-based research, Dawson et al. (2021) defined a 'trait' as 'a measurable characteristic (morphological, phenological, physiological, behavioural, or cultural) of an individual organism that is measured at either the individual or other relevant level of organisation'. While the definition implies that traits are quantitative variables (e.g. predator–prey size ratio, body mass, carbon content), qualitative or categorical traits (e.g. feeding mode or reproductive strategy) are also frequently used to describe organisms. A more specific term is 'functional trait', which implies that the trait directly influences individual Darwinian fitness through processes of growth, reproduction, or survival (Violle et al. 2007, Demetrius and Ziehe 2007).

Ecological research can regularly involve organismal characteristics or traits, but in the past three decades, studies with a trait-based focus have proliferated (Green et al. 2022). The theories and tools surrounding the trait-based approach formally emerged from terrestrial plant ecology, which is the domain that still dominates the field (Green et al. 2022). Nonetheless, the use of trait-based approaches has revolutionized the mechanistic understanding of ecological systems in both terrestrial and aquatic realms (Meunier et al. 2017, Martini et al. 2021, Green et al. 2022). Reviews describing trait-based approaches particularly on zooplankton have provided frameworks in linking traits to organismal and ecosystem functions (Litchman et al. 2013, Hébert et al. 2016a, Martini et al. 2021). Data on zooplankton traits have long been collected and compiled before the field of trait-based approaches was formalized, but it is only recently that these were integrated into standardized digital formats (Pata and Hunt 2023). The trait-based approach has led to significant insights in zooplankton ecology (see the section "Trait-based approaches") and resources on zooplankton trait data (see the section 'Trait data resources').

Trait-based approaches have widespread advantages and applications, as well as open challenges across different ecological scales and domains (Fig. 1). The use of traits can significantly simplify zooplankton community structure and overcome the lack of data or the varying resolution of taxonomic identification. This provides a common currency for comparing the functional characteristics of taxonomically diverse and different regions. Although for some questions, it is ideal for trait data to be measured in tandem with organismal sampling, trait-based approaches can also be applied retrospectively to existing community datasets and can be updated when more trait data become available, potentially from different sampling devices and observational scales not present in the original dataset (e.g. Benedetti et al. 2023). More importantly, trait-based approaches assign organismal traits to ecological functions that can be scaled up to processes at the ecosystem level, which allows for the development of mechanistic explanations and models (Kiørboe et al. 2018).

Despite existing frameworks and data for zooplankton ecology, widespread applications of trait-based approaches are limited due to the diversity of standards and methods for acquiring, organizing, and describing zooplankton trait data. Furthermore, data types, formats, and management practices vary among research groups and the systems they work in. Advances in trait-based zooplankton research will therefore be linked to improved findability, accessibility, interoperability, and reusability (FAIR) of trait data (Wilkinson et al. 2016). Adhering to FAIR principles will facilitate common standards and practices when working with trait data, which will promote further innovation. FAIR trait data practices are critical to improving the longevity and reach of zooplankton data beyond project-specific study periods and geographies, potentially leading to innovative strategies to monitor, model, and predict impacts such as those caused by global warming and biodiversity loss.

Recent reviews articulate the benefits of FAIR data (Wilkinson et al. 2016), trait datasets (e.g. Keller et al. 2023, Morim et al. 2023), and trait-based approaches (e.g. Martini et al. 2021).

Here, we highlight the strengths, applications, and challenges of trait-based approaches and the adoption of FAIR principles in zooplankton research. Finally, we outline pathways to improve FAIR trait-based approaches that promise to advance zooplankton ecology. The ideas presented in this paper emerged from the workshop *Approaches towards findable, accessible, interoperable and reusable (FAIR) zooplankton trait data as stepping stones to improved functional ecology* held during the 7th ICES-PICES Zooplankton Production Symposium in March 2024 in Hobart, Tasmania.

Landscape of what we know on zooplankton trait-based approaches and data resources

Trait-based approaches

Several studies have used trait-based approaches in zooplankton research, highlighting the breadth of applications that have already been implemented (Table 1). Trait-based approaches have been applied in empirical studies at different levels of biological organization and from the local to global scale. At the individual level, traits were used to demonstrate trade-offs that govern organismal processes (e.g. Kiørboe and Hirst 2014). At the community level, trait-based approaches have characterized the functional composition and diversity of zooplankton (e.g. Pomerleau et al. 2015). Studies that explicitly link traits to biodiversity and ecosystem functioning

