Naturalis Repository

Mediterranean zooplankton limits species-level monitoring accuracy

Janna Peters , Aitor Albaina , Leocadio Blanco-Bercial , Katja T.C.A. Peijnenburg [et al.]

Downloaded from
https://doi.org/10.1093/icesjms/fsaf077

Article 25fa Dutch Copyright Act (DCA) - End User Rights
This publication is distributed under the terms of Article 25fa of the Dutch Copyright Act (Auteurswet) with consent from the author. Dutch law entitles the maker of a short scientific work funded either wholly or partially by Dutch public funds to make that work publicly available following a reasonable period after the work was first published, provided that reference is made to the source of the first publication of the work.

This publication is distributed under the Naturalis Biodiversity Center 'Taverne implementation' programme. In this programme, research output of Naturalis researchers and collection managers that complies with the legal requirements of Article 25fa of the Dutch Copyright Act is distributed online and free of barriers in the Naturalis institutional repository. Research output is distributed six months after its first online publication in the original published version and with proper attribution to the source of the original publication.

You are permitted to download and use the publication for personal purposes. All rights remain with the author(s) and copyrights owner(s) of this work. Any use of the publication other than authorized under this license or copyright law is prohibited.

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the department of Collection Information know, stating your reasons. In case of a legitimate complaint, Collection Information will make the material inaccessible. Please contact us through email: collectie.informatie@naturalis.nl. We will contact you as soon as possible.

ICES Journal of Marine Science, 2025, Vol. 82, Issue 6, fsaf077
https://doi.org/10.1093/icesjms/fsaf077
Received: 13 September 2024; **revised:** 5 March 2025; **accepted:** 30 March 2025
Review Article

Taxonomic uncertainty in North Atlantic and Mediterranean zooplankton limits species-level monitoring accuracy

Janna Peters[1,*], Aitor Albaina[2], Leocadio Blanco-Bercial[3], Ann Bucklin[4], Iole Di Capua[5], Antonina Dos Santos[6,7], Tone Falkenhaug[8], Mariluz Fernandez de Puelles[9], Elaine Fileman[10], Rade Garić[11], Sabine Holst[1], Aino Hosia[12], Silke Laakmann[13,14], Sanna Majaneva[15,16], Maciej K. Mańko[17], Maria Grazia Mazzocchi[5], Todd O'Brien[18], Katja T.C.A. Peijnenburg[19,20], Jasmin Renz[1], Sven Rossel[21], Agata Weydmann-Zwolicka[17], Gesche Winkler[22], Lidia Yebra[23], Astrid Cornils[14]

[1]German Centre for Marine Biodiversity Research, Senckenberg am Meer, Martin-Luther-King Platz 3, 20146 Hamburg, Germany
[2]Department of Zoology and Animal Cell Biology, Faculty of Science and Technology, University of the Basque Country (UPV/EHU), BarrioSarriena s/n, 48940 Leioa, Bizkaia, Spain
[3]Bermuda Institute of Ocean Sciences (BIOS), Arizona State University, 17 Biological Station, St Georges GE 01, Bermuda
[4]Department of Marine Sciences, University of Connecticut, 1080 Shennecossett Road, Groton, Connecticut 06340, United States of America
[5]Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Naples, Italy
[6]Portuguese Institute for Sea and Atmosphere (IPMA), Av. Doutor Alfredo Magalhães Ramalho 6, 1495-165 Algés, Portugal
[7]Interdisciplinary Centre of Marine and Environmental Research, Terminal de Cruzeiros do Porto de Leixões, Av. General Norton de Matos s/n 4450-208 Matosinhos, Portugal.
[8]Institute of Marine Research, Flødevigen Research Station, Nye Flødevigveien 20, NO-4817 His, Norway
[9]Instituto Español de Oceanografía (IEO/CSIC), Centro Oceanográfico de las Islas Baleares (COB), Muelle de Poniente s/n, 07015 Palma de Mallorca, Spain
[10]Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL1 3DH, United Kingdom
[11]Institute for Marine and Coastal Research, University of Dubrovnik, Kneza Damjana Jude 12, 20000 Dubrovnik, Croatia
[12] University Museum of Bergen, Department of Natural History, P.O. Box 7800, NO-5020 Bergen, Norway
[13]Helmholtz Institute for Functional Marine Biodiversity (HIFMB) at the University of Oldenburg (HIFMB) , Im Technologiepark 5, 26129 Oldenburg, Germany
[14]Alfred Wegener Institute Helmholtz Center for Polar and Marine Research (AWI), Am Handelshafen 12, 27570 Bremerhaven, Germany.
[15]Akvaplan-niva, Framsenteret, Postboks 6606, Stakkevollan, 9296 Tromsø, Norway.
[16]Norwegian University of Science and Technology (NTNU), Biologisk stasjon Trondheim, Bynesveien 46 , 7491 Trondheim, Norway
[17]Faculty of Oceanography and Geography, University of Gdańsk, Department of Marine Biology and Biotechnology, al. Marszałka Piłsudskiego 46, 81–378 Gdynia, Poland.
[18]National Oceanic and Atmospheric Administration (NOAA), 1315 East West Highway, Silver Spring, Maryland 20910-3282, United States of America
[19]Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, Netherlands
[20]Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, Science Park 904, 1098 XH Amsterdam, Netherlands
[21]German Centre for Marine Biodiversity Research, Senckenberg am Meer, Südstrand 44, 26382 Wilhelmshaven , Germany
[22]Institut des Sciences de la Mer (ISMER), Québec-Océan, Université du Québec à Rimouski, 310 Allée des Ursulines, Rimouski, G5L 3A1, Québec, Canada
[23]Centro Oceanográfico de Málaga (IEO, CSIC), Explanada de San Andrés (Muelle 9), Puerto de Málaga, 29002 Málaga, Spain

[*]Corresponding author. German Centre for Marine Biodiversity Research, Senckenberg am Meer, Martin-Luther-King Platz 3, 20146 Hamburg, Germany. E-mail: janna.peters@senckenberg.de

Abstract

Taxonomic discussions often permeate the broader scientific community slowly, yet they may hold more relevance than typically assumed. In many zooplankton groups, identification issues arise from cryptic species complexes, increasingly revealed by molecular approaches, and from groups with high morphological similarity. These challenges can lead to substantial uncertainties in species-level identification, questioning whether the expected species are truly covered and whether those sharing names across ecosystems are indeed distinct entities. This review provides a condensed overview on identification challenges of key species in the ICES zooplankton time series from the North Atlantic and adjacent seas. Examples are given across all relevant groups, including copepods, gelatinous plankton, and meroplanktonic larvae. The high prevalence of challenging species complexes underscores the need to further explore the implications of an accurate species assignment for understanding what defines a species' role in an ecosystem. This review highlights the dynamic nature of taxonomy, with species being split and cryptic species eventually becoming morphologically distinguishable. It provides examples showing that relying solely on molecular methods without deep taxonomic expertise poses significant risks. It also aims to serve as a starting point for delving deeper into the taxonomy of the ICES zooplankton time series.

Keywords: zooplankton; cryptic species; species complexes; ICES time series

Introduction

Marine zooplankton time series are essential tools to understand the variability of biodiversity patterns and productivity processes in the ocean. Within the International Council for the Exploration of the Sea (ICES) area, monitoring is a critical tool for providing advice. From an ecosystem-based assessment approach, multiple time-series analyses are crucial for the understanding of ecosystem change due to climate and anthropogenic impacts. The ICES Working Group on Zooplankton Ecology (WGZE) and its Zooplankton Status Reports cover over a hundred time series sites, located in western and eastern North Atlantic, Nordic, Barents, Baltic, North, and Mediterranean Seas. The comprehensive examination of long-term changes of dominant zooplankton species and food web dynamics can provide improved model parameterizations and a pan-regional view of the relationships between the physical–chemical environment and plankton communities in the context of climate change (reviewed in Ratnarajah et al. 2023). However, zooplankton monitoring is not a straightforward task. Taxonomic identification of the zooplanktonic organisms requires a high level of specialization, and the number of expert taxonomists is rapidly declining. Considering this, a new series of the ICES Leaflets for the identification of plankton was initiated by the WGZE revising morphological identification keys and providing additional molecular information on key zooplankton groups. In many monitoring programs, taxa are morphologically identified at the class or family level, and only some groups (e.g. copepods) are routinely identified at the genus or species level. Even well-known or very abundant species are not always effectively identified due to the presence of sibling, cryptic, and pseudocryptic species, or absence of apparent morphological characters to separate species.

In the last two decades, the use of molecular tools in zooplankton research has led to a revolution in species delineation and identification as well as in the assessment of ecosystem diversity (Laakmann et al. 2020, Bucklin et al. 2021a). The increasing application of DNA-based species research has resulted in a stronger recognition of the existence and importance of species complexes in marine ecosystems (Fig. 1). However, recent taxonomic findings on newly revealed species complexes, or on uncertainties of identification in some taxa, are often quite slow to penetrate the broader scientific community. This is due in part to the relatively low number of journals of common interest, a general persistence of established terminologies in regions and data sets, and the lack of resources to routinely reassess taxonomic knowledge on all important taxa in the ecosystem.

This review therefore aims (i) to provide condensed up to date information on various important taxa from the zooplankton time series in the North Atlantic and adjacent seas, including the Baltic and Mediterranean Seas; (ii) to pinpoint important species complexes as well as identification issues for some key taxa; and (iii) to assess the relevance of potentially hidden diversity (cryptic species complexes) or nonaccessible diversity (highly laborious identification) for ecosystem and time series studies.

In essence, this review is based on the collective expertise of the ICES Working Groups on Integrated Morphological and Molecular Taxonomy (WGIMT) and Zooplankton Ecology (WGZE) and seeks to shed light on critical issues in the field of zooplankton taxonomy in time series data. Yet, we acknowledge the inherent limitations of our exploration, as it merely scratches the surface of the taxonomic complexity of zooplankton communities and the inherent questions on the role of species identification for ecosystem studies. However, we believe that it can be a good starting point for discussion on exploring taxonomic challenges and the significance of species complexes in zooplankton time series.

Key taxa

Taxonomic challenges, such as identification of specimens from cryptic species complexes or species groups with high morphological similarity, are not a minor issue restricted to rare taxa. These challenges exert a significant impact on taxa identification in many zooplankton time series. A qualitative meta-analysis (based on top 10 taxa lists for each station according to expert evaluation) summarizing abundant taxa from 19 monitoring stations in the North Atlantic Ocean and Mediterranean (Fig. 2) has identified 60 species groups, or taxon groups, to be of high importance in the various ecosystems. Most of them belong to the calanoid copepods (mainly to the genera *Acartia*, *Temora*, *Calanus* as well as *Para*-, *Pseudo*-, and *Clausocalanus*), the cyclopoid genus *Oithona*, to meroplanktonic larvae or gelatinous plankton (ICES 2021). The group of Diplostraca (formerly known as Cladocera) has high impact in several ecosystems, but species are varying between different areas.

Some widely distributed species that rank in the top ten at many stations (Table 1) are readily identifiable based on current knowledge and are assumed to be conspecific throughout their range. One example is *Temora longicornis* that is among the most abundant copepods found in the coastal and neritic waters of the northern hemisphere (Di Capua 2021). Other groups, however, are commonly merged into a very high taxonomic level in routine analyses, or species classification differs between regions due to uncertainties in identification. For example, the calanoid copepod *Paracalanus parvus* is reported in the top ten taxa from more than 50% of the monitoring stations. However, recent studies revealed that diagnostic characters of *Paracalanus* congeners are variable and that a larger complex of species is commonly grouped under the species name *P. parvus* (Cornils and Held 2014, Kasapidis et al. 2018, Khelifi-Touhami and Ounissi 2023). *Oithona* and *Acartia* species exhibit high abundance across all stations. The taxonomic lists for both genera, as well as for the genera *Pseudocalanus*, *Paracalanus*, and *Clausocalanus*, reveal that species-level identification is not straightforward, as many monitoring stations report them as unidentified species or as groups with mixed genera. They are often referred to as “P-Cal” or “PCPCalanus” categories that comprise the copepodites of the three abovementioned genera plus *Ctenocalanus* (Albaina and Irigoien 2007, Uriarte et al. 2016).

In addition to the top 10 list coming from expert evaluation on the different sites, this review incorporates several taxa that we believe are of significant importance and pose challenges for taxonomic identification. These taxa are missing in the species ranking, e.g. due to marked seasonality or suboptimal sampling strategy, which is a critical factor for many gelatinous groups. We therefore also included the hydrozoans *Obelia*, *Clytia*, and *Muggiaea*, the scyphozoans *Aurelia*, *Cyanea*, and *Rhizostoma*, as well as the ctenophore *Beroe* as they can be of seasonally high importance at regional scale. Further challenges in time series analysis may arise from

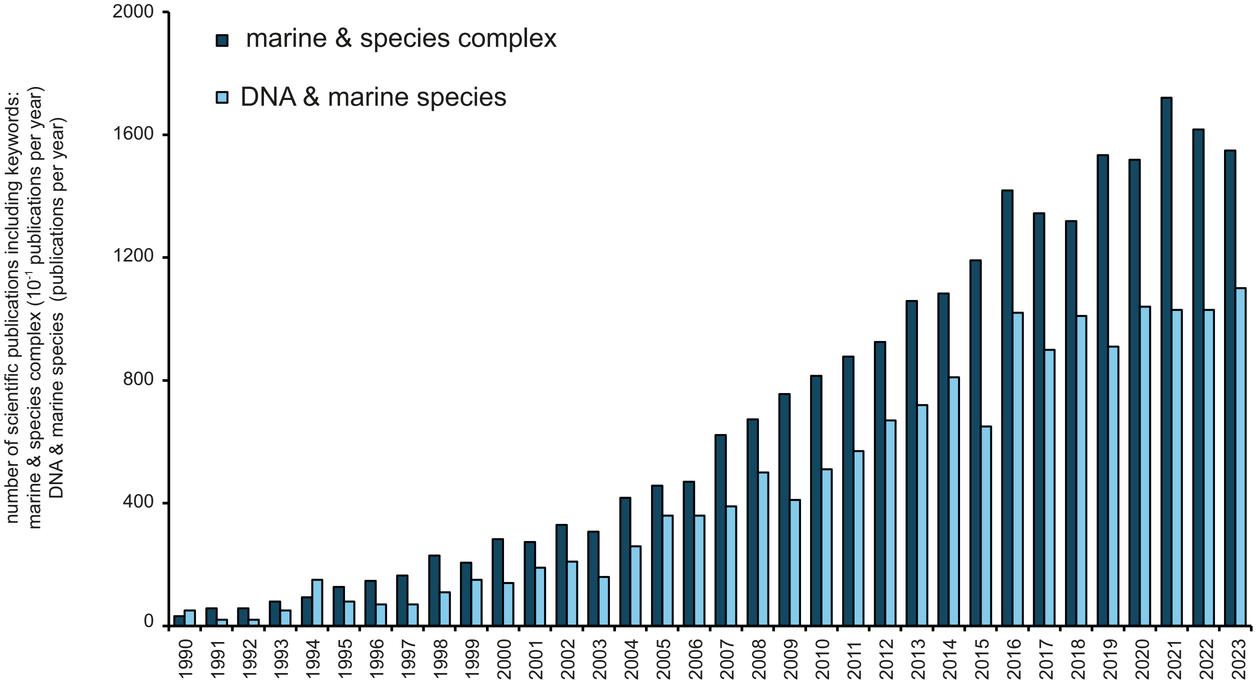

Figure 1. Number of publications per year on "DNA and marine species" and "species complex and marine" based on literature search Web of Science, January 2024.