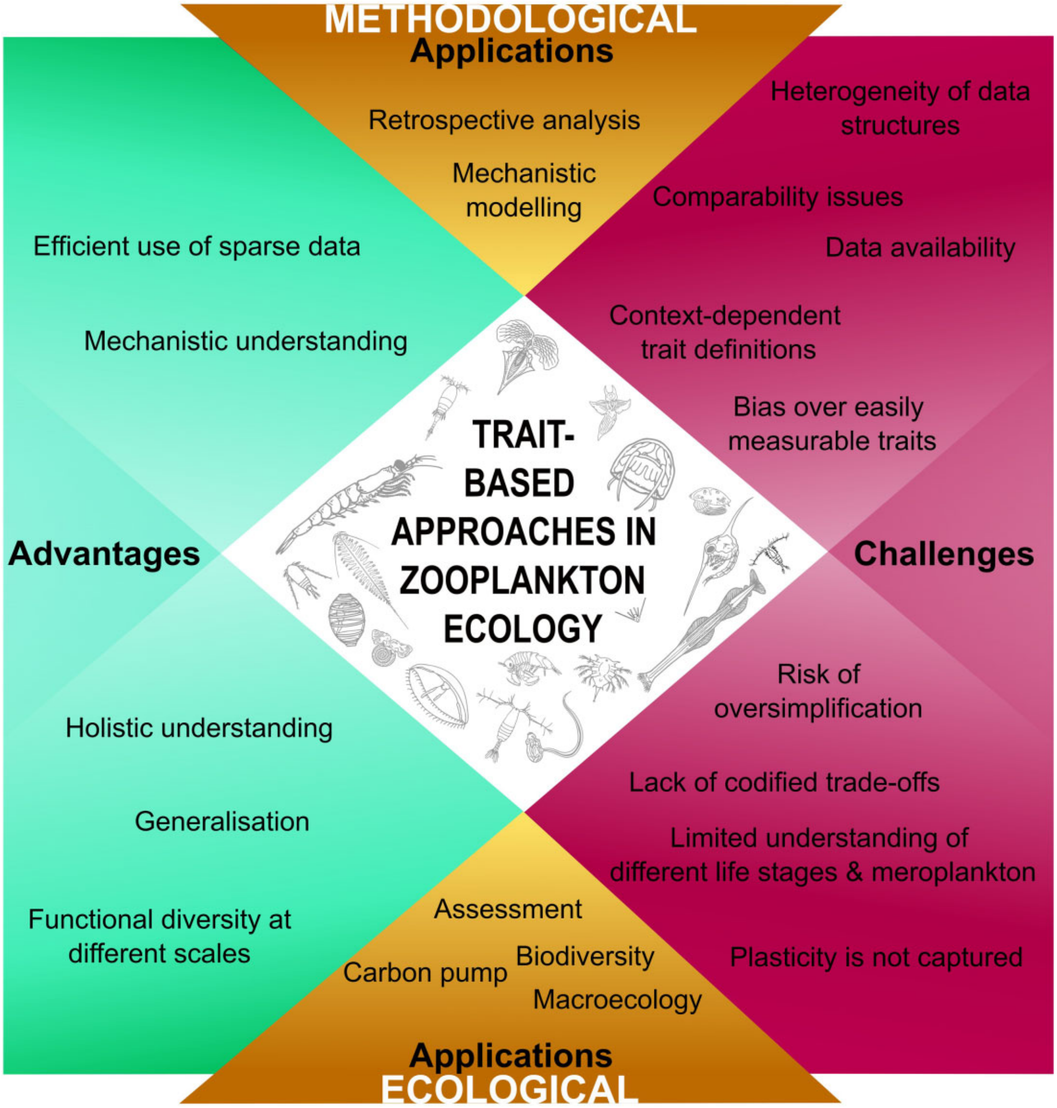

Figure 1. Characteristics of trait-based approaches in zooplankton ecology listed as advantages, challenges, and methodological or ecological applications. Zooplankton vectors adapted from Pata, P. (2023). Marine organism line art. https://doi.org/10.5281/zenodo.13685461.

Table 1. Examples of applications of trait-based approaches in zooplankton ecology categorized thematically based on the study topic.

Category	References
Individual-level analysis, trade-offs between traits	Kiørboe (2008), Gorokhova et al. (2013), Bianco et al. (2014), Kiørboe and Hirst (2014), Kiørboe et al. (2015)
Population-level analysis	García et al. (2007), Frances et al. (2021), Ilić et al. (2021), Shaw et al. (2021)
Community-level analysis	Litchman et al. (2013), Pomerleau et al. (2015), Romagnan et al. (2015), Benedetti et al. (2016, 2023), Hébert et al. (2016b), Teuber et al. (2019), Becker et al. (2021), Vilgrain et al. (2021), Cornils et al. (2022), Feuilloley et al. (2022), Li et al. (2022), Beck et al. (2023), Perhirin et al. (2024)
Biodiversity and ecosystem functioning	Barnett et al. (2007), Hébert et al. (2016a), St.-Gelais et al. (2023)
)M)odeling biogeography	Barton et al. (2013), Brun et al. (2016), Prowe et al. (2019), Drago et al. (2022)
Modelling food webs, including size-based ecosystem models	Heneghan et al. (2016), Prowe et al. (2019, 2020, 2023), Everett et al. (2022), Negrete-García et al. (2022), Clerc et al. (2023)
Modeling biogeochemistry	Renaud et al. (2018), Archibald et al. (2019), Luo et al. (2020), Wright et al. (2021), Serra-Pompei et al. (2022), Pinti et al. (2023), Clerc et al. (2024)

This table is an open access source that can be updated regularly, and we invite all zooplankton researchers to contribute to its future version at this link https://osf.io/gqu53.

were explored for zooplankton (Hébert et al. 2016a, St.-Gelais et al. 2023), yet linking traits to the effects of multiple anthropogenic stressors on biodiversity (Butt et al. 2022) needs to be further developed for zooplankton. Models that capture the functional diversity of zooplankton have begun to look into the climate change impacts on ecosystem functioning as modulated by traits (Clerc et al. 2023, Heneghan et al. 2023). By focusing on the individual-level processes determined by traits, ecosystem models can mechanistically link functional groups and environmental drivers. Moreover, applications of trait data to global models that have synthesized zooplankton occurrence and biomass data lead to new insights into the drivers of macroscale distribution of traits and the resulting ecosystem functions (Prowe et al. 2019, Drago et al. 2022, Benedetti et al. 2023).

Zooplankton trait data are also essential when building, parameterizing, and validating models. Traits help to simplify the complexity of ecosystems and facilitate the representation of a broad range of organisms in mechanistic ecosystem models, across large ranges of traits and functional trait trade-offs (e.g. Prowe et al. 2019, Heneghan et al. 2020). Trait-based modeling also improves the connection between the representation of zooplankton physiology and biogeochemical processes, especially with regard to carbon cycling (Stemmann and Boss 2012, Renaud et al. 2018, Serra-Pompei et al. 2022). Poor resolution of zooplankton traits in biogeochemical models has been identified as the largest source of uncertainty in projections of climate impacts on the carbon cycle (Rohr et al. 2023). Increasing the number of empirical trait values, therefore, is critical to improving parameterization and validation of these models. Strategies to improve zooplankton representation in models include using functional types and continuous trait distributions (e.g. Wright et al. 2021, Clerc et al. 2023, Heneghan et al. 2023).

Recent advancements in technologies and tools for sampling, such as high-throughput sequencing, environmental DNA (eDNA), biochemical tracers, and advanced imaging techniques, have significantly enhanced trait measurement capabilities. These tools enable more comprehensive and near-real-time monitoring across zooplankton phyla, large size ranges, and gradients of trait distributions, likely at finer spatial and temporal scales than previously possible (Martini et al. 2021). Monitoring biodiversity using DNA metabarcoding and eDNA-based techniques is valuable for assessing species, especially by revealing the hidden biodiversity for species richness. Associating biodiversity with trait distributions is possible but is limited by the reliability of the species' relative abundance estimates based on DNA reads. These molecular tools also allow sampling in a broader range of habitats, especially in remote and seasonally ice-covered areas that are not easily accessible by traditional net sampling (Thomsen and Willerslev 2015, Deiner et al. 2017, Lacoursière-Roussel et al. 2018). Additionally, biochemical tracers, including stable isotopes and fatty acids, can provide information for traits related to feeding behaviour and nutritional quality and insights into dietary relationships and the trophic roles of zooplankton in the food web (Laakmann and Auel 2010, Visconti et al. 2018).

Plankton imaging devices, similar to molecular approaches, are becoming widespread and have a variety of technical approaches for sampling the full spectrum of plankton size classes (Romagnan et al. 2015, Lombard et al. 2019, Greer et al. 2020). Many morphological traits that are difficult or labour-intensive to quantify with microscopy can be measured automatically with *in situ* or benchtop imaging methods (Irisson et al. 2022, Orenstein et al. 2022), albeit at the expense of lower taxonomic resolution. For example, some morphological traits can be directly measured on the images (e.g. size, shape, colour, presence of elongations/spines), while others can be inferred by the values of the measured traits and related to behavioural or physiological characteristics and the life stage category such as lipid content, gonadal maturity, and feeding activity (Vilgrain et al. 2021, Orenstein et al. 2022, Maps et al. 2024). *In situ* imaging systems can also produce trait data at finer spatial scales (∼1–10 m) and overcome detection biases due to the fragility of some zooplankton (Biard et al. 2016), and are thus able to investigate habitat transition zones that are difficult to capture with coarser traditional sampling methods (Greer et al. 2015, McManus et al. 2021). Imaging systems can substantially reduce the cost and duration of data analysis, allowing the study of time series of morphological traits over long time intervals or at a high frequency (Feuilloley et al. 2022, Beck et al. 2023).

Trait data resources

The use of trait-based approaches is facilitated by the extensive resources publicly available online for trait data collection, curation, processing, and analysis. Extensive digitization efforts over the past decade have enabled the integration of historical data from original species descriptions, research articles, and field studies into the compilation of many organismal trait databases and several comprehensive online resources dedicated to the study of zooplankton traits (Supplementary Table). Some of the early databases with zooplankton trait data have focused on copepods (Benedetti et al. 2016, Hébert et al. 2016b, Brun et al. 2017, Razouls et al. 2005–2024). Recently, these databases were harmonized along with other datasets and publications to include a broader range of zooplankton taxonomic groups and >50 traits in the 'Global Zooplankton Trait Database' (Pata and Hunt 2023). This harmonized database is focused on marine species only and is mostly limited to holoplanktonic mesozooplankton. Trait data for some meroplankton and micronekton are available in other databases that do not explicitly focus on zooplankton (Madin et al. 2016, Gleiber et al. 2024, Degen and Faulwetter 2019, Faulwetter et al. 2014), while trait data for freshwater zooplankton are stored in separate databases (Barnett et al. 2007, Hébert et al. 2016b).

Although broader in scope, other valuable resources and repositories of zooplankton trait data include the Encyclopedia of Life (EOL), TraitBank (Parr et al. 2016), the Marine Traits Portal of the World Register of Marine Species (WoRMS), SeaLifeBase, and the Global Biodiversity Information Facility (GBIF). These resources primarily focus on taxonomic information, but also contain detailed entries for many zooplankton species with some trait information and extensive occurrence data that can be used to infer traits related to distribution and environmental preferences or to collate and incorporate trait data (Hébert et al. 2016a). Moreover, several zooplankton trait resources can be extracted by consulting datasets archived among the main biodiversity and marine data portals (e.g. PANGAEA, OBIS).

The development of comprehensive molecular databases (Wang et al. 2009, Sayers et al. 2020) and repositories such as GenBank, Barcode of Life Data Systems (BOLD, doi.org/10.17616/R3PP7J), and MetaZooGene Atlas and Database (Bucklin et al. 2021, O'Brien et al. 2024) provide an additional source of taxonomic data that can be integrated with trait data and facilitate interspecies comparisons and the linkage of genetic information with phenotypic traits. Another emerging trait data resource is Ecotaxa (https://ecotaxa.obs-vlfr.fr/), the largest database of sorted plankton images containing ~450 million images, which is dedicated to the taxonomic identification of images of plankton and includes measurements of morphological traits (Picheral et al. 2017).

Collectively, these resources support the advancement of trait-based research in zooplankton ecology by providing readily accessible information, courses, and documentation of FAIR data practices to researchers worldwide. The repositories also have implemented quality assurance (QA) and quality control (QC) measures to maintain high standards of data submission. Users collaborate through defined responsibilities shared among data providers, data curators, and reviewers, and provide direct support and guidance to facilitate data preparation and submission. This ensures rigorous QC through evaluation processes that may include pre-entry checks, formal criteria assessments, and content review. However, trait data resources remain decentralized and widely dispersed across the Web, which makes it challenging to develop robust information systems to aggregate and disseminate data according to FAIR principles. To date, there has been no specific online repository dedicated to zooplankton traits. Nevertheless, the Open Traits Network (OTN) represents one of the major efforts to provide a centralized hub for trait-related data (https://opentraits.org). It includes a collection of trait datasets, often specific to a particular taxonomic domain or biogeographic region, with some datasets including zooplankton taxa. Similarly, a catalogue of trait databases for a plethora of aquatic organisms, including zooplankton, has been provided in Martini et al. (2021).