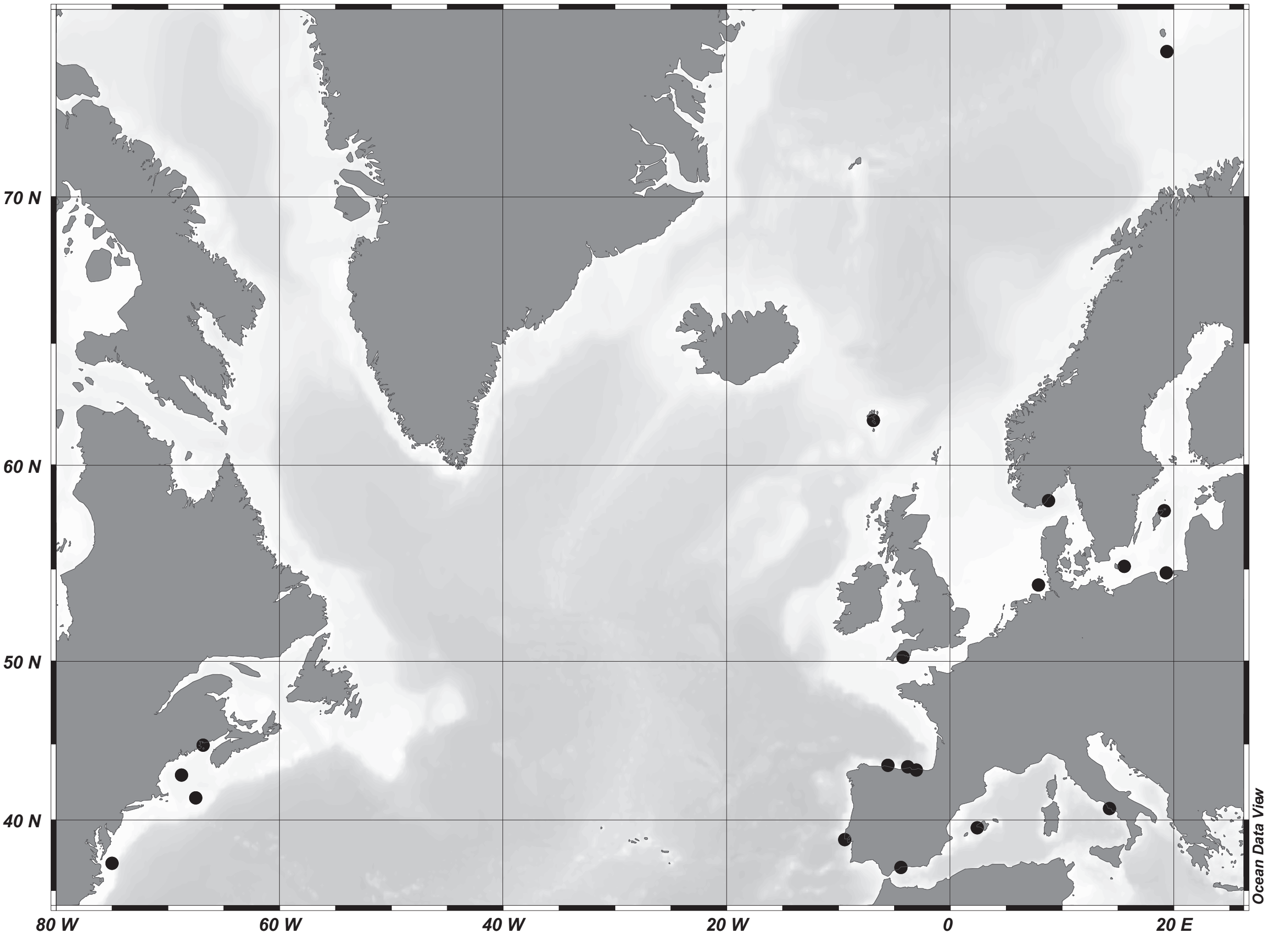

Figure 2. Time-series stations (black dots) in the ICES area and the Mediterranean included in the meta-analysis of key taxa, modified from the WGZE report (ICES 2021).

Table 1. Overview of key taxa listed in time series within the ICES eco-regions based on expert evaluation from program scientists on the different sites (overview in Fig. 2) supplemented by taxa selection by authors of this study. The categories of prominence (Prom.) are specified as: x: prominence not reported, 1: occasional prominence, i.e. <20% of all sites, 2: frequent prominence, i.e. 20%–40% of all sites, and 3: predominant prominence, i.e. >40% of all sites. Please note that the time series use different taxonomic resolutions for the different taxa.

Taxon as referred to in LTER	Prom.	Taxonomic challenge
Copepoda		
Acartia spp.	2	Species identification laborious, also cryptic species
Acartia bifilosa	2	No cryptic complex reported so far
Acartia clausi	2	No cryptic complex reported so far
Acartia longiremis	1	No cryptic complex reported so far
Acartia tonsa	1	Cryptic species complex
Calanus spp.	1	Species identification laborious
Calanus finmarchicus	2	Reliable separation from *C. glacialis* only via molecular methods or for later copepodite stages (CV and adults)
Calanus helgolandicus	1	Reliable separation from *C. finmarchicus* via molecular methods or for later copepodite stages (CV and adults)
Centropages spp.	1	Species identification laborious
Centropages hamatus	2	No cryptic complex reported so far
Centropages typicus	2	No cryptic complex reported so far, but may be misidentified as *C. chierchiae*
Clausocalanus spp.	1	Species identification laborious
Clausocalanus arcuicornis	1	No cryptic complex reported so far
Clausocalanus furcatus	1	No cryptic complex reported so far
Clausocalanus lividus	1	No cryptic complex reported so far
Clausocalanus paululus	1	No cryptic complex reported so far
Clausocalanus pergens	1	No cryptic complex reported so far
Para-/Clausocalanus spp.	1	Species identification laborious for young stages
Paracalanus parvus	3	Cryptic species complex
Pseudo-/Paracalanus spp.	1	Only separable as older copepodite stages/adults
Pseudocalanus spp.	2	Complex morphometry needed to seperate species
Pseudocalanus acuspes	1	Complex morphometry needed to seperate species
Pseudocalanus elongatus	1	Complex morphometry needed to seperate species
Pseudocalanus minutus	1	Complex morphometry needed to seperate species
Metridia spp.	1	Difficult species complex
Metridia lucens	2	Difficult species complex
Pseudodiaptomus marinus	1	NIS, species identification possible
Temora longicornis	3	No cryptic complex reported so far
Temora stylifera	1	No cryptic complex reported so far
Euterpina acutifrons	2	Cryptic species complex suspected
Oithona spp.	2	Species identification laborious, also cryptic species
Oithona davisae	1	NIS, might be overlooked or misidentified
Oithona longispina	1	Species identification laborious
Oithona nana	2	Cryptic species complex suspected
Oithona plumifera	1	Species identification laborious
Oithona similis	3	Cryptic species complex
Oncaea spp.	1	Species identification laborious
Oncaea media	1	Cryptic species complex suspected
Eurytemora carolleeae	x	NIS, might be overlooked or misidentified
Eurytemora affinis	x	Cryptic species complex, mainly estuarine and brackish waters
Tachidius discipes	1	No cryptic complex reported
Microcalanus spp.	1	Cryptic species complex (Cornils, unpublished data)
Nannocalanus minor	1	No cryptic complex reported so far
Calanipeda aquaedulcis	1	No cryptic complex reported so far
Diplostraca		
Penilia avirostris	1	Only species in genus, no cryptic complex reported
Podon intermedius	1	No cryptic complex reported
Podon spp.	1	No cryptic complex reported, *P. leuckartii* and *P. intermedius* only species in genus, *Pleopis* (formerly *Podon*) *polyphemoides* morphol. similar
Evadne nordmanni	1	No cryptic complex reported
Bosmina coregoni maritima	1	No cryptic complex reported
Evadne spinifera	1	No cryptic complex reported
Cergopagis pengoi	1	No cryptic complex reported
Cnidaria		
Muggiaea atlantica	1	Eudoxid stage not separable from that of *Muggiaea kochii*
Aurelia spp.	x	Cryptic species complex
Cyanea spp.	x	Unresolved taxonomy, laborious species identification
Obelia spp.	x	No differentiation on medusae stage
Clytia spp.	x	No differentiation on medusae stage
Rhizostoma spp.	x	Species identification laborious

Table 1. Continued

Taxon as referred to in LTER	Prom.	Taxonomic challenge
Ctenophora		
Pleurobrachia pileus	1	Larval morphology similar for most Tentaculate ctenophore species, i.e. no clear morphological differences between species
Beroe spp.	x	Unresolved taxonomy, difficult identification
Mollusca		
Bivalvia larvae	1	Morphology similar for most species, i.e. species identification not possible/restricted to experts
Limacina spp.	1	Several cryptic species complexes
Cirripedia		
Cirripedia larvae	1	Morphology similar for most species, i.e. species identification not possible/restricted to experts
Decapoda		
Decapod larvae	1	Species identification laborious, restricted to experts, often only genus or family level
Rotifera		
Synchaeta spp.	1	Species identification laborious, restricted to experts, about 20 marine/brackish species
Appendicularia		
Appendicularia	1	Identification beyond family level restricted to experts, *Oikopleura dioica* and *O. longicauda* are cryptic species complexes
Fritillaria borealis	x	
Oikopleura spp.	x	
Chaetognatha		
Sagitta spp.	x	Species identification laborious, restricted to experts

species exhibiting low abundance but potentially high ecological impact, such as chaetognaths as well as from non-indigeneous species (NIS) with marked morphological similarity to native taxa. The latter may be overlooked in routine analyses and are a major challenge for monitoring. This concerns, for example, the copepods *Eurytemora carolleeae*, *Oithona davisae*, and several *Acartia* species. Furthermore, we included selected species with potential hidden diversity, such as the copepod species complexes *Eurytemora* and *Metridia*, which are often not prominent in coastal monitoring but can be of regionally high importance.

Please note that for simplification purposes, we use only genus and species names in the main manuscript without referencing the author of the original description. Even though it would be formally correct to include subgenus or subspecies nomenclature for some taxa, we have also omitted these for simplicity. A list of all mentioned taxa including the authors of the original descriptions and the taxonomic status according to the World Register of Marine Species can be found in Table S1.

Species complexes

The advent of the genetic revolution in taxonomy has sparked a surge in the usage of the term “cryptic species” in the context of diversity assessments. Nonetheless, the definition and usage of the term “cryptic species complex” remains a topic of ongoing debate (Korshunova et al. 2019, Shin and Allmon 2023). This term is frequently employed to denote congeners that exhibit substantial molecular divergence, but lack discernible differences in phenotype and external morphology. However, in many instances, these species groups have not been subjected to sufficient morphological examination in light of molecular-based knowledge. In such cases, the term “pseudo-cryptic” may more accurately capture the taxonomic status, rather than “cryptic” (Lajus et al. 2015). Several authors even argue that the term cryptic can only be used on a temporary basis and with on-going refinement of morphological identification, differences would finally be identified (Korshunova et al. 2017). Within this review, we will address complexes that consist of genetically diverged but so far hidden and undescribed species as being a “cryptic species complex,” acknowledging that these may be of only temporary existence.

The challenges in routine zooplankton identification are diverse. Some taxa cannot be identified to the species or genus level throughout their entire pelagic phase due to a lack of diagnostic characters. Others are cryptic species, which are indistinguishable from closely related species based on established morphological traits. Additionally, congeneric species often require extensive, labor-intensive identification. A common risk among these taxa is that NIS of the same genus may have been overlooked in recent years. NIS are prevalent in marine zooplankton communities worldwide and although not all NIS become invasive, some can out-compete native species or multiply into pest proportions. NIS have transformed coastal marine habitats around the world and pose a serious threat to biodiversity. Small invertebrate species like copepods are scarcely listed in invasive species databases (Zenetos et al. 2005). In this context, it is very important to strengthen taxonomic initiatives, as well as cooperation and knowledge comparison. In marine time series, the risk of undetected NIS poses a significant challenge, specifically since some taxa are only identified to genus level.

This overview is neither all-encompassing nor intended to serve as a comprehensive inventory. Rather it aims to highlight some of the key issues and raise awareness for the hidden diversity in zooplankton time series.

Taxa with elusive identity in the pelagic phase

Early life stages of many planktonic species are difficult to identify, but there are some species that cannot be identified to species level during their whole pelagic phase. Particularly challenging are meroplankton organisms, defined as those organisms that spend only part of their life cycle in a planktonic stage, for example, fish larvae and dispersive larval stages of benthic invertebrates. Meroplankton taxa often exhibit specific regional patterns connected to the characteristics of local benthic communities, species phenology, and environmental conditions. In many ICES regions, particularly coastal areas, meroplankton taxa are characterized by strong seasonal variations and can be dominant components of zooplankton communities (e.g. Highfield et al. 2010, Hidalgo et al. 2014, Michelsen et al. 2017, Weydmann-Zwolicka et al. 2021). However, these important contributors to zooplankton communities are often underestimated during routine time-series analyses because most meroplanktonic larvae of benthic animals are difficult to identify. In some cases, identification is not possible beyond the phylum level, mainly due to their small sizes and the lack of easily visible taxonomic features. Meroplankton species-, or at least, genus-identification is often only possible with molecular methods (e.g. Heimeier et al. 2010, Brandner et al. 2017, Walczyńska et al. 2019) but it can be costly and time-consuming, thus difficult to apply during the routine zooplankton time-series analyses. Metabarcoding plays a pivotal role in addressing these groups, offering rapid and cost-effective qualitative assessment of zooplankton diversity through high-throughput DNA sequencing of unsorted samples (Lindeque et al. 2013, Schroeder et al. 2020, Di Capua et al. 2021, Ohnesorge et al. 2023). Almost all meroplanktonic groups are more or less affected by these taxonomic difficulties. We chose decapods as an example to highlight these issues, which are also inherent in polychaetes, mollusks, echinoderm larvae, and some hydromedusae.

Decapods are a greatly diverse group of species, ranging from shrimps to crabs, containing some economically important species, possessing large genetic variability, and a high level of cryptic diversity (e.g. Matzen da Silva et al. 2011). Consequently, their larvae exhibit much morphological diversity, requiring extensive knowledge of various morphotypes and access to a wide range of bibliographic resources. In addition to the great diversity of forms and morphological characters that decapod larvae exhibit, making their identification challenging in plankton samples, they also undergo changes throughout their larval development. The decapod larval cycle comprises three morphologically different phases: nauplius, zoea, and decapodid. As a result, the first larval stage can be considerably different from the last stage within the same species (e.g. Martin et al. 2014). Although molecular techniques have been used to identify larval decapod species (e.g. Torres et al. 2014, Carreton et al. 2019), these techniques are not yet generalized and are unable to separate larval stages. Information on the larval morphologies of the various groups of decapods is summarized in Martin et al. (2014), and keys to the morphological identification of the species are available (Dos Santos and González-Gordillo 2004, Buckland et al. 2017).

Certain species are identified easily due to their characteristic morphology (e.g. shrimp larvae *Lysmata*; De Sousa et al. 2022), or some types of larval stage can be assigned to certain taxon groups, e.g. the typical zoea larva as belonging to brachyuran crabs (e.g. Paula and Dos Santos 2000). However, some decapod groups are difficult to distinguish (e.g. Carideae and Upogebiidae larvae), and others possess larval stages that are morphologically indistinguishable (e.g. Polybiinae species). Upogebiidae larvae can only be distinguished from all the caridean (shrimp) larvae by the size of the second posterior process of the telson. In the case of the Polybiinae larvae and Palaemon larvae, groups common in North Atlantic coastal waters, the first zoeal stage is morphologically similar for most of the species and identifying them to species level requires a high level of expertise, looking for very small details under the microscope and to have a pool of different stages of the same species in the sample. In other cases, identification at the species level is prevented because the larval morphology of all species of a given group is still unknown. A concerted effort to produce high quality morphological identification is provided by the new series of the ICES Identification Plankton Leaflets, of which five are already dedicated to decapod larvae and more are in progress. However, a greater effort in the use of integrative taxonomy would have to be made to find a reliable tool or method for the identification of decapod larvae.

Taxa with challenging identification (congeneric and cryptic species)

Distinguishing among congeneric species can be a difficult task, especially when the identification process requires resources and taxonomic expertise beyond what is feasible in time series analyses. This is especially true for species with difficult-to-access or very small morphological characters that would require routine dissection and even mounting on microscope slides to distinguish, especially when highly abundant taxa are involved. In addition, it is typical that fragile body parts, such as antennae and swimming legs, are the ones that have specific characteristics and these break easily when collecting samples. It is particularly challenging to preserve features using fixatives for gelatinous planktonic organisms in routine sampling. We structured this chapter into hard-bodied plankton and gelatinous plankton and generally refer only to the older developmental stages, as some species cannot be identified in certain pelagic phases (e.g. in larval or juvenile stages).

Hard-bodied plankton

Acartia spp.

The calanoid copepod genus *Acartia* requires a revision as many of the original descriptions are incomplete (Boxshall and Halsey 2004, Belmonte 2021). Recently, an updated ICES plankton leaflet presented a key to the 21 species occurring in the North Atlantic and adjacent seas (Belmonte 2021). Taxonomic classification is mainly based on the morphology of the fifth pair of thoracic legs and spinules or fine hairs on the last cephalothoracic segment. The main taxonomic challenge in this genus is a high plasticity of morphological characters, probably reflecting the ability to adapt to variable and stressful environments (Sasaki and Dam 2019). Highly variable setulation of female urosome segments or in the fifth pair of thoracic legs were reported for *Acartia bifilosa* (Brylinski 1984, Hirst and Catro-Longoria 1998), leading to the discussion about different varieties in the past. Different morphology in the genital somite of females and in the fifth thoracic leg in males in *A. discaudata* suggest the existence of a species variety *A. discaudata* var. *mediterranea* (Bradford-Grieve 1999a, Belmonte 2021). This variability within the same species may hide the presence of cryptic species (Brylinski 1984), which are difficult to confirm by morphological studies alone.

Phylogenetic studies on this genus are confounded by numerous morphological misidentifications of *Acartia* species deposited in GenBank (Figueroa et al. 2020). In addition, exceptionally high and uncommon divergence to other calanoid copepods was observed in the genus *Acartia* when analyzing 18S rDNA, which highlights the need for further morphological and molecular taxonomic studies to resolve uncertainties within this genus (Laakmann et al. 2013). Also, high intraspecific genetic divergence has been found in some species, when analyzing different gene–enzyme systems, which may indicate the presence of multiple cryptic species (Cervelli et al. 1995). For instance, molecular studies suggest that *A. tonsa* represents a complex of several cryptic species (Caudill and Bucklin 2004, Chen and Hare 2008, da Costa et al. 2011, Plough et al. 2018, Figueroa et al. 2020). Analyses of DNA sequences of the mtCOI, and rRNA 16S have revealed several phylogenetic clades of *A. tonsa* in the northwestern Atlantic and Europe, which are mainly geographically separated, but in some cases, they occur in sympatry (Caudill and Bucklin 2004, Figueroa et al. 2020). Although no morphological differences between the cryptic species in *A. tonsa* have been identified yet, differences may exist in size and chemical composition (Plough et al. 2018). Signs of crypsis are also found for *A. clausi*, with distinct subclades without detectable gene flow between the North Sea and the Mediterranean Sea (Di Capua et al. 2022).

The ability to produce resting eggs and tolerance to brackish or hyperhaline environments, enables *Acartia* copepod species to spread to new habitats. Some species of this genus have been introduced to Europe by human activities, such as *A. tonsa*, *A. margalefi*, *A. teclae*, and *A. omorii*, and are classified as NIS. *Acartia tonsa* is reported as invasive in some coastal areas, where they may exclude local indigenous species (Sei et al. 1996, Aravena et al. 2009, Belmonte et al. 2011). Just recently, the species *Acartia hudsonica* has been identified several times in the North Sea (Ohnesorge et al. 2023), the Limfjord (Ohnesorge et al. 2024), and the Baltic Sea (Hahn and Brennan 2024, Ohnesorge et al. 2024) based on molecular techniques. This species is generally distributed in the North Pacific and the Northwest Atlantic Ocean (OBIS 2024a), but the recurring identification of this species in European waters indicates its presence in this area. It remains to be clarified (Hahn and Brennan 2024) whether this is a NIS in the North and Baltic Seas, or whether this species was previously overlooked and is hence native to the North and Baltic Seas; note that this species was a subspecies of *A. clausi* before it was considered as a single species (Bradford 1976, Ueda 1986).

Eurytemora spp.

The calanoid copepod *Eurytemora affinis* complex is divided into at least six major genetically divergent clades, four native to the North American continent and one in Europe, revealed by two mitochondrial gene regions: 16S rRNA and cytochrome oxidase I (COI; Lee 1999, 2000). Subsequently, three geographically separated subclades in Western Europe were identified showing sequence divergence of 1.7%–2.1% on the COI gene (Winkler et al. 2011). The East Atlantic subclade is present in the Gironde and the Loire, the North Sea English Channel subclade spans from the Seine, the Scheldt and the Elbe rivers, and the third subclade is restricted to the Baltic Sea (Winkler et al. 2011, Sukhikh et al. 2016). Morphological stasis of sexual characteristics was marked among clades, except the European one (Lee and Frost 2002). However, an increased effort in the last decade, revealed differentiation at the fine scale of morphological characteristics and led to the description of two new species within the complex, *E. carolleeae* (Alekseev and Souissi 2011) and *E. caspica* (Sukhikh and Alekseev 2013). *Eurytemora carolleae*, formerly the Atlantic clade, is considered native to brackish waters of North America and has invaded freshwater environments, such as the Great Lakes (Winkler et al. 2008, Lee 2016, Vasquez et al. 2016) and more recently European waters (Sukhikh et al. 2013, 2019, Labuce et al. 2018, 2020). Besides the identification of the cryptic species using molecular approaches (Favier and Winkler 2014, Cabrol et al. 2015), morphometry on adults can help to distinguish the species and clades of the species complex (Sukhikh et al. 2013, Lajus et al. 2020). Three morphometric indices are well distinguished based on the caudal rami, the shape of the female genital segment, and the exopodite first segment in male leg P5. Shortcomings of this method, however, are that these measurements are time consuming, thus not likely to be applied in routine time series zooplankton identification and furthermore this morphometry approach is restricted to adult individuals for the moment. Alternatively, a relatively simple quantitative polymerase chain reaction (qPCR) approach might be a cost and time efficient solution, to detect the occurrence of the invasive *E. carolleeae* in samples (Avila et al. 2024).

Oithona spp.

The cyclopoid copepod genus *Oithona* is common and very diversified in the ICES regions (Wootton and Castellani 2017), though many surveys report generically about *Oithona* spp. (e.g. John et al. 2001, Licandro et al. 2001, Continuous Plankton Recorder Survey Team 2004, Eloire et al. 2010). The most common species occurring in the North Atlantic and adjacent seas have been recently presented in an ICES plankton leaflet (Mazzocchi 2019) that is mainly based on the comprehensive taxonomic review of Nishida (1985). *Oithona* species are mostly small and thin copepods whose abundance is certainly underestimated in mesozooplankton samples due to the typical use of 200 μm mesh nets (Gallienne and Robins 2001), and whose specific identification in routine analyses is in many cases rather difficult because it is based on the ornamentation of the swimming legs and mouthparts as well as the shape of the rostrum (Nishida 1985).

A clear latitudinal gradient appears in the distribution of *Oithona* richness, with only three species occurring in the Arctic and subArctic regions, seven in the eastern North Atlantic, and up to 23 in the Mediterranean Sea (Razouls et al. 2024). In this latter basin, the cooccurrence of congeneric species is characterized by their distinct seasonal peaks (e.g. Mazzocchi and Ribera d'Alcalà 1995), and contrasting distributional preferences in the horizontal (Mazzocchi et al. 2014) or vertical space (Scotto di Carlo et al. 1984, Lindegren et al. 2020). For example, *O. atlantica*, common in the ICES area, is quite difficult to distinguish from the closely allied *O. longispina* (Nishida 1985) with which it shares the Mediterranean epipelagic habitat. Similarly, *O. decipiens*, occurring in the Mediterranean Sea and in the Ibero-Moroccan area, is very similar to *O. similis* in its general shape and differentiates for spinulation on thoracic leg exopods.

Molecular analyses suggest that the cosmopolitan and often abundant *O. similis* is likely a species complex with distinct lineages separated by climate zones (polar and temperate), oceans (Atlantic and Pacific), and hemispheres (Arctic and Antarctic) (Cornils et al. 2017). Although no morphological differences have been described so far for the putative species within *O. similis* s.l. (Cornils et al. 2017), it is likely that morphometric diagnostic characters do exist. Shuvalov (1972) described significant differences in prosome lengths and cephalon shape between *O. similis* specimens from Arctic and North Atlantic water masses and based on these results he stated that *O. similis* might be a polytypic species with distinct temperature preferences. It has also been speculated whether *O. helgolandica* described by Claus (1863) and *O. similis* are synonymous (see review in Cepeda et al. 2016). Both descriptions, however, are incomplete and the description of *O. helgolandica* may also match with *O. nana* (Sars 1918).

Oithona setigera may also be a species complex that is widely distributed in the ICES regions. This is supported by Farran's (1929) previous suggestion of two groups for the Irish and Pacific specimens, as well as differences in size and other minor morphological characters that have been observed in open Mediterranean populations (MG Mazzocchi, personal observations).

The copepod species *O. davisae* has become increasingly abundant in the ICES area or has replaced native species such as *O. similis* or *O. nana* (Cornils and Wend-Heckmann 2015, Isinibilir et al. 2016, Pansera et al. 2021). *Oithona davisae* is native to the eutrophic coastal waters of East Asia with pronounced seasonality in hydrography and food availability (Nishida 1985, Uye and Sano 1998). During the past two decades, it has been introduced to many European coastal regions including e.g. the Black Sea (Temnykh and Nishida 2012, Isinibilir et al. 2016), the North Sea (Cornils and Wend-Heckmann 2015), the Bay of Biscay (Uriarte et al. 2016, Barroeta et al. 2020), and the Mediterranean Sea (Saiz et al. 2003, Terbıyık Kurt and Beşiktepe 2019, Vidjak et al. 2019, Pansera et al. 2021). The most likely vectors of its introduction are the ballast water tanks of ships, as has been suggested for the North Pacific (Choi et al. 2005). *Oithona davisae* is characterized by a strong ventrally pointed rostrum and thus easily distinguishable from indigenous species such as *O. similis* or *O. nana* in the Northern Atlantic (Ferrari and Orsi 1984, Cornils and Wend-Heckmann 2015). Additional morphological information is available in Nishida (1985) or Temnykh and Nishida (2012).

Paracalanus spp.

Species of the calanoid copepod genus *Paracalanus* are abundant in the pelagic shelf ecosystems of the Northern Atlantic and the Mediterranean Sea (Siokou-Frangou 1996, OBIS 2024b). Of the 12 accepted species (Walter and Boxshall 2024), 6 occur in the ICES area of the Northern Atlantic Ocean and the Mediterranean Sea: *P. aculeatus*, *P. denudatus*, *P. indicus*, *P. nanus*, *P. parvus*, and *P. quasimodo* (Razouls et al. 2024). One species, *P. tropicus*, occurs in subtropical to tropical regions of the Northern Atlantic Ocean (Khelifi-Touhami and Ounissi 2023). A molecular phylogeny confirmed the separation of the *Paracalanus* genus into two species groups (Cornils and Blanco-Bercial 2013): the *P. aculeatus* group (with *P. denudatus*) and the *P. parvus* group (all other *Paracalanus* species). Morphologically, the *P. aculeatus* and the *P. parvus* species group differ from each other in the segmentation of the antennules (Sewell 1929), and the morphometry of the fourth pair of thoracic legs (Cornils and Blanco-Bercial 2013).