As more trait data become available, collaborative projects and initiatives are establishing standardized methods for producing FAIR trait data (Gallagher et al. 2015, Schneider et al. 2019, Keller et al. 2023). In recent years, particular attention has been paid to addressing issues of heterogeneity in terminologies of trait data in units or categorical variables by applying standardized definitions. One of the most important examples of improving the annotation, standardization, and interoperability of trait data and metadata is the Ecological Trait-data Standard (ETS) vocabulary (Schneider et al. 2019). The ETS vocabulary is a single resource terminology that provides a starting point for the development of a common language and terminology around traits and trait-based research across disciplines. Specifically, for zooplankton, the Zooplankton Trait Thesaurus (https://ecoportal.lifewatch.eu/ontologies/ZOOPLANKTRAITS) was initiated to make zooplankton-related trait terminologies machine-readable and actionable, to ensure data consistency, and to promote zooplankton data harmonization and integration across studies. This resource provides standards mainly for morphological traits and is currently being improved and extended to include standards for physiological, behavioural, and life-history traits. Furthermore, this thesaurus has been merged with the Phytoplankton Trait Thesaurus (Rosati et al. 2017), the Macroalgae Trait Thesaurus, and the Fish Trait Thesaurus in a unique resource: the Traits Thesaurus (https://www.doi.org/10.48373/sa6p-ta25). The ultimate goal of this Traits Thesaurus is to interact with the ETS and to be linked and aligned with other existing biodiversity and trait data terminology initiatives within The Biodiversity Information Standards (https://www.tdwg.org/). Establishing clear trait definitions and semantically annotating trait terminologies with rich metadata using controlled vocabularies is essential for standardizing traits and associated information, such as units of measurement, the location or environment where the trait was measured, the level of measurement (e.g. individual or species), and the protocol or instrument used. This limits confusion during data aggregation and allows for accommodating multiple trait records for a single species, which facilitates documenting intraspecific variation.

Recently, the identification of zooplankton and the collection of trait-based measurements have seen significant advances through the integration of image processing pipelines, machine learning applications, and various analytical tools, Web services, and open-source code and software (Supplementary Table). Among these, Ecotaxa is a valuable example of an interactive database that allows collaborative image processing and classification according to a universal taxonomy and machine learning techniques to automate the identification process, thereby reducing manual effort and improving data consistency. Ecotaxa uses the UniEuk taxonomic framework, which is based on curated molecular phylogenies and has established new standards relevant to marine biodiversity image networks (Irisson et al. 2022, Martin-Cabrera et al. 2022). Other openly available analytical services for zooplankton trait data acquisition, processing, analysis, and modelling include The LifeWatch Data Explorer, Plankton Toolbox, Plankton Identifier, Plankton Lifeform Extraction Tool, and Plankton Inversion Model (Supplementary Table). The Zoo and Phytoplankton EOV Product from the Blue-Cloud VRE and the Plankton Genomics VLab are examples of Virtual Lab (VLab) and VREs that promote e-Science and collaborative research (Supplementary Table). They do so through platforms that provide integrated access to data, computational resources, and analytical workflows for interpolating sparse *in situ* measurements and modelling phytoplankton–zooplankton interactions, and for in-depth assessment of plankton distributions by mining biomolecular, imaging, and environmental data. All of these data resources and Web services have the potential to greatly motivate researchers to organize, share, and use trait data, fostering the adoption of common protocols and analytical processes in accordance with the FAIR principles.

Existing challenges in zooplankton trait-based approaches

Despite the growing interest in trait-based approaches in zooplankton ecology, their application in fundamental and generalizable ecological research is limited by (i) data availability, (ii) data FAIRness, and (iii) some inherent shortcomings and uncertainties in recent implementations of trait-based approaches.

Trait data availability

There are significant gaps in the taxonomic coverage of zooplankton trait information where most available data are extracted from morphological information (e.g. size, shape, body mass) or categorical behavioural traits, with less available information on physiological, biochemical, and life-history traits (Pata and Hunt 2023). The existing databases mainly focus on crustaceans, with other taxa, such as pelagic cnidarians, ctenophores, and tunicates, largely absent. Important zooplankton groups that need to be incorporated into or linked with global zooplankton trait databases include meroplankton, microzooplankton, macrozooplankton, and freshwater species. Additionally, several important traits, such as growth rates, clearance rates, reproduction frequency, vertical migration, motility, and size at maturation, are largely missing from the available databases even for relatively well-studied species.

A strategy for resolving the gaps in trait data availability is to use available data as proxies for the traits of interest or estimating trait values through broad taxonomic generalizations, allometric scaling equations, or imputation (Litchman et al. 2021, Thorson et al. 2023). Standardization of these estimation procedures is necessary, with recommendations provided by de Bello et al. (2021). The accuracy of these various methods in estimating zooplankton traits was found to be strongly dependent on the number of existing trait records (Pata and Hunt 2023). Thus, acquiring new trait data is essential.

It is not clear whether the limitations on zooplankton trait data's findability and accessibility stem from actual gaps in data availability or from the scarcity of FAIR zooplankton trait data. At the same time, zooplankton trait data that are not available in public open data repositories but are stored in log books or on computer hard drives and discs in research laboratories need to be identified, digitized, and uploaded to appropriate data repositories. Furthermore, trait data can also be 'hidden' in publications that collect these data for other purposes and are therefore not incorporated in trait databases. However, mining for all the hidden data would require extensive manual effort to harmonize the datasets and integrate them into trait data repositories.

Trait data FAIRness

Beyond the challenges in data availability, the majority of available zooplankton trait data are decentralized, and, currently, there is no single access point or repository specifically tailored for accessing zooplankton trait data and metadata. As a result, many available data exist primarily as trait datasets attached to publications or uploaded to general-purpose data repositories such as Figshare, Zenodo, ResearchGate, and Data Dryad. Although these general-purpose repositories are open source and provide DOIs, they typically allow data to be archived with minimal standards for metadata documentation and data interoperability, resulting in variable tabular structures and labelling conventions for trait variables. Therefore, they often do not fully meet the requirements of FAIR principles. Beyond general-purpose data repositories, zooplankton trait data and metadata are also often scattered across multiple domain-specific repositories for marine and freshwater systems (Supplementary Table) or available through institutional websites and e-Science research infrastructure (e.g. LifeWatch, Long Term Ecological Research Network, European Marine Biological Resource Centre, European Multidisciplinary Seafloor and water column Observatory). In addition, FAIR data practices and data quality assurance measurements are still not consistent across research data hosting centres and vary considerably depending on the repository used (Kindling and Strecker 2022). Thus, the scattered data are complicated to extract and subsequently reuse. This issue is exacerbated by the occurrence of multiple parallel and concurrent efforts that may share the same objectives but employ their own approaches to data FAIRness and data and metadata quality assurance, resulting in differences in the metadata schemas, data formats, standards used, and individual approaches to QA/QC assessment. Currently, the lack of common agreement, linkage, and interoperability among these data resources underscores the urgent need for alignment and harmonization. Moreover, similar to the peer review of research papers, research on the assessment and certification of data repositories is needed to improve the value of data, policies, procedures, and services for data management and sharing.

Another source of misunderstanding that limits data FAIRness is, fundamentally, in the definition of what a trait is, which previous studies have attempted to constrain (Violle et al. 2007). Trait-based approaches include a heterogeneity in the sources of trait observations and in the level of biological organization in which traits were measured. Thus, practically, ecologists use varying, although closely related, definitions of what a trait is (Dawson et al. 2021). Beyond resolving the term 'trait', the terminologies and units of the traits themselves are context-dependent and remain challenging to standardize and decode.

In recent years, the DarwinCore (DwC) standard (Wieczorek et al. 2012) and DwC-Archive have gained popularity for biodiversity data. However, the recommended data architecture was created with the intention of harmonizing occurrence data and does not provide standards for trait data. The 'Ecological Trait-data Standard' (ETS; Schneider et al. 2019) addresses this gap, providing a vocabulary for trait datasets with essential terms such as 'trait name', 'trait value', and 'trait units'. The ETS, however, does not offer standardized descriptions for trait names and units, which can be domain specific. There are currently a number of glossaries aimed at standardizing terminology and facilitating communication between trait-based research communities (e.g. Marine Species Traits, BIOTIC, ICES vocabulary, Ecotaxonomy). However, a common problem is that many of these glossaries often lack the ability to create linked data, as they do not provide Uniform Resource Identifiers (URIs) for terms that are required to connect between different datasets and resources (Parr et al. 2016, Schneider et al. 2019). This limitation in interoperability hinders their usefulness in automated systems and data integration efforts and is further exacerbated by the lack of alignment between the semantic resources mentioned previously.

Another key challenge when integrating and ensuring the FAIRness of zooplankton trait data lies in the quality of the metadata associated with the collected trait data, which can be widely heterogeneous (e.g. various levels of taxonomic specificity, non-systematic information about the location and time of sampling). Due to the rapid changes in marine environments caused by climate change, harmonized metadata are needed to evaluate and establish trait baselines, as well as to track the changes over time and to test their robustness. In particular, the recurrent absence of spatial metadata for zooplankton traits poses difficulties for understanding ecological and biogeographical patterns and limits the ability to relate trait variations with environmental conditions.

Trait-based approaches

Trait selection is limited by the amount of available information from literature and the cost of making new trait measurements. Reliance on analysing only the functional traits that are deemed to have sufficiently available information introduces a risk of oversimplification that may fail to capture the functional diversity or ecological process of interest. One outcome of this is focusing mainly on some easily measurable traits such as size, shape, and body mass (or biovolume), and putting less emphasis on behavioural or physiological traits, which may require more detailed analyses and more specific equipment to obtain accurate and reliable trait data (Petchey and Gaston 2006). To address this, we recommend identifying the relevant traits *a priori* and explicitly linking these to the associated organismal or ecosystem processes of interest. This approach is consistent with the work already undertaken within the Essential Ocean Variables (EOVs) and the Essential Biodiversity Variables (EBVs), which provide international coordination on best practices for observing and producing data (Muller-Karger et al. 2018). The EOV and EBV frameworks demonstrate the value of recommended and commonly agreed standards and protocols for data collection and management at the international level to ensure interoperability and integrability of data from local to global scales. Furthermore, since trait information could be derived from various levels of biological organization, focusing only on taxonomic level trait values (e.g. using the same trait value for all individuals of the same species) will effectively miss the intrataxa variability. This presents a particular challenge when trait plasticity is ecologically relevant, whether from developmental changes in life history, regional variability in environmental conditions, or from the long-term responses to environmental changes. The appropriateness of trait records obtained from data compilations needs to be evaluated based on the ecological context for when the trait was measured, which are ideally provided by the metadata. This would be consistent with FAIR data practices necessary for utilizing trait data to address ecological questions.

The selection of measured or applied traits can affect estimates and applications of trait data (de Bello et al. 2021). For practical reasons, researchers tend to focus on understanding the ecosystem effects of a single or a few traits. The use of a 'representative trait' approach, often involving a single trait (i.e. size), may oversimplify the interpretation of these ecological aspects. For instance, recent work documenting morphological traits of mesozooplankton revealed that carbon export may be more influenced by body transparency (i.e. more transparent individuals are often gelatinous) than by their size (Perhirin et al. 2024). Instead, measuring more traits may better represent the functional diversity and variation of the community (Maire et al. 2015), although measuring a large number of traits at different levels of ecological complexity quickly becomes impractical, requiring increased sampling effort and costs for analysis. Traits are, however, known to intersect in the organismal processes they capture and so identifying the commonalities between traits in the statistical trait space (Vilgrain et al. 2021) would be useful for trait selection.