In the ICES region, species of the *P. parvus* group are often abundant. While *P. nanus* is morphologically easy to distinguish from the other species due to its small size and the short antennules, the separation of the other three species, namely *P. parvus*, *P. indicus*, and *P. quasimodo* is based mainly on the differences in serration of the distal outer edges of the third exopods of the swimming legs and the shape of the cephalothorax (Bowman 1971, Bradford 1978, Bradford-Grieve et al. 1999, Khelifi-Touhami et al. 2007). Due to net sampling however, the distal parts of the swimming legs are often broken, making correct morphological identification often impossible. Recent molecular studies using the mitochondrial COI gene have shown that the abovementioned diagnostic characters of the three species are not persistent and that our knowledge on their distribution has to be revised (Cornils and Held 2014, Kasapidis et al. 2018, Di Capua et al. 2022). It was long assumed that the species *P. parvus* was widely distributed in the ICES region and also in other oceans. Based on the molecular results, the species *P. parvus* s.s., originally described from the North Sea (Claus 1863) appears to be restricted to the Northeastern Atlantic Ocean, including the Mediterranean Sea (Cornils and Held 2014, Kasapidis et al. 2018) and is not a panmictic species. Specimens from the northwestern Atlantic Ocean are morphologically indistinguishable from *P. parvus* s.s., but are genetically divergent and thus belong to a putative new species (Cornils and Held 2014). In the Mediterranean Sea, a molecular study revealed that not *P. parvus*, but the subtropical *P. quasimodo* is the most abundant *Paracalanus* species (Kasapidis et al. 2018). *Paracalanus parvus* s.s. is only found in the northern parts of the Mediterranean and the Black Sea. The subtropical *P. indicus* occurs in low numbers in the Mediterranean Sea.

Pseudocalanus spp.

In contrast to the species complexes in the previous chapters, in which recent molecular studies revealed a whole species complex hidden behind a single species name, interspecific morphological differentiation and potential cooccurrence of cryptic species have been discussed for the calanoid copepod genus *Pseudocalanus* for some time. Based on morphology, Frost (1989) suggested that the genus comprises seven species in total (*P. acuspes*, *P. elongatus*, *P. moultoni*, *P. minutus*, *P. major*, *P. mimus*, and *P. newmani*), using e.g. the shape of the cephalosome, ornamentation of the thoracic segments, and length ratios between urosome segments. Today, the validity of *P. major* is subject to discussion leaving six accepted species for this genus (Walter and Boxshall 2024). All species have been reported to occur in the North Atlantic Ocean (Corkett and McLaren 1979, Frost 1989). However, the species are remarkably similar morphologically and several lack diagnostic characters preventing routine microscopic identification, while the mitochondrial COI barcode region has proven to be reliable for discriminating and identifying the species (Bucklin et al. 1998, 2001, 2003, Unal et al. 2006, Aarbakke et al. 2011, Laakmann et al. 2013, Bailey et al. 2016, Questel et al. 2016). Species delimitation by morphological parameters seems to be less unambiguous than originally assumed. And while investigations show morphological differences between species that have so far been overlooked (Markhaseva et al. 2012), this species group is often being assigned to a cryptic species complex highlighting the fluidity of the taxonomic categories used in this review.

The congeners have been shown to exhibit unique life history characteristics and distinct ecological roles in the pelagic ecosystem (Cleary et al. 2016, Aarbakke et al. 2017, Crouch et al. 2020, Ershova et al. 2021) as well as different patterns of population connectivity and phylogeography in the

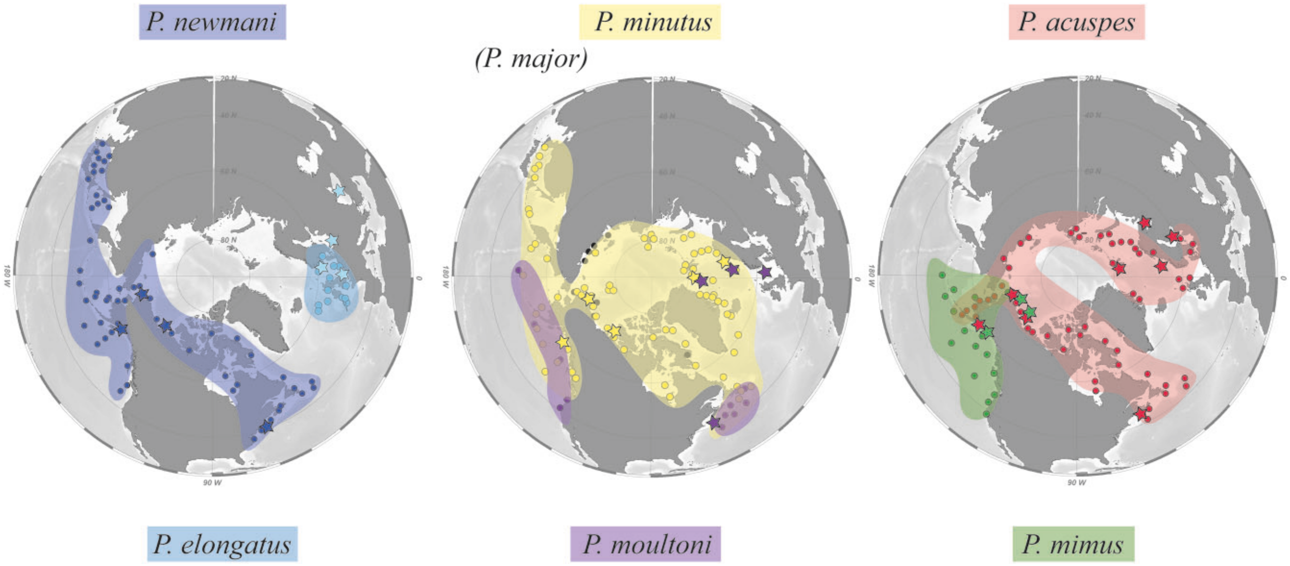

Figure 3. *Pseudocalanus* species in the North Atlantic and adjacent seas, modified from Aarbakke et al. (2014), dots or squares = species detected by morphological species identification modified from Frost (1989) and Markasheva et al. 2012 stars = species detected by genetic species identification modified from Bucklin et al. (1998, 2001, 2022), Questel et al. (2016), Unal et al. (2006), Grabbert et al. (2010), Aarbakke et al. (2011), Holmborn et al. (2011), Laakmann et al. (2013), Crouch et al. (2020), Ershova et al. (2021).

Atlantic (Aarbakke et al. 2011, 2014). They exhibit distinct biogeographical distributions, although with significant areas of overlap. This species complex exemplifies how integrating genetic and morphological studies can complement and validate each other (Fig. 3), effectively characterizing species distributions. For instance, this approach facilitated the detection of *P. moultoni* in the North Sea (Laakmann et al. 2013) and identified distributional boundaries with potentially low abundances, such as *P. elongatus* in the Baltic Sea (Grabbert et al. 2010).

Clausocalanus spp.

Clausocalanus, one of the calanoid copepod genera most widespread worldwide, occurs in the ICES basins with 11 of its 13 species (Razouls et al. 2024). The most common representatives in those regions are *C. arcuicornis*, *C. furcatus*, *C. jobei*, *C. lividus*, *C. mastigophorus*, *C. parapergens*, *C. paululus*, and *C. pergens* (e.g. Williams and Wallace 1975, Fragopoulu et al. 2001, Continuous Plankton Recorder Survey Team 2004, Licandro and Icardi 2009, Mazzocchi et al. 2014, Wootton and Castellani 2017). These species occur both in offshore and coastal waters and inhabit mainly the epipelagic layers, although some of them have a more extensive vertical distribution (Scotto di Carlo et al. 1984). Clear differentiations of their ecological niches have been revealed, for the most abundant species, based on their seasonal occurrence and succession (Mazzocchi and Ribera d'Alcalà 1995, Peralba and Mazzocchi 2004, Mazzocchi et al. 2011) and latitudinal distribution (Schnack-Schiel et al. 2010, Peralba et al. 2017). The ecological, biological, and taxonomic features of *Clausocalanus* have been recently synthesized in an updated ICES plankton leaflet (Mazzocchi 2020). The morphological identification of *Clausocalanus* species is not straightforward because, for females, it is based on the shape of the seminal receptacle (Frost and Fleminger 1968). Although this character is visible at high magnification at the stereomicroscope in specimens fixed with formalin, it is more difficult to distinguish in samples fixed with ethanol. Males are even more arduous to discern (Frost and Fleminger 1968), and copepodites are often grouped with those of *Paracalanus*, *Pseudocalanus*, and *Ctenocalanus* because of their similar general characteristics. Molecular tools such as a restriction fragment length procedure can facilitate the identification of these stages (Blanco-Bercial and Alvarez-Marques 2007), also allowing to separate them from the other genera. The ability to identify both sexes and the juvenile stages will improve our knowledge of *Clausocalanus* diversity and population structure (e.g. Peralba et al. 2017) to further understand their adaptations to the different ICES regions. Molecular investigations on intraspecific divergence are scarce in *Clausocalanus* and have only been found in *C. lividus* differentiating Atlantic and Pacific populations so far (Blanco-Bercial et al. 2011), but none pertains to the ICES region.

Calanus spp.

Some taxa play key roles in marine ecosystems, due to their numbers and biomass, or may be used as indicators of water masses. Therefore, their correct identification is extremely important, although sometimes it requires highly laborious identification with efforts that might be beyond resources for routine, time-series analyses. A good example of such taxa present in the ICES area are four representatives of the calanoid copepod *Calanus* species complex: *C. helgolandicus*, *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*, which are morphologically similar, especially as young development stages. Although they have overlapping geographic ranges, there is a latitudinal gradient in their distribution: *C. helgolandicus* is regarded as a more temperate species, *C. finmarchicus* as a North Atlantic one, and *C. glacialis* and *C. hyperboreus* are the Arctic congeners; however, the northern species are being gradually replaced by the respective southern ones due to climate change (Beaugrand et al. 2002a, Chust et al. 2014, Weydmann et al. 2014a). While *C. hyperboreus* copepodites of stage 4 and older are easily identified by morphology and size (Brodskii et al. 1983), the identification of the congeneric species *C. helgolandicus*, *C. finmarchicus*, and *C. glacialis* is still problematic, especially in the areas of their cooccurrence (North Sea and the European Arctic, respectively). Morphological differences between these three species, such as: structure of the first basipodite of female fifth pair of thoracic legs and structure of fifth pair of legs in males, shape of forehead and its internal structures, and shape of posterolateral margin of the last thoracic segment and the genital segment, as well as the pore signature patterns of female urosome (Fleminger and Hulsemann 1977), are hardly used in ecological research due to their time-consuming examination and limitation of the method to older life stages. Therefore, in a long-term time series, such as the Continuous Plankton Recorder, only species-specific abundance for the copepodite stage 5 and adults of *C. helgolandicus* and *C. finmarchicus* are reported (Wilson et al. 2015). A common method to distinguish *C. finmarchicus* and *C. glacialis* is based on differences in size of the prosome, although this approach is inaccurate because the species may overlap in sizes in areas where they cooccur (Lindeque et al. 2006, Weydmann and Kwaśniewski 2008, Gabrielsen et al. 2012) and show high plasticity depending on environmental conditions (Trudnowska et al. 2020). Despite species morphological similarities, genetic identification of *Calanus* congeners is possible at any development stage with the use of different molecular tools (Hill et al. 2001, Lindeque et al. 2006, Gabrielsen et al. 2012, Weydmann et al. 2014b, Weydmann et al. 2017, Choquet et al. 2018).

There has been an ongoing discussion about hybridization between *C. finmarchicus* and *C. glacialis* (Parent et al. 2012, 2021, Choquet et al. 2020, 2023). However, a recent publication with advanced genetic tools (SNPs and transcriptomes) and a reassessment of existing genetic data has found no evidence for hybridization in these two species (Choquet et al. 2023), suggesting that despite their morphological similarity and sympatric occurrence, the reproductive timing may act as a barrier for hybridization.

Metridia spp.

In the ICES regions, seven species of the calanoid copepod genus *Metridia* have been found: *M. brevicauda*, *M. discreta*, *M. longa*, *M. lucens*, *M. pacifica*, *M. princeps*, and *M. venusta* (O'Brien et al. 2024). The most widespread species in temperate and boreal waters of the Atlantic and Pacific Oceans is *M. lucens*. In the Arctic Ocean, this species is considered as an expatriate species of Atlantic origin (Kosobokova et al. 2011). Originally, *M. lucens* was described from the North Sea off the Norwegian coast (Boeck 1865). Based on morphological differences in the shape of the head and the length of the setae of the fifth swimming leg of the females, Brodsky (1950) described a new, closely related species from Northern Pacific waters (*M. pacifica*), although these characteristics are variable (Bradford-Grieve 1999b).

First molecular results confirmed a separation of North Atlantic and North Pacific specimens (Bucklin et al. 1995). However, not all specimens of Pacific origin can be attributed to *M. pacifica* described by Brodsky (1950), as they show a variation of morphological characteristics intermediate between *M. lucens* and *M. pacifica* (Mazzocchi et al. 1995, Bradford-Grieve 1999b). However, a recent study confirmed the presence of both *M. pacifica* and *M. lucens* with distinct biogeographies in the northern Pacific (Hirai et al. 2022). Further research comparing COI haplotypes showed that *M. lucens* significantly differed between ocean basins (Atlantic–Pacific), and also regional isolation between the NW Atlantic and the NE Atlantic Ocean was observed (Blanco-Bercial et al. 2014). Similar regional isolation and evidence of cryptic species has been observed in *M. lucens* north and south of the Polar front in the Southern Ocean (Stupnikova et al. 2013). Further investigations are necessary to elucidate the status of *M. pacifica* and the putative cryptic speciation within *M. lucens*.

Oncaea spp.