Currently, the relationships between traits and associated ecological functions are poorly investigated and understood (Degen et al. 2018). Furthermore, the trade-offs between resource acquisition and defence govern the diversity of communities, as they allow the coexistence of many trait configurations with similar fitness (Hébert et al. 2017). The execution of any one of these functions, however, may conflict with the others, as they cannot all be maximized simultaneously (Bremner et al. 2006). Thus, quantifying the risks and trade-offs associated with key traits is necessary to predict the morphology, behaviour, and physiology that optimizes the fitness of an organism in any environment (Violle et al. 2007), which requires cross-disciplinary investigations.

Finally, an important challenge to address in zooplankton ecology is understanding how zooplankton traits and processes contribute to and interact within the overall food web, from virioplankton to large marine mammals. Other than body size, there are traits that are common across trophic groups (Litchman et al. 2021) and the use of these cross-trophic level traits will stimulate trait-based research on entire ecosystems (Martini et al. 2021). Moreover, it will be worthwhile to learn from other ecological domains, such as terrestrial plants, that may have led to the development of trait-based approaches in terms of trait data infrastructure, forming expert networks, and applying traits for predictive studies (Green et al. 2022).

Future directions

Although trait-based approaches have been used in ecological research for some time, coordinated efforts in trait data collection, harmonization, and analysis are needed to realize the full potential of zooplankton trait-based approaches. Broadly, future zooplankton trait-based research involves the need to incorporate new sources of trait data and facilitate how trait-based studies utilize common standards, practices, and technologies for FAIR data to achieve a more cohesive and comprehensive understanding of zooplankton trait-based knowledge. We believe that several steps are necessary to coordinate and promote the collection and standardization of zooplankton trait data and the increase of FAIR zooplankton trait data (Fig. 2).

Enabling zooplankton trait data findability and accessibility

Continuing to collect zooplankton trait data from field and laboratory studies, as well as finding and synthesizing trait records from literature into existing databases, is an ongoing effort that will advance trait-based approaches. This process involves digitizing existing data and metadata, extracting information from papers and grey literature, and encouraging potential data holders to standardize and share their data in domain-specific repositories through persistent identifiers (PIDs). It is essential to establish structured connections between zooplankton data and related information through high-quality and rich metadata. This includes detailed descriptions of the methodology, environmental conditions of the trait measurements, data provenance, and other relevant attributes. For image data, assigning a unique identifier to high-resolution images will allow for potential revisions or additions to the trait measurements. When publishing, it is crucial to share data and metadata openly through domain-specific repositories rather than in supplementary materials, ensuring that the data and metadata have a PID. Additionally, the published data need to be associated with a clear usage licence. The high volume and diversity of trait data generated by different systems and research groups underscore the critical