The Oncaeidae is a large family of planktonic copepods, very abundant from neritic areas to open seas and from epipelagic to deep waters (e.g. Boxshall and Halsey 2004, Razouls et al. 2024, 2024). The ecological traits and the role played by Oncaeidae in planktonic communities are poorly known (Böttger-Schnack 1992, Böttger-Schnack and Schnack 2009) and many aspects of their biology are still not completely understood. The taxonomic allocation of Oncaeidae is currently under debate. This family is within the order Cyclopoida (Walter and Boxshall 2024), while some authors place Oncaeidae within Poecilostomatoida (e.g. Boxshall and Halsey 2004, Razouls et al. 2024). Also, at genus level the classification is debatable (Heron and Frost 2000, Boxshall and Halsey 2004, Di Capua et al. 2017). Currently, 70 different species of the genus *Oncaea* are reported worldwide (Razouls et al. 2024, 2024). A combination of several microscopic characters is necessary to identify species within the genus *Oncaea s.s.* (Böttger-Schnack 2001). In recent years, further morphological studies have been carried out to improve oncaeid taxonomy and additional morphological characters have been proposed to distinguish *Oncaea* species (e.g. Böttger-Schnack 1999, 2001, Di Capua and Boxshall 2008, Böttger-Schnack and Schnack 2013). Overall, *Oncaea* species identification requires advanced taxonomic expertise, and, in many cases, diagnostic morphological details are visible only using scanning electron microscopy technique. The revised genus *Oncaea s. str.* includes eight species *(O. venusta*, *O. mediterranea*, *O. media*, *O. scottodicarloi*, *O. curta*, *O.waldemari*, *O. clevei*, and *O. paraclevei*), five of which occur in ICES basins. Taxonomic studies have shown that many apparently well-known species, such as *O. venusta* and *O. media*, are complexes of closely related, yet distinct, species (Heron and Frost 2000, Elvers et al. 2006, Böttger-Schnack and Machida 2011). Only few molecular studies have been conducted so far to disentangle the phylogenetic relationship and connectivity within the Oncaeidae (Böttger-Schnack and Machida 2011, Di Capua et al. 2017). Taxonomic features of *Oncaeidae* have been recently synthesized in an updated ICES plankton leaflet (Böttger-Schnack and Schnack 2025).

Temora spp.

Only three copepod species of *Temora* are known from the North Atlantic, all of which are distinct in morphology (Di Capua 2021) and COI barcodes (GenBank). Based on current knowledge, no cryptic speciation is suspected within the genus. The reason for including this genus anyway in the review despite this, is that there is a high degree of morphological similarity between the congeners *T. turbinata* and *T. longicornis*, with differences observed primarily in the caudal rami and anal segment length. This similarity poses a high risk of misidentification and undetected invasion. *Temora turbinata* was classified as a NIS in Brazilian waters (Soares et al. 2018) and was reported once from the English Channel (OBIS 2024c) as a potential indicator of warm water inflow (Beaugrand et al. 2002b). While it has been observed regularly in neritic water of the NW Atlantic (OBIS 2024c), its distribution in European waters is much less certain.

Euterpina acutifrons

The copepod *Euterpina acutifrons* is recognized as a globally distributed warm-water species. It spans diverse regions from the southern coast of Norway to the Brazilian coast, with extensive records in Oceania, the Mediterranean, and both North American coasts (Lang 1948, Walter and Boxshall 2024). It has been found in ballast water tanks as confirmed morphologically in the Mediterranean and European coastal waters (Choi et al. 2005, David et al. 2007, Cabrini et al. 2019). Metabarcoding studies indicate its presence to British Columbia, Svalbard, and Australian waters (Takahashi et al. 2020, Van den Heuvel-Greve et al. 2021, Bailey et al. 2022). However, the presence in metabarcoding studies, coupled with the prior absence of observations of the species e.g. in the Arctic, suggests a recent introduction, still low in abundance. Morphological variability within *E. acutifrons* has been observed, particularly in males (Haq 1965, Stancyk and Moreira 1988), resulting in distinctly different male-types. Breeding experiments indicate that these differences are rather intraspecific variation and not an indication of a sympatric species complex (Haq 1972). While morphological and molecular approaches seemingly agree on a cosmopolitan distribution, molecular data of the East Atlantic population introduces the possibility of undiscovered cryptic diversity within *E. acutifrons* (Blanco-Bercial et al. 2014). Further scrutiny, especially in remote locations, is recommended to unravel potential hidden diversity within this species (Blanco-Bercial et al. 2014)

Diplostraca

Only eight diplostracan branchiopod species (formerly known as cladocerans) from five genera are truly marine (Egloff et al. 1997): *Evadne nordmanni* and *E. spinifera*, *Pleopis polyphemoides* and *P. schmackeri* (the latter mainly distributed outside the North Atlantic area), *Podon leuckartii*, *P. intermedius*, *Pseudevadne tergestina*, and *Penilia avirostris*. Furthermore, the endemic *Bosmina coregoni* as well as the NIS Ponto-Caspian *Cercopagis pengoi* and *Evadne anonyx* occur in the brackish environment of the Baltic Sea (Möllmann et al. 2002, Telesh and Ojaveer 2002, Rodionova and Panov 2006, Telesh et al. 2008). This introduction of NIS diplostracan species is observed also in other basins. For example, *P. schmackeri* of Indo-Pacific origin has recently arrived into the Levantine Sea (Eastern Mediterranean), where it was found for the first time in 2012 and has become abundant since then (Terbiyik-Kurt and Polat 2018). For the currently known and described marine taxa, as well as for *B. coregoni* and *C. pengoi* in the Baltic Sea, the challenges in identification are mainly due to the small size of the organisms and their delicate bodies, as all these species are well described and easily distinguishable by distinct morphological characteristics (see Onbé 1999 and references therein). The occurrence of cryptic species has not been mentioned so far in marine diplostracans. A phylogenetic analysis of six marine species, based on COI, has supported an ancient radiation of Podonidae and a recent worldwide expansion of Sididae and has highlighted the identity or high similarity of haplotypes in different oceans (Durbin et al. 2008). The worldwide distribution of *P. avirostris* has been reviewed by Della Croce and Venugopal (1972) and that of six of the seven marine podonid species by Mordukkai-Boltovskoy and Rivier (1987).

Gelatinous plankton

Sagitta spp.

Chaetognaths are a small phylum with only two orders and 120 species, but are widely distributed in many marine ecosystems. In ICES ecoregions, 28 epi- and mesopelagic species occur of which 20 species belong to the genus *Sagitta* (Pierrot-Bults 2020). Identification of chaetognaths is not straightforward, requires substantial taxonomic expertise and chaetognaths are often only identified in time series samples to genus or phylum levels. The general morphological simplicity of the phylum has led to much debate about chaetognath taxonomy specifically whether to divide the genus *Sagitta* into multiple genera or to maintain the original classification (Tokioka 1965, Bieri 1991). Resolving this taxonomic debate will likely require a comprehensive approach integrating both morphological and molecular data. Several studies examining mitochondrial DNA variation within species uncovered unusually high levels of genetic variation, often combined with spatial genetic structure, and suggest the presence of cryptic species (Peijnenburg et al. 2004, 2006, Jennings et al. 2010, Miyamoto et al. 2012, Kulagin et al. 2014). For example, the coastal species *Sagitta setosa* (accepted as *Parasagitta setosa*), which is abundant in the North East Atlantic, Mediterranean, and Black Sea, shows genetic isolation among populations in different European basins (Peijnenburg et al. 2004, 2006). Additionally, highly divergent mitochondrial lineages were found that did not match morphology, geography or nuclear DNA (Peijnenburg et al. 2005, 2006). Marlétaz et al. (2017) showed that by analyzing entire mitochondrial genomes combined with nuclear genetic markers, chaetognaths have unusual patterns of mitochondrial evolution and can have extreme levels of mitochondrial diversity without reproductive isolation. Therefore, conclusions about cryptic speciation in chaetognaths cannot be drawn in the absence of information from the nuclear genome.

Aurelia spp.

The cosmopolitan genus *Aurelia* hides considerable cryptic diversity (Dawson and Jacobs 2001, Schroth et al. 2002, Dawson 2003, Lawley et al. 2021) and the number of valid species remains subject to ongoing debate (Mayer 1910, Kramp 1965, Dawson and Jacobs 2001, Jarms and Morandini 2019, Collins and Morandini 2025). By 2021, WoRMS listed 11 described *Aurelia* species, out of which 7 were genetically characterized (Dawson and Jacobs 2001, Dawson et al. 2005, Scorrano et al. 2016, Brown et al. 2021, Collins and Morandini 2025), while genetic studies had identified 17 additional clades, which were previously only numbered. Lawley et al. (2021) attempted to resolve the problem by classifying several of these clades based solely on genetic data without accompanying morphological descriptions, an approach that also faced criticism (Brown and Gibbons 2022, Lawley et al. 2022).

Based on the current taxonomic status, the moon jelly *A. aurita* is not the only species observed in the ICES region (Lawley et al. 2021, Moura et al. 2023) as there are at least seven recorded *Aurelia* species: *A. hyalina* (Greenland), *A. coerulea* (NE Atlantic and Mediterranean), *A. aurita* (North Atlantic, Black Sea, and Baltic Sea), *A. solida* (Mediterranean), recently described *A. pseudosolida* (Adriatic Sea), *A. relicta*

(Adriatic Sea—Mljet lakes), and *A. persea* (East Mediterranean) (Scorrano et al. 2016, Lawley et al. 2021, Garić and Batistić 2022, Gittenberger et al. 2023). *Aurelia solida* seems to be the main bloom forming species in the coastal waters of the Mediterranean Sea, while *A. aurita* is the same for the Black Sea, North Atlantic, and Baltic area. *Aurelia coerulea* inhabits ecosystems with less stable hydrological conditions compared to the open sea (Scorrano et al. 2016). *Aurelia relicta* is an endemic species from marine Mljet lakes (Adriatic), while *A. persea* is a recently resurrected species based on genetic data of an *Aurelia* species from the East Mediterranean (Lawley et al. 2021). A recent paper by Moura et al. (2023) presented morphological and genetic evidence for another two *Aurelia* species from the Azores, which are still not formally described.

Overall, the *Aurelia* species complex remains challenging as species are very difficult to identify based on morphology. Morphological characters are e.g. the number of marginal tentacles, the morphology of gonads, manubrium, and rhopalia or the number and organization of radial canals. Many species can only be reliably identified through genetic analysis. Some authors overcome this challenge by referring to *A. aurita* s.l. (e.g. Suzuki et al. 2018, Goldstein and Javidpour 2023). We want to emphasize here that species identification and the use of the term *A. aurita* in many publications has to be approached with caution.

Cyanea spp.

The taxonomy of the scyphozoan genus *Cyanea*, which is widely distributed in neritic waters of the target region and beyond, is not fully resolved. While WoRMS currently lists 18 species of *Cyanea* as valid (Collins and Morandini 2025), assessing the actual diversity in the genus is currently not possible (Jarms and Morandini 2019), and a taxonomic revision integrating morphological and molecular data is required. Recent molecular studies have suggested undescribed cryptic diversity among *Cyanea* from Canadian waters (Hotke 2015), and studies on *Cyanea* specimens collected at the northwest Atlantic coast (Niantic River, Chesapeake Bay, and Gulf of Mexico) revealed the occurrence of two species not identical to *Cyanea capillata* (Bayha 2005). Agassiz (1862) already differentiated three species with morphological differences in color, shape of marginal lappets, size of oral folds, and the dimensions of the subumbrellar muscles and with successive core distribution areas along the east coast of North America from north to south: *C. arctica*, *C. fulva*, and *C. versicolor*. Fewkes (1881) interpreted the morphological differences between the three species as variations and combined them under the name *C. arctica*. Later *C. arctica*, *C. fulva*, and *C. versicolor* were considered to be varieties of *C. capillata* (Mayer 1910, Stiasny and van der Maaden 1943, Kramp 1961). To clarify whether *C. fulva* and *C. versicolor* are valid species in the northwestern Atlantic as recently suggested (Jarms and Morandini 2019, Collins and Morandini 2025), additional studies combining molecular and morphological approaches are needed. Three species are known to occur in European waters: *C. capillata*, *C. lamarckii*, and the recently described *C. tzetlinii* (Kolbasova et al. 2015). *Cyanea capillata* is found throughout the region and is sympatric with both *C. lamarckii*, which has the core of its distribution in the North Sea and around the British Isles, and *C. tzetlinii*, which has so far only been recorded from the White Sea. The main diagnostic difference between *C. capillata* and *C. tzetlinii* is the presence of a rhopalial bulb with an eyespot in the latter species (Kolbasova et al. 2015). Combined morphological and molecular genetic analysis confirmed that *C. capillata* and *C. lamarckii* can be differentiated by diagnostic morphological features as well as by mitochondrial (COI) and nuclear (18S rDNA) gene fragments (Holst and Laakmann 2014). However, a morphological differentiation between the two species requires close inspections whereas the simple identification based on the bell color is not reliable, because of high color variations in the "blue jellyfish" *C. lamarckii*, which can also be yellow (Holst and Laakmann 2014). Gastrovascular intrusions into the circular and radial muscle folds are present in *C. capillata* in specimens with a rhopalar diameter >10 mm but are not found in *C. lamarckii* specimens in any size, whereas *C. lamarckii* medusae with a rhopalar diameter of <10 mm can be distinguished from *C. capillata* by the presence of conspicuous papillae at the central exumbrella (Holst and Laakmann 2014). As these characters require closer morphological scrutiny of the specimens, reliable identification is probably often only made to the genus level (e.g. Køhler et al. 2022).

Rhizostoma spp.

All three species of the rhizostome jellyfish genus *Rhizostoma*: *R. pulmo*, *R. octopus*, and *R. luteum* occur in European waters, and studies integrating molecular data suggest that these three species are indeed valid (Prieto et al. 2013). *Rhizostoma octopus* occurs in Atlantic waters of western Europe with a distribution range from the Scottish Clyde Sea area down to the Bay of Biscay (Russel 1970, Lilley et al. 2009, Lee et al. 2013), while *R. luteum* is found in Atlantic waters from Portugal down the west coast of Africa and in the western Mediterranean (Alboran Sea) (Kienberger and Prieto 2018). *Rhizostoma pulmo* is distributed in the Mediterranean Sea and adjacent waters, e.g. Black Sea and Adriatic Sea (Mariottini and Pane 2010, Leoni et al. 2021). All three species can reach large bell diameters of >600 mm (Elliot et al. 2017, Kienberger et al. 2018). *Rhizostoma octopus* and *R. pulmo* often appear in blooms and haplotype network analyses revealed that both species occur in geographically separated populations (Lee et al. 2013, Glynn et al. 2015, Ben Faleh et al. 2017). The two species have very similar morphology, and thus, *R. octopus* has been regarded as a variety of *R. pulmo* by some earlier authors (Mayer 1910, Kramp 1961), leading to incorrect reports of *R. pulmo* in the North Sea (e.g. Dittrich 1988). To date, there is only one obvious morphological character that can be used to distinguish the two species: the number of velar lappets that is on average ten per octant in *R. octopus* but has been reported to be always eight per octant in *R. pulmo* (Russel 1970, Kienberger and Prieto 2018). However, species identification by this morphological difference should be regarded with caution, since the number of velar lappets increases with medusa growth (Russel 1970). Moreover, detailed observations have shown that the number of velar lappets is not only variable between specimens but also varies between octants of the same specimen in *R. octopus* (Russel 1970), as well as in *R. pulmo* (Holst and Laakmann, unpublished). *Rhizostoma luteum* has been regarded as a rare species (Prieto et al. 2013) before it was frequently reported from the Alboran Sea, where its distribution overlaps with *R. pulmo* (Kienberger and Prieto 2018). Although the morphology of *R. luteum* differs remarkably from its congeners in lacking the distinct blue color of the marginal lappets and in forming very long oral arm appendages, it is likely that, in the past, the species has often been misidentified in the Mediterranean Sea. It can be confused with the Mediterranean species *R. pulmo*, or the morphologically similar rhizostome medusa *Catostylus tagi*, that differs from species of the genus *Rhizostoma* only by the structure of its oral arms (Kienberger and Prieto 2018).

Muggiaea spp.

Only four species of the siphonophore hydrozoan jellyfish genus *Muggiaea* are recognized globally (Schuchert 2024), of which only *M. delsmani* does not occur in the ICES ecoregions (Totton 1965). *Muggiaea bargmannae* is considered a bipolar species, but in the Northern Hemisphere it has been detected as far as mid-Atlantic Ridge near the waters off the British Isles (Hosia et al. 2008). The remaining two congeneric forms, *M. atlantica* and *M. kochii*, are frequently found within European waters (Blackett et al. 2017, and references therein). Although taxonomic identification of the two is possible, it is tedious, since their nectophore morphology differs only in the depth of hydroecium and the length of somatocyst (Totton 1965). Moreover, this applies only to the nectophore-bearing polygastric stage in their life cycle, whereas the sexually reproducing eudoxids remain morphologically indistinguishable (Totton 1965). These species represent differing thermal preferences, with *M. atlantica* more typical for warmer waters, and *M. kochii* preferring colder waters (Blackett et al. 2014). Spatial avoidance between the two species has been suggested (Mackie et al. 1988) and distinguishing between them in surveys is of interest as climate-driven changes in their distributions and relative dominance have been proposed (e.g. Licandro et al. 2012, Batistić et al. 2013).

Obelia spp.

More than 100 species of Hydrozoa *Obelia* have been described over the years, but to the date, only four valid species with wide or cosmopolitan distributions are recognized: *O. bidentata*, *O. dichotoma*, *O. geniculata*, and *O. longissima* (Cornelius 1975, 1982, 1990). While several morphotypes of *Obelia* medusae have also been described, these cannot be unambiguously connected to specific hydroids, and reliable morphological species identification is not possible for the medusae (Laakmann and Holst 2014), but only for the hydroid stage (Cornelius 1990, 1995). However, more recent molecular data suggest that the cosmopolitan species recognized by Cornelius (1990) may indeed contain cryptic diversity (e.g. Govindarajan et al. 2005), and the 299 public records with sequences in the BOLD database form no less than 29 BINs (clusters) (boldsystems.org, accessed 24 May 2024). It is thus prudent to identify the planktonic *Obelia* hydromedusae to genus level only.

Clytia spp.

The medusa-producing *Clytia hemisphaerica* and *C. gracilis* are by far the most commonly recorded species in the genus, which comprises over 50 accepted species (Schuchert 2024), with 3952 and 736 globally distributed records, respectively, out of the total 7585 records of *Clytia* in the Global Biodiversity Information Facility (GBIF) (24 May 2024). Both species are common in the ICES region. However, these two supposedly cosmopolitan and ubiquitous species are part of a larger, poorly resolved species complex. The medusa stages of *C. gracilis* and *C. hemisphaerica* cannot be reliably separated based on morphology, and genetic identification within the genus is also fraught with peril. Sequences assigned to *C. hemisphaerica* or *C. gracilis* in BOLD and GenBank fall in numerous clusters, suggesting cryptic diversity, and there is reason to suspect that many specimens connected to these sequences may also have been misidentified. Cornelius (1995) states that difficulties in identification within the genus make nearly all records supporting the near-cosmopolitan distribution of *C. hemisphaerica* suspect. The conspecific medusa *C. languida* has also been recorded from the North Sea, based on a comparison with sequences from GenBank (Laakmann and Holst 2014). However, the medusa stage of *C. languida* is morphologically inseparable from *C. hemisphaerica* and solely identified based on area of occurrence (Kramp 1959), and is currently regarded as synonymous to *C. hemisphaerica* (Schuchert 2024). Therefore, morphological identification of *Clytia* medusae of type *C. hemisphaerica/gracilis* should not be attempted, and caution should also be exercised if assigning a species based on molecular data from e.g. GenBank.

Beroe spp.

Species identification and delimitation of the ctenophore genus *Beroe* is often uncertain and many species may become synonymized in future studies (Mills 2024) or new species being described. In 2024, the European Register of Marine Species lists four species as occurring in European waters: *B. cucumis*, *B. forskalii*, *B. gracilis*, and *B. ovata*. However, also *B. abyssicola* has been commonly observed in the European side of the Arctic (Ciambelli 2023; A. Hosia and S. Majaneva, personal observation), as well as in the Norwegian and Icelandic Seas (Licandro et al. 2015, Neitzel et al. 2021).

There has been considerable confusion particularly regarding *B. cucumis* and *B. ovata* (Bayha et al. 2004, Shiganova and Abyzova 2022) further compounded by the suggested existence of two potentially undescribed species named *B. "norvegica"* and *B. "anatoliensis"* along the coast of Norway and Turkey (Johansson et al. 2018). However, a subsequent study (Shiganova and Abyzova 2022) synonymized *B. "norvegica"* with north Atlantic *B. cucumis* (see Table S1), and *B. "anatoliensis"* with *B. mitrata*, native to the Mediterranean. Shiganova and Abyzova (2022) also clarified some of the confusion around the nomenclature of *B. cucumis* and *B. ovata*, concluding (1) that the species name *B.ovata* should be used for the species native to the western Atlantic coasts, and (2) that the Mediterranean species, which was first incorrectly characterized as *B. ovata*, and later as *B. cucumis* (*sensu* Mayer 1912) is genetically distinct from *B. cucumis*, and was thus described as *B. pseudocucumis* sp. nov. However, the latter species is currently unaccepted in WoRMS due to not being compliant with the ICZN code.

Overall, the collection and preservation of ctenophores is challenging, and of all observations logged in the GBIF, 30% are identified to genus level only (GBIF.org accessed 03 June 2024). It is important to emphasize that even when species level identification exists, the use of the names *B. cucumis* and *B. ovata* in particular in many publications should be approached with caution. For young specimens, accurate species identification is dependent on molecular tools, yet sometimes requiring use of multigene approach, but for live larger specimen morphological identification is possible, although hampered by the lack of identification literature. In addition to the body shape, which can be somewhat plastic, characters such as the branching and anastomoses of the meridional canals, the relative lengths of the comb rows, and macrocilial patterns can be diagnostic.

Appendicularia

Appendicularians are often determined only to the class level (Appendicularia) or the family level (Oikopleuridae, Fritillariidae, and Kowalevskiidae). Species-level identification is challenging for nonexperts due to subtle morphological differences and the general fragility of these organisms, which are frequently damaged during sampling with plankton nets (Hopcroft 2005). There have been indications of cryptic diversity within Appendicularia, based on slight morphological differences in some species. For instance, variations in the arrangement of oikoblasts in *Oikopleura longicauda* (Flood 2005) and differences in tail morphology in *O. villafrancae* and *Fritillaria fagei* from different basins (Hopcroft 2005, Hopcroft and Robison 2005) suggested cryptic diversity. To this date the true number of Appendicularia species remains an open question (Garić and Batistić 2010) with speculations that the actual number could be twice the current estimate (Hopcroft 2005). The advent of molecular methods has raised hopes for resolving appendicularian cryptic diversity (Hopcroft 2005). However, the presence of poly-T inserts in mtDNA in many appendicularian species (Albaina et al. 2024) and the scarcity of taxonomists have limited genetic diversity and cryptic species investigations in this group (Sherlock et al. 2017, Masunaga et al. 2022). Recent investigations have provided evidence of existence of cryptic species within two commonest coastal oikopleurid species: *O. dioica* and *O. longicauda*. *Oikopleura dioica* is now understood to be a complex of at least three cryptic species (Masunaga et al. 2022). This is likely also true for *O. longicauda*, as suggested by morphological (Flood 2005) and genetic evidence (Garić et al. 2018, Albaina et al. 2024). Given the limitations of using mtDNA genes in appendicularian diversity research, alternative markers are needed. One promising alternative seems to be the ITS (Internal transcribed spacer) region (Masunaga et al. 2022).

Limacina spp.

The most abundant species of shelled pteropods belong to the Limacinoidea, which are characterized by thin left-coiling shells up to 1 mm in size. The species that has been referred to as “the most abundant gastropod in the world” is *Heliconoides inflatus*, formerly known as *Limacina inflata* (Janssen 2012). This species is easily recognized by the “inflated shell,” has a worldwide distribution and is highly abundant in Atlantic and Mediterranean waters. The genus *Limacina* is currently composed of six accepted species (MolluscaBase 2024) with five species commonly found in ICES ecoregions. There are three warm-water species with (sub)tropical distributions: *L. bulimoides*, *L. trochiformis*, and *L. lesueurii*, and two cold-water species with bipolar or antitropical distributions: *L. helicina* and *L. retroversa*. Though nominal species can be fairly easily recognized based on shell shape, at least as adults (e.g. Choo et al. 2023a), *Limacina* spp. are generally not identified to species level in time series samples. Molecular data has revealed substantial genetic diversity within the nominal species *L. bulimoides* (Choo et al. 2021, 2023b), *L. helicina* (Hunt et al. 2010, Sromek et al. 2015, Kohnert et al. 2020, Shimizu et al. 2021) and *L. retroversa* (Peijnenburg and Spagliardi, unpublished data) suggesting the presence of cryptic species. Specifically, using mitochondrial and >100 000 genome-wide SNP markers on worldwide samples of *L. bulimoides*, Choo et al. (2023b) showed that there are at least three genetic lineages. These lineages are reproductively isolated, yet morphologically indistinguishable based on shell shape and are thus regarded as cryptic species. For the cold-water species, variations in shell shape and genetic differentiation are reported, usually associated with different geographic areas, and several subspecies are described leading to considerable confusion. Taxonomic revision integrating molecular and morphological data with original species descriptions and type material is urgently needed, especially as these cold-water species are the most commonly used as bioindicators, and the most impacted by ocean acidification (e.g. Mekkes et al. 2021, Hofmann Elizondo et al. 2024).

Relevance of species complexes for understanding ecosystem dynamics

Species identification is a cornerstone in biodiversity research, crucial for understanding ecosystem dynamics and guiding ecosystem conservation efforts. We have highlighted the taxonomic challenges of achieving precise species-level identification in many zooplankton groups, revealing a substantial uncertainty in species-resolved data, even within key taxa in pelagic coastal ecosystems. This, in turn, may affect not only the uncertainty of biodiversity assessments but also of the ecological interpretations resulting from the data. We have shown that integrative approaches in taxonomy, using morphological characters and molecular markers, often paint a more complex picture of species and ecosystems (Hirai et al. 2017, Semmouri et al. 2021) and sometimes reveal unexpected high numbers of cryptic species under a single species name (Adams et al. 2014). Ultimately, these challenges posed by species complexes unveil that the true essence lies in understanding what defines a species.

The concept of what constitutes a species has been a subject of debate among taxonomists for centuries. Since Carl von Linné established a morphological basis for species identification nearly 300 years ago (Linné 1735), various species concepts have emerged, each addressing different aspects of species differentiation. The “Biological Species Concept,” introduced by Ernst Mayr, defines species based on their reproductive isolation (Mayr 1942). Based on this concept, Theodosius Dobzhansky developed his evolutionary ideas regarding the significance of genetic variation within the “Biological Species Concept” (Dobzhansky 1963) laying the foundation for the development of the “Molecular Species Concept,” which is finally based on genetic divergence. The practical applicability of this concept was boosted by the fundamental discovery of the structure of DNA (Watson and Crick 1953) and has continued to evolve with studies using a variety of single and multiple genetic markers as well as whole-genome information and single nucleotide polymorphisms to assess genetic diversity and to delineate species. However, this delineation can be more complex than commonly assumed. Genetic diversity within a potential species can vary significantly, and the interpretation of the “barcoding gap” as a species boundary is not equally reliable across all taxa. Recent research on chaetognaths, for example, challenges the molecular species concept, as extreme mitochondrial divergence occurs within several sympatric lineages of a morphospecies (Marlétaz et al. 2017). Other species concepts are focusing on common ancestry, defining a species as the smallest group of individuals that share a parental pattern of descent as defined in the “Phylogenetic Species Concept,” proposed by Joel Cracraft (Cracraft 1983). Some concepts follow a more functional approach, such as the "Ecological Species Concept," discussed by Robert Sokal and Peter Sneath, and later by Daniel Levin, which considers ecological niches or functions, proposing that species are sets of organisms adapted to a particular set of resources (niches) in the environment (Sokal and Sneath 1963, Levin 1979). While morphological species have historically been the primary taxonomic unit in time series studies, molecular species delineated by genotypic characteristics are increasingly prevalent in the routine identification of zooplankton.

Regardless of whether we are dealing with cryptic or difficult-to-resolve species, taxonomic information is very often lost in routine monitoring, or species identification comes with a certain bias. The extent to which this missing or imprecise information will influence our understanding of ecosystem dynamics depends very much on the function of the taxon in the ecosystem and remains one key question in biodiversity research. In theory, undetected sympatric cryptic species will lead to an underestimation of species number in an ecosystem and an overestimation of the respective species abundances. Missing cryptic species not only has implications for understanding the dynamics of specific ecosystems but also exerts an influence on our global understanding of diversity and the effects of climate change on species and species richness. The existence of nonresolved allopatric cryptic species, for instance, can result in an overestimation of geographical distribution ranges and subsequently lead to erroneous evaluations regarding connectivity, adaptive potential, niche ranges, species vulnerability, and invasiveness estimations (e.g. Darling and Carlton 2018, Chenuil et al. 2019, Cerca et al. 2020, Starko et al. 2023).