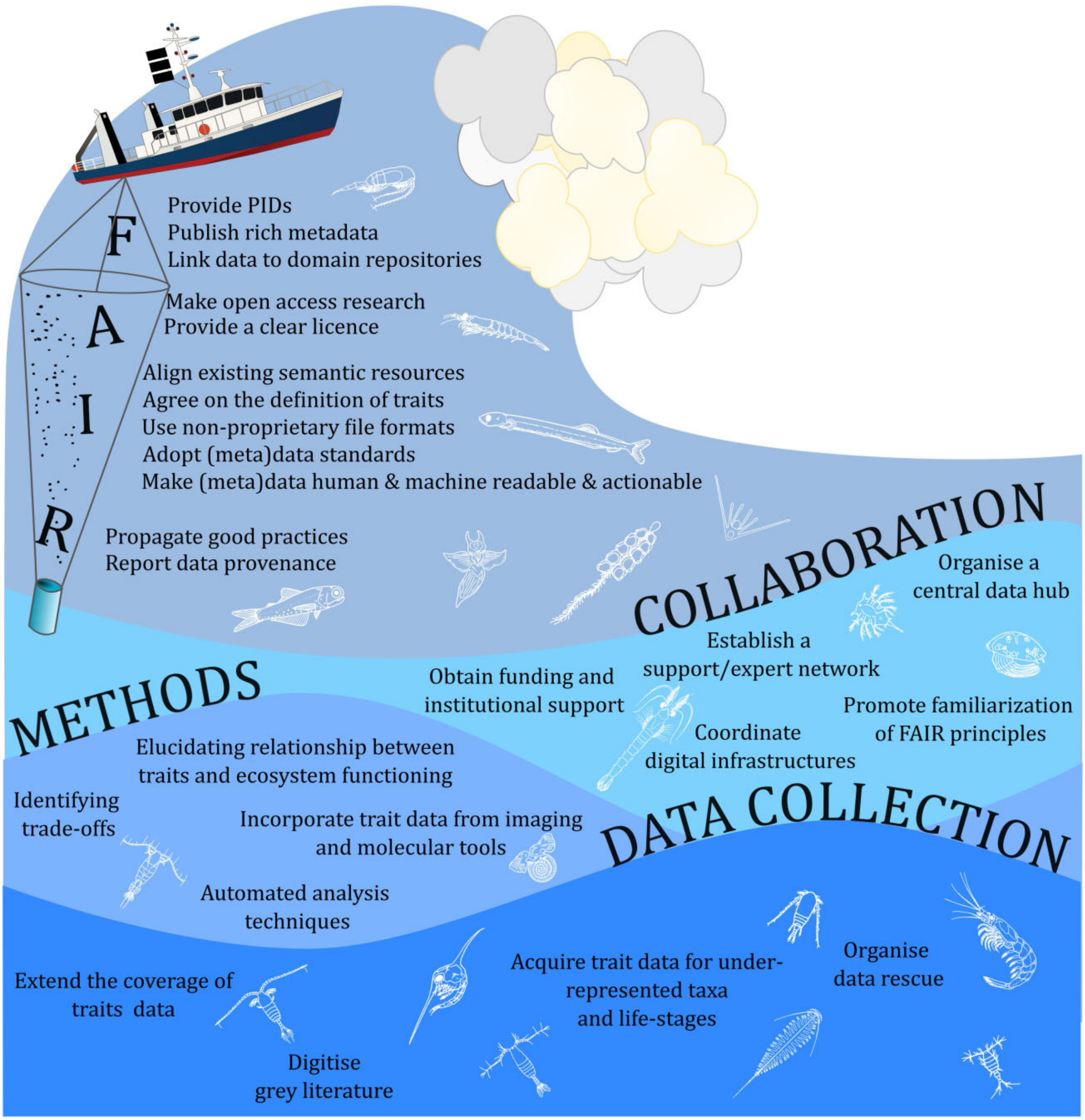

Figure 2. Summary of next steps to achieve FAIRness in zooplankton trait-based research. Recommendations are listed thematically for next steps related to FAIR data practices, collaboration within the scientific community, methods in trait data analysis, and expanding trait data collection. Sources: Illustration of the UMCES research vessel, *RV Rachel Carson*, adapted from Tracey Saxby, Integration and Application Network (ian.umces.edu/media-library), CC BY-SA 4.0. Zooplankton vectors adapted from Pata, P. (2023). Marine organism line art. https://doi.org/10.5281/zenodo.13685461.

importance of reproducible and platform-independent data management strategies.

To support these efforts, a dedicated data rescue working group should be established, potentially within the ICES framework, to facilitate connections and common practices and to provide technical support in adjusting existing data to fit the structure of databases. The contributions of data providers to making data FAIR and harmonized must be acknowledged, credited, and incentivized, thereby increasing the value of data reuse and promoting even more the adoption of FAIR data management practices. Additionally, centralized databases such as the Plant Trait Database (TRY, https://www.try-db.org/de/TabDetails.php) and FishBase (https://fishbase.org) have demonstrated that providing accessible resources in a single access point facilitates innovation in terrestrial plant and fish functional ecology. Since there is currently no specific online repository dedicated to zooplankton traits, the zooplankton research community must decide on a suitable path forward. Options include improving data FAIRness across existing repositories by aligning and standardizing FAIR data management practices along the different repositories or developing a centralized trait database or data portal specific for zooplankton traits. A centralized platform has the potential to benefit zooplankton ecologists by facilitating the findability, accessibility, and integration of zooplankton trait data into their studies. However, managing a centralized repository is challenging and requires consistent funding to remain operational and ongoing investment in technical digital infrastructure, staff, and user support to maintain their functionality. Collaborations with digital research infrastructure, academic institutions, funding bodies, and data-sharing consortia can help ensure the long-term sustainability of the repository.

Enabling zooplankton trait data interoperability

Even if trait data are available in open data repositories, data interoperability seems to be the most challenging aspect, especially among data generated by different devices and research groups (Bi et al. 2024). A critical first step in adhering to FAIR principles is the need for semantic and syntactic data standardization in zooplankton ecology. This includes standardizing data and metadata from disparate trait data collection systems into interoperable and reusable formats and adopting widely used protocols and manuals for zooplankton trait measurements (e.g. Harris et al. 2000). For this reason, zooplankton ecologists must achieve a general agreement on the definitions of specific traits and how these are measured. This would require developing agreed-upon trait terminologies and trait measurement protocols and the need for more Linked Open Data (LOD) for sharing machine-readable and actionable interlinked data on the Web. This should be achieved by the improved use of existing standards and controlled vocabularies for biodiversity and trait data annotation (Supplementary Table). Although initial steps have been taken to include species traits as EBVs, and several datasheets, templates, and guidelines for trait data collection have been proposed (Muller-Karger et al. 2018), progress is slow for integrating and operationalizing species traits in global monitoring. This is due partly to the challenges highlighted in this paper, such as the lack of a clear consensus on what is considered a 'trait' and insufficient standardization of trait data and metadata from data providers. In this context, developing tools to assist in aligning datasets to data templates and in mapping the measured traits to trait-based semantic resources remains a useful and ongoing task. These tools should include software for Web-based access to trait data and semantic Web standards.

Pre-configured spreadsheet templates for capturing trait data may be an efficient way to identify and share a consistent structure and terminology extracted from controlled vocabularies (i.e. thesauri, ontologies) for trait data collection that can be used in workflow analyses through Web services and Virtual Research Environments (VREs) . Similar initiatives already exist for occurrence data and phytoplankton trait data (i.e. PhytoplanktonData Template, https://www.phytovre.lifewatchitaly.eu/phyto-data-template/). For plankton imaging data management, best practices and recommendations have already been individuated among EMODnet Biology, OBIS, and EurOBIS networks (Martin-Cabrera et al. 2022) and some specific data templates and standard terminologies have been suggested (De Pooter et al. 2017). However, usually, data templates have limitations, as they can be restrictive, inflexible, and may not cover all possible scenarios exhaustively. An alternative approach is to use template generators, such as The Nansen Legacy Template Generator for DwC and CF-NetCDF (Marsden and Schneider 2024), which enables the addition of terms such as the Climate and Forecasting convention standard names and DwC terms to spreadsheets, allowing scientists to create semantically aware templates without needing to understand the underlying technology. Similar initiatives should be shared in the zooplankton community to provide open source easily built templates with standardized structures for trait data collection and acquisition that is flexible enough to ideally contain the details related to the trait record (e.g. the prey type and concentrations used when measuring feeding rates).