While the importance of hidden diversity for understanding the functioning of a marine ecosystem seems intuitive, its essential role remains largely unverified within the marine system. This raises the provocative question of how crucial species-level resolution of challenging taxa is in routine monitoring within a specific ecosystem, given the high resource costs involved. Some real-world examples advocate for species-level identification, even when the effort required is substantial. One such instance is the common grouping of the highly abundant congener copepods *A. bifilosa* and *A. longiremis* into *Acartia* spp. in the Baltic Sea (e.g. Musialik-Koszarowska et al. 2019), despite the two (noncryptic) species likely being affected very differently by ecological drivers: *A. longiremis* is a marine species with a boreal–Arctic distribution, probably persisting in the Baltic Sea near its physiological limit (Dutz and Christensen 2018), while *A. bifilosa* is a brackish warm water species. We currently have only limited knowledge about the physiological variation within morphologically cryptic species complexes in zooplankton. Field studies have attempted to differentiate the ecophysiology and ecological roles of cryptic species, revealing e.g. differences in food selection within the *Eurytemora* species complex in a Canadian estuary (Cabrol et al. 2015), as well as within the species group of *P. minutus*, *P. newmani*, and *P. acuspes* in the Bering Sea (Cleary et al. 2016).

Molecular identification significantly facilitated the discovery of cryptic diversity. High-throughput sequencing of both zooplankton bulk samples and eDNA promises new insights into the role of species complexes in LTER data and databases such as GenBank and BOLD offer swift species identification. However, the lack of clarity in data calibration and the risk of outdated or even incorrect species identifications may result in inaccurate assignments. It is also crucial to acknowledge that relying solely on molecular species identification without deep taxonomic expertise of the morphospecies and detailed expertise of the local and regional fauna poses inherent risks. This is exemplified by the case of the copepods *Calanus euxinus* and *C. helgolandicus*, which are morphologically nearly indistinguishable and cannot be differentiated based on genetic markers (Papadopoulos et al. 2005, Unal et al. 2006, Yebra et al. 2022, Ohnesorge et al. 2023). Despite their genetic similarity, these species are still recognized as distinct (Walter and Boxshall 2024), yet there is ongoing discussion regarding their status as populations rather than species (Yebra et al. 2011). Another example illustrating the risks of relying solely on molecular units is evident in the case of the decapods *Polybius holsatus* and *Polybius henslowii*, of which the larvae are widespread in the North Sea and thus occur in LTERs. Despite displaying distinct differences in morphology and behavior during adulthood (Hazerli et al. 2022), these two species cannot be genetically delineated based on various mitochondrial markers (Plagge et al. 2016) and are nearly indistinguishable morphologically as larvae. These instances exemplify the importance of understanding species communities and their potential challenges, serving as but two among numerous others. A strong synergy of molecular techniques with morphological taxonomic and ecological knowledge would help to unravel diversity within natural systems. Extensive regional or seasonal sampling efforts and application of genetic tools can discover cryptic species in sympatry, a good case study is the detection of seasonally and regionally occurring cryptic hydrozoan species in the Gulf of Mexico (Miglietta and Pruski 2023). But these approaches require a wise allocation of resources in monitoring to balance taxonomic precision on the one hand and temporal or spatial resolution on the other.

The high number of challenging species complexes in marine zooplankton communities calls for a deeper exploration of species identification. Are we truly covering the expected species in the LTER stations? Might those sharing names across ecosystems actually be distinct entities? Should we rather follow a polytypic species concept, subdividing biological species geographically (Lukhtanov 2024)? It is essential to recognize that species concepts extend beyond singular definitions and defining every lineage as putative (cryptic) species without evidence for reproductive isolation bears a risk of taxonomic inflation in species numbers (Dufresnes et al. 2023). Overall, we hope to have shown in this review compelling evidence that species concepts and species complexes are not solely of interest to specialist taxonomists, but hold significance in many ICES zooplankton time series. The uncertainties inherent in the taxa utilized in time series datasets lead to challenges in connecting datasets or ecological knowledge through these entities. This will be particularly significant for scientists working with highly comprehensive community and ecosystem data, as it is impossible to have taxonomic expertise across all groups. Therefore, a close integration of taxonomy and data science remains essential for informed ecological research and conservation efforts.

Food for thought for the future of zooplankton taxonomy

A central premise of this study is that molecular methods have revealed species identity to be even more complex than what already highlighted by morphological taxonomy. This even applies for the most common taxa in well-studied epipelagic neritic systems right on our doorstep, let alone the broader ecological implications of resolving these species complexes. What actions should be taken based on this knowledge, and which insights does this review aim to provide?

Our initial recommendation is a pragmatical one. First, to adapt to the rapidly evolving advancements in analytical methods, it will be necessary to anticipate imminent and prospective requirements for sample collection, fixation, and storage. At its core, this requires parallel fixation suitable for DNA analysis (e.g. ethanol) within established sampling regimes and long-term storage of at least a subset of material suitable for future analyses (e.g. cold storage). It is essential not only to maintain morphological-based repositories (e.g. museum collections, digitalization of type individuals by microCT scanning or laser confocal microscopy) and molecular-based databases (e.g. BOLD or GenBank), but also to develop sustainable repositories (e.g. biobanks) of specimens, tissue, or genetic material that is suitable for future access to molecular information on ecosystems and their inhabitants. Conversely, when developing new methods, it is essential to consider not only their future value but also their applicability to existing material. Only this approach would allow calibration and retrospective species resolution.

Second, we encourage having an open-mind to methods beyond the well-established morphological and genetic approaches. Morphological taxonomy generally relies on specific diagnostic traits, much like molecular identification often depends on specific genetic markers. These traits can be difficult to access and may require extensive specimen preparation. Expanding our taxonomic toolbox by incorporating other phenotypic characters, such as proteomic fingerprints or morphometric traits, may offer a promising path forward. For example, using metric data of many easy-accessible morphological traits simultaneously may provide a less qualitative but more quantitative method for species delimitation, and could even be integrated into automated systems.

Our third recommendation is of a more strategic perspective regarding the role of taxonomy in modern biodiversity research. In recent years, significant investments have been made in developing novel methodologies for species detection and their integration into field research, not only in marine ecosystems but also across diverse areas of ecosystem and biodiversity science. While we highly welcome this progress, this manuscript also conveys a note of caution. Alongside the advancement of techniques, there has been a corresponding severe decline in morphological-based taxonomic knowledge and expertise within the community. Beyond the confines of museums and collections, there is a paucity of opportunities and supports for young scientists to engage with taxonomy in a sustained manner. There is growing concern that the expertise of traditional taxonomists is at serious risk of being lost. Given the exponential growth of artificial intelligence capabilities, we may envision the development of systems that not only preserve the vast legacy of historical taxonomic literature and the profound expertise of retiring taxonomists, but also enhance this knowledge through machine learning and semantic integration. However, such a path must be taken with caution. While AI may replace classical taxonomic keys with accessible, dynamic, and integrative platforms to advance global biodiversity research, human expertise does remain essential to ensure quality control and taxonomic rigor.

Finally, we would like to highlight that “not all that glitters is gold.” Genetic barcoding and molecular databases such as BOLD and GenBank have indeed revolutionized how we collect molecular information about species, unlocking new possibilities and revealing an increasing number of species. However, there is a concomitant risk that molecular identification could become isolated and self-contained, thereby severing its connection to morphological taxonomy and compromising quality control. Reliable ground-truthing remains essential. The quality-controlled MetaZooGene database, which focuses on marine zooplankton, may serve as a good example of integrating molecular and morphological taxonomists (Bucklin et al. 2021b). Molecular taxonomy often raises more questions than it answers, and we are still far from fully understanding the implications of molecular diversity and entities in terms of species and ecology. More effort must be dedicated to understanding the relationship between taxonomic units—whether morphological or molecular—and the variation in ecological niches, physiology, or adaptation potential. Many approaches to understanding ecosystems necessitate an initial simplification of complex relationships, often focusing more on traits than on taxonomic units. As a result, the choice of species on which to base such assessments may become less critical in these cases. Nevertheless, we should continue to sensitize the community engaged in species-based research to the inherent limitations of our taxonomic knowledge and the associated uncertainties, even within well-studied and highly abundant species complexes.

Acknowledgement

This work is a product of the ICES Working Groups on Integrated Morphological and Molecular Taxonomy (WGIMT) and on Zooplankton Ecology (WGZE).

We also thank both reviewers for their insightful and helpful comments, which contributed substantially to improving this work.

Author contributions

Conceptualization was done by J.P., A.C., E.F., and J.R., investigation and writing of the original draft by all coauthors, visualization by J.P., T.O.B., J.R., and A.B., supervision, project administration and writing the review & editing by J.P. and A.C., funding aquisition by J.P.

Supplementary data

Supplementary data is available at *ICESJMS* online.

Conflict of interest: None declared.

Funding

J.P. was supported by the German DFG initiative 1991 “Taxon-omics” (grant numbers RE2808/3–1 and RE2808/3–2), R.G. was supported by the Croatian Science Foundation (grants HRZZ-UIP-2020–02-3907 and HRZZ-IP-2019–04-9043), L.Y. was supported by the Andalusian Government (Consejería de Economía, Innovación y Ciencia) and EU (European Regional Development Fund) through project MICROZOO-ID (P20_00743) and by the Spanish Ministry for the Ecological Transition under project ESMARES3 (20243TE020). A.C. was supported by the German Ministry for Education and Research (BMBF; grant number 03F0917A

MOSAiC 3). A.d.S. was partially supported by EMODnet (EASME/EMFF/2016/1.3.1.2-Lot5/SI2.750022-Biology). L.B.B. was supported by the US NSF grant OCE-1948162. S.L. and A.C. were financially supported through the POF IV, subtopic 6.1 research program of the HIFMB and AWI, respectively, as part of the Helmholtz Association of German Research Centres.

Data availability

No new data were generated or analysed in support of this research.

References

Aarbakke ONS, Bucklin A, Halsband C *et al.* Comparative phylogeography and demographic history of five sibling species of *Pseudocalanus* (Copepoda: calanoida) in the North Atlantic Ocean. *J Exp Mar Biol Ecol* 2014;**461**:479–88. https://doi.org/10.1016/j.jembe.2014.10.006

Aarbakke ONS, Bucklin A, Halsband C *et al.* Discovery of *Pseudocalanus moultoni* (Frost, 1989) in Northeast Atlantic waters based on mitochondrial COI sequence variation. *J Plankton Res* 2011;**33**:1487–95. https://doi.org/10.1093/plankt/fbr057

Aarbakke ONS, Fevolden S-E, Weydmann A. Relative summer abundances and distribution of *Pseudocalanus* spp. (Copepoda: calanoida) adults in relation to environmental variables in the Nordic Seas and Svalbard fjords. *Pol Biol* 2017;**40**:51–9. https://doi.org/10.1007/s00300-016-1923-0

Adams M, Raadik TA, Burridge CP *et al.* Global biodiversity assessment and hyper-cryptic species complexes: more than one species of elephant in the room?. *Syst Biol* 2014;**63**:518–33. https://doi.org/10.1093/sysbio/syu017

Agassiz L. *Contributions to the Natural History of the United States of America*. Boston, MA: Little, Brown and Company, 1862, p. 450. https://www.biodiversitylibrary.org/item/54510

Albaina A, Garić R, Yebra L. Know your limits; miniCOI metabarcoding fails with key marine zooplankton taxa. *J Plankton Res* 2024;**46**:581–95. https://doi.org/10.1093/plankt/fbae057

Albaina A, Irigoien X. Fine scale zooplankton distribution in the Bay of Biscay in spring 2004. *J Plankton Res* 2007;**29**:851–70. https://doi.org/10.1093/plankt/fbm064

Alekseev VR, Souissi A. A new species within the *Eurytemora affinis* complex (Copepoda: calanoida) from the Atlantic Coast of USA, with observations on eight morphologically different European populations. *Zootaxa*, 2011;**2767**:41–56. https://doi.org/10.11646/zootaxa.2767.1.4

Aravena G, Villate F, Uriarte I *et al.* Response of *Acartia* populations to environmental variability and effects of invasive congenerics in the estuary of Bilbao, Bay of Biscay. *Estuar Coast Shelf Sci* 2009;**83**:621–8. https://doi.org/10.1016/j.ecss.2009.05.013

Avila L, Martinez-Silva M, Sirois P *et al.* *Eurytemora* unmasked: the trophic role of a cryptic copepod complex in early life stages of rainbow smelt. *Mar Ecol Progr Ser* 2024;**751**:153–71. https://doi.org/10.3354/meps14744

Bailey J, Durbin EG, Rynearson T. Species composition and abundance of copepods in the morphologically cryptic genus *Pseudocalanus* in the Bering Sea. *Deep Sea Res Part II Top Stud Oceanogr* 2016;**134**:173–80. https://doi.org/10.1016/j.dsr2.2015.04.017

Bailey SA, Brydges T, Casas-Monroy O *et al.* First evaluation of ballast water management systems on operational ships for minimizing introductions of nonindigenous zooplankton. *Mar Pollut Bull* 2022;**182**:113947. https://doi.org/10.1016/j.marpolbul.2022.113947

Barroeta Z, Villate F, Uriarte I *et al.* Differences in the colonization success and impact of non-indigenous and other expanding copepod species on the zooplankton of two contrasting estuaries of the Bay of Biscay. *Biol Invas* 2020;**22**:3239–67. https://doi.org/10.1007/s10530-020-02320-7

Batistić M, Lučić D, Carić M *et al.* Did the alien calycophoran *Muggiaea atlantica* outcompete its native congeneric *M. kochi* in the marine lakes of Mljet Island (Croatia)?.*Mar Ecol* 2013;**34**:3–13. https://doi.org/10.1111/maec.12021

Bayha KM, Richard Harbison G, Mcdonald JH *et al.* Preliminary investigation on the molecular systematics of the invasive ctenophore *beroe ovata*. In: H Dumont, TA Shiganova, U Niermann (eds), *Aquatic Invasions in the Black, Caspian, and Mediterranean Seas*. Dordrecht: Kluwer Academic Publishers, 2004, 167–75. http://link.springer.com/10.1007/1-4020-2152-6_7 (8 March 2024, date last accessed).

Bayha KM. *The Molecular Systematics and Population Genetics of Four Coastal Ctenophores and Scyphozoan Jellyfish of the United States Atlantic and Gulf of Mexico*. Newark, DE: University of Delaware, 2005.

Beaugrand G, Ibañez F, Lindley JA *et al.* Diversity of calanoid copepods in the North Atlantic and adjacent seas. *Mar Ecol Progr Ser* 2002;**232**:179–95. https://doi.org/10.3354/meps232179

Beaugrand G, Reid PC, Ibañez F *et al.* Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 2002;**296**:1692–4. https://doi.org/10.1126/science.1071329

Belmonte G, Scirocco T, Denitto F. Zooplankton composition in Lake Varano (Adriatic Sea coast, Italy). *Ital J Zool* 2011;**78**:370–8. https://doi.org/10.1080/11250003.2011.561261

Belmonte G. Acartiidae sars G.O, 1903. In: *ICES Identification Leaflets for Plankton*. Vol. **194**. Copenhagen: ICES, 2021, pp. 1–29.