Although the use of data templates may be helpful in trait data harmonization, they have limited applications if data interoperability is weak. Therefore, there is a strong need to identify mappings among already existing trait-based semantic resources and align these resources. In this context, the use of semantic technologies that promote automated ontology matching approaches is a promising solution to the semantic heterogeneity problem. Moreover, trait-based terminologies included in glossaries and vocabularies with no URIs should be assigned with URIs to facilitate the sharing and reuse of LOD on the Web. Thus, in the case of zooplankton data, providing the specific standardized definitions of traits and units through the Traits Thesaurus will enable an automated tool to extract relevant parameters from these diverse data sources. It is essential that each type of measurement is uniquely identifiable and accessible in a machine-readable format. The list of possible traits is extensive, yet many are seldom measured or recorded as continuous data, but rather as categorical descriptions. With regard to categorical traits, each value or level of a trait would require standardized definitions as well. As a result, there is an increasing demand for domain-specific thesauri and ontologies tailored to address these limitations and improve annotation and specificity, ensuring machine-readability and actionability. These actions, aligned with preexisting government-backed frameworks and product distribution initiatives, should result as synergistic efforts for enhancing the information available for existing EBVs. This would also facilitate inclusion of species traits as EBVs, particularly within the zooplankton domain.

Enabling zooplankton trait data reusability

Once zooplankton trait data are findable, accessible, and interoperable, it is essential to enhance their full reusability by documenting the analytical workflow. This will ensure that zooplankton trait data are not only accessible but also reusable in different analytical contexts, thus maximizing the value of the data collected. Since the handling and processing of large amounts of zooplankton trait data is difficult to perform manually, the development of efficient tools for data integration, analysis, and modelling, open-source codes, user-friendly Web services, workflows, and VREs specifically designed for zooplankton trait-based data analysis should be strongly encouraged by digital research infrastructure and IT developers. Reusability also includes the appropriate recognition of the data providers and preserving the history of the PIDs linked to the data. Digital research infrastructure plays an important role in propagating good practices in data use and citation through providing user interfaces and tools that facilitate reusability. In plankton imaging, significant advances in machine learning and computer vision algorithms have led to an immense increase in recorded data quantity and quality (Orenstein et al. 2022). These data are now part of large-scale monitoring programmes, such as the Canadian Aquaculture Monitoring Program (Finnis et al. 2023). Efforts are underway to make these images and associated processing algorithms available for broad-scale plankton analyses of taxa and functional traits (Picheral et al. 2017, Drago et al. 2022, Dugenne et al. 2024), with initiatives such as iFDO providing standards and frameworks for FAIR marine images (https://marine-imaging.com/fair/ifdos/iFDO-overview/).

The promotion of open-source codes and software, workflows, and pipelines for data processing can support high-throughput data analyses, and various statistical and computational techniques and modelling, including machine learning, and enhance the scalability of research efforts. Dedicated virtual zooplankton labs and VRE should be promoted as collaborative spaces where researchers can work together on zooplankton trait data analysis, sharing tools, resources, and data, facilitating collaboration and knowledge sharing. In addition, incorporating more traits into models allows for multi-platform analyses that comprehensively address trait-based ecological questions and improve predictive power. These models can simulate different ecological scenarios and help predict the effects of environmental changes on zooplankton communities. By implementing these strategies, the zooplankton community can augment the reusability of zooplankton trait data, driving advances in ecological research and supporting sustainable ecosystem management.

Collaborating towards FAIR trait-based zooplankton research

All the steps previously stated depend heavily on support from the institutions and digital research infrastructure that are revolutionizing data management practices across a range of scientific disciplines. They are essential frameworks that facilitate the organization, storage, and dissemination of the vast amounts of research data produced worldwide. However, the effectiveness of this infrastructure depends on the commitment of individual researchers to be open and to improve the FAIRness of their own research, together with the support of data curators and data managers. The existing digital research infrastructure could play an important role in providing funding and professional support in maintaining data centres. In the future, the funding, development, and promotion of a network of aligned physical and digital research infrastructure will be a major asset to the trait-based research community.

Strengthening collaboration and networking in zooplankton research is the basis for integrating diverse expertise, methodologies, and data sources. Stronger networks and collaborative efforts will lead to improved data standardization, and more robust and accurate analytical processes and models. Collaboration will be facilitated through forming working groups to establish expert networks with the skills necessary to navigate the complexities of FAIR data principles. Future working groups would need to solicit financial support specifying the funds and labour necessary for data management.

Encouraging the development of specialized programmes that integrate training in computer science, zooplankton ecology, and data management is also essential. These actions may have the potential to cultivate new professionals who have expertise in both ecological science and data management, fostering dialogue and collaboration and ultimately advancing research in both fields. Furthermore, implementing workshops and courses related to open science and zooplankton trait data management will facilitate the dissemination of FAIR zooplankton trait data. These initiatives should be promoted early in scientific careers, even at the undergraduate level, and within the framework of digital research infrastructure, which plays a key role in enabling data-driven research by providing digital resources, tools, and Web services. Moreover, connecting with and learning from experts in other domains of ecology, such as marine microbes, fishes, and terrestrial plants, who have more extensive experience in organizing trait data and applying trait-based approaches, would be helpful in acquiring best practices for zooplankton ecology.

Finally, incentives must be generated to foster a culture of data sharing in the scientific community. Improving the way we attribute datasets in peer-reviewed research and academic evaluations is critical. Recognizing and rewarding data sharing efforts through proper citation and academic credit can provide avenues for professional advancement for researchers contributing their data to public repositories. By treating datasets and data papers as research outputs on par with traditional publications, the scientific community can foster a more collaborative and transparent research environment. Future trait data rescue and data standardization activities should consider how to promote the achievements of the scientists generating the original trait data.

The pathways forward are paved with FAIR data practices, and strengthening collaborations among the zooplankton research community with the existing FAIR initiatives and frameworks is much needed. By adhering to FAIR principles and practices, trait-based approaches in zooplankton research hold significant promise for transforming trait data into actionable knowledge leading to a more holistic understanding of the critical role of zooplankton in aquatic ecosystems and biogeochemical cycles. Working towards establishing a consolidated network of trait data providers, stewards, and users will be key in promoting the benefits of FAIR data practices and in achieving the steps we outlined towards converting traits to ecological insights.

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Author contributions

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Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

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Data availability

No new data were generated or analysed in support of this research. Information containing the contents of Table 1 and the supplementary table are archived in this Open Science Framework project link (https://osf.io/gqu53/).

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