Ben Faleh A, Allaya H, Armani A *et al.* Significant genetic differentiation among meroplanktonic barrel jellyfish *Rhizostoma pulmo* (Cnidaria: scyphozoa) in the Mediterranean Sea. *Afr J Mar Sci* 2017;**39**:1–8. https://doi.org/10.2989/1814232X.2017.1303395

Bieri R. Systematics of the Chaetognatha. In: Q Bone, H Kapp, AC Pierrot-Bults (eds), *The Biology of Chaetognaths*. Oxford: Oxford University Press, 1991, 122–36. https://doi.org/10.1093/oso/9780198577157.001.0001

Blackett M, Licandro P, Coombs SH *et al.* Long-term variability of the siphonophores *Muggiaea atlantica* and *M. kochi* in the Western English Channel. *Progr Oceanogr* 2014;**128**:1–14. https://doi.org/10.1016/j.pocean.2014.07.004

Blackett M, Lucas CH, Cook K *et al.* Occurrence of the siphonophore *Muggiaea atlantica* in Scottish coastal waters: source or sink?.*J Plankton Res* 2017;**39**:122–37. https://doi.org/10.1093/plankt/fbw082

Blanco-Bercial L, Álvarez-Marqués F, Bucklin A. Comparative phylogeography and connectivity of sibling species of the marine copepod *Clausocalanus* (Calanoida). *J Exp Mar Biol Ecol* 2011;**404**:108–15. https://doi.org/10.1016/j.jembe.2011.05.011

Blanco-Bercial L, Álvarez-Marqués F. RFLP procedure to discriminate between *Clausocalanus* Giesbrecht, 1888 (Copepoda, Calanoida) species in the Central Cantabrian Sea. *J Exp Mar Biol Ecol* 2007;**344**:73–7. https://doi.org/10.1016/j.jembe.2006.12.016

Blanco-Bercial L, Cornils A, Copley N *et al.* DNA barcoding of marine copepods: assessment of analytical approaches to species identification. *PLoS Curr* 2014;**6**:24987576. https://currents.plos.org/treeoflife/?p=5721 (14 March 2024, date last accessed).

Boeck A. Oversigt over de ved Norges Kyster jagttagne Copepoder henhorende til Calanidernes, Cyclopidernes og Harpactidernes Familier. In: *Forhandlinger i Videnskabs-Selskabet i Christiania*. Urbana, IL: University of Illinois Urbana Champaign, 1865, 226–82.

Böttger-Schnack R, Schnack R. Oncaeidae Giesbrecht W., 1893. *ICES Identification Leaflets for Plankton* 2025. https://doi.org/10.17895/ices.pub.28955810.v1

Böttger-Schnack R, Machida RJ. Comparison of morphological and molecular traits for species identification and taxonomic grouping of oncaeid copepods. *Hydrobiologia* 2011;**666**:111–25. https://doi.org/10.1007/s10750-010-0094-1

Böttger-Schnack R, Schnack D. Definition of species groups of Oncaeidae (Copepoda: Cyclopoida) as basis for a worldwide identification key. *J Nat Hist* 2013;**47**:265–88. https://doi.org/10.1080/00222933.2012.708453

Böttger-Schnack R, Schnack D. Taxonomic diversity and identification problems of oncaeid microcopepods in the Mediterranean Sea. *Mar Biodiver* 2009;**39**:131–45. https://doi.org/10.1007/s12526-009-0013-8

Böttger-Schnack R. Community structure and vertical distribution of cyclopoid and poecilostomatoid copepods in the Red Sea. III. Re-evaluation for separating a new species of *Oncaea*. *Mar Ecol Progr Ser* 1992;**80**:301–4. https://doi.org/10.3354/meps080301

Böttger-Schnack R. Taxonomy of Oncaeidae (Copepoda, Poecilostomatoida) from the Red Sea.-I. 11 species of *Triconia* gen. nov. and a redescription of *T. similis* (Sars) from Norwegian waters. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut,* 1999;**96**:37–128.

Böttger-Schnack R. Taxonomy of Oncaeidae (Copepoda: Poecilostomatoida) from the Red Sea. II. Seven species of *Oncaea* s. str. *Bull Nat Hist Mus Lond* 2001;**67**:25–84.

Bowman TE. The distribution of calanoid copepods off the southeastern United States between Cape Hatteras and southern Florida. In: *Smithsonian Contributions to Zoology*. Washington, DC: Smithsonian Institution Press, 1971, 1–58. https://doi.org/10.5479/si.00810282.96

Boxshall GA, Halsey SH. *An Introduction to Copepod Diversity*. London: The Ray Society, 2004, p. 2.

Bradford JM. *Paracalanus indicus* Wolfenden and *Corycaeus aucklandicus* Kraemer, two neritic pelagic copepods from New Zealand. *J R Soc New Zeal* 1978;**8**:133–41. https://doi.org/10.1080/03036758.1978.10429386

Bradford JM. Partial revision of the *Acartia* subgenus *Acartiura* (Copepoda: calanoida: acartiidae). *New Zeal J Mar Freshwater Res* 1976;**10**:159–202. https://doi.org/10.1080/00288330.1976.9515606

Bradford-Grieve JM, Markhaseva EL, Rocha CEF *et al.* Copepoda. In: D. Boltovskoy (ed.), *South Atlantic Zooplankton*. Vol. **2**. Leiden: Backhuys Publishers, 1999, 869–1098.

Bradford-Grieve JM. Copepoda: calanoida: acartiidae, paracartia, pteriacartia. In: *ICES Identification Leaflets for Plankton*. Vol. **181**. Copenhagen: ICES, 1999a, 1–18.

Bradford-Grieve JM. *The Marine Fauna of New Zealand: Pelagic Calanoid Copepoda ; Bathypontiidae, Arietellidae, Augaptilidae, Heterorhabdidae, Lucicutiidae, Metridinidae, Phyllopodidae, Centropagidae, Pseudodiaptomidae, Temoridae, Candaciidae, Pontellidae, Sulcanidae, Acartiidae, Tortanidae*. NIWA biodiversity memoir. Wellington: National Institute of Water and Atmospheric Research (NIWA), 1999b. 268.

Brandner MM, Stübner E, Reed AJ *et al.* Seasonality of bivalve larvae within a high Arctic fjord. *Pol Biol* 2017;**40**:263–76. https://doi.org/10.1007/s00300-016-1950-x

Brodskiĭ KA, Vyshkvartseva NV, Kos MS *et al.* Copepods (Copepoda: Calanoida) of the seas of the USSR and adjacent waters. Zoological Institute USSR Academy of Sciences, In: *Keys to the fauna of the USSR*. Vol. **135**. Leningrad: Nauka, 1983, p. 358.

Brodsky KA. Calanoida of the far-eastern seas and polar basin of the USSR. Veslonogie rachki (Calanoida) dalnevostochnykh morei SSSR i pol'yarnogo basseina. Opredeliteli po Faune SSSR, Leningrad: Nauka, 1950. https://www.marinespecies.org/aphia.php?p=sourcedetails&id=79559 (6 June 2024, date last accessed).

Brown M, Scorrano S, Kuplik Z *et al.* A new macromedusa from the coast of Mozambique: *A urelia mozambica* sp. nov. (Scyphozoa: ulmaridae). *Zootaxa* 2021;**4933**:263–276. https://doi.org/10.11646/ZOOTAXA.4933.2.5

Brown MK, Gibbons MJ. Cautioning the move from morphology to molecules in the taxonomy of metazoa: comments on Lawley et al. (*PeerJ* 2022 2021;9:e11954) and a plea for considered integration. *South Afr J Sci* 2022; **118**. https://sajs.co.za/article/view/12590 (Accessed 6 June 2024).

Brylinski JM. Anomalies morphologiques chez le genre *acartia* (Crustacea, Copepoda): description et essai de quantification. *J Plankton Res* 1984;**6**:961–6. https://doi.org/10.1093/plankt/6.6.961

Buckland C, Castellani C, Lindley AJ *et al.* *Crustacea: Decapoda*. Oxford: Oxford University Press, 2017. https://academic.oup.com/book/25513/chapter/192767849 (15 March 2024, date last accessed).

Bucklin A, Batta-Lona PG, Questel JM *et al.* COI metabarcoding of zooplankton species diversity for time-series monitoring of the NW Atlantic continental shelf. *Front Mar Sci* 2022;**9**:867893. https://doi.org/10.3389/fmars.2022.867893

Bucklin A, Bentley AM, Franzen SP. Distribution and relative abundance of *Pseudocalanus moultoni* and *P. newmani* (Copepoda: calanoida) on Georges Bank using molecular identification of sibling species. *Mar Biol* 1998;**132**:97–106. https://doi.org/10.1007/s002270050375

Bucklin A, Frost B, Bradford-Grieve J *et al.* Molecular systematic and phylogenetic assessment of 34 calanoid copepod species of the Calanidae and Clausocalanidae. *Mar Biol* 2003;**142**:333–43. https://doi.org/10.1007/s00227-002-0943-1

Bucklin A, Frost BW, Kocher TD. Molecular systematics of six *Calanus* and three *Metridia* species (Calanoida: copepoda). *Mar Biol* 1995;**121**:655–64. https://doi.org/10.1007/BF00349301

Bucklin A, Guarnieri M, McGillicuddy DJ *et al.* Spring evolution of *Pseudocalanus* spp. abundance on Georges Bank based on molecular discrimination of *P. moultoni* and *P. newmani*. *Deep Sea Res Part II Top Stud Oceanogr* 2001;**48**:589–608. https://doi.org/10.1016/S0967-0645(00)00128-4

Bucklin A, Peijnenburg KTCA, Kosobokova K *et al.* New insights into biodiversity, biogeography, ecology, and evolution of marine zooplankton based on molecular approaches. *ICES J Mar Sci* 2021;**78**:3281–7. https://doi.org/10.1093/icesjms/fsab198

Bucklin A, Peijnenburg KTCA, Kosobokova KN *et al.* Toward a global reference database of COI barcodes for marine zooplankton. *Mar Biol* 2021;**168**:78. https://doi.org/10.1007/s00227-021-03887-y

Cabrini M, Cerino F, De Olazabal A *et al.* Potential transfer of aquatic organisms via ballast water with a particular focus on harmful and non-indigenous species: a survey from Adriatic ports. *Mar Pollut Bull* 2019;**147**:16–35. https://doi.org/10.1016/j.marpolbul.2018.02.004

Cabrol J, Winkler G, Tremblay R. Physiological condition and differential feeding behaviour in the cryptic species complex *Eurytemora affinis* in the St Lawrence estuary. *J Plankton Res* 2015;**37**:372–87. https://doi.org/10.1093/plankt/fbu111

Carreton M, Company JB, Planella L *et al.* Morphological identification and molecular confirmation of the deep-sea blue and red shrimp *Aristeus antennatus* larvae. *PeerJ* 2019;7:e6063. https://doi.org/10.7717/peerj.6063

Caudill CC, Bucklin A. Molecular phylogeography and evolutionary history of the estuarine copepod, *Acartia tonsa*, on the Northwest Atlantic coast. *Hydrobiologia* 2004;**511**:91–102. https://doi.org/10.1023/B:HYDR.0000014032.05680.9d

Cepeda GD, Sabatini ME, Scioscia CL *et al.* On the uncertainty beneath the name *Oithona similis* Claus, 1866 (Copepoda, Cyclopoida). *ZooKeys* 2016;**552**:1–15. https://doi.org/10.3897/zookeys.552.6083

Cerca J, Meyer C, Purschke G *et al.* Delimitation of cryptic species drastically reduces the geographical ranges of marine interstitial ghostworms (Stygocapitella; Annelida, Sedentaria). *Mol Phylogenet Evol* 2020;**143**:106663. https://doi.org/10.1016/j.ympev.2019.106663

Cervelli M, Battaglia B, Bisol RM *et al.* Genetic differentiation in the genus *Acartia* from the lagoon of Venice. *Vie et Milieu /Life Environ* 1995;**45**:117–22. https://hal.sorbonne-universite.fr/hal-03051553v1

Chen G, Hare MP. Cryptic ecological diversification of a planktonic estuarine copepod, *Acartia tonsa*. *Mol Ecol* 2008;**17**:1451–68. https://doi.org/10.1111/j.1365-294X.2007.03657.x

Chenuil A, Cahill AE, Délémontey N *et al.* Problems and questions posed by cryptic species: a framework to guide future studies. In:

E Casetta, J Marques Da Silva, D Vecchi (eds), *From Assessing to Conserving Biodiversity*. Cham: Springer International Publishing, 2019, 77–106. https://link.springer.com/10.1007/978-3-030-10991-2_4 (25 April 2024, date last accessed).

Choi K-H, Kimmerer W, Smith G *et al.* Post-exchange zooplankton in ballast water of ships entering the San Francisco Estuary. *J Plankton Res* 2005;**27**:707–14. https://doi.org/10.1093/plankt/fbi044

Choo LQ, Bal TMP, Goetze E *et al.* Oceanic dispersal barriers in a holoplanktonic gastropod. *J Evol Biol* 2021;**34**:224–40. https://doi.org/10.1111/jeb.13735

Choo LQ, Spagliardi G, Malinsky M *et al.* Genome-wide phylogeography reveals cryptic speciation in the circumglobal planktonic calcifier *Limacina bulimoides*. *Mol Ecol* 2023;**32**:3200–19. https://doi.org/10.1111/mec.16931

Choo LQ, Spagliardi G, Peijnenburg KTCA. The use of hand-sanitiser gel facilitates combined morphological and genetic analysis of shelled pteropods. *Mar Biodiver* 2023;**53**:77. https://doi.org/10.1007/s12526-023-01384-7

Choquet M, Burckard G, Skreslet S *et al.* No evidence for hybridization between *Calanus finmarchicus* and *Calanus glacialis* in a subarctic area of sympatry. *Limnol Oceanogr* 2020;**66**:314–25.

Choquet M, Kosobokova K, Kwaśniewski S *et al.* Can morphology reliably distinguish between the copepods *Calanus finmarchicus* and *C. glacialis*, or is DNA the only way?. *Limnol Oceanogr Methods* 2018;**16**:237–52.

Choquet M, Lizano AM, Le Moan A *et al.* Unmasking microsatellite deceptiveness and debunking hybridization with SNPs in four marine copepod species of *Calanus*. *Mol Ecol* 2023;**32**:6854–73. https://doi.org/10.1111/mec.17183

Chust G, Castellani C, Licandro P *et al.* Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach. *ICES J Mar Sci* 2014;**71**:241–53. https://doi.org/10.1093/icesjms/fst147

Ciambelli A. Gelatinous zooplankton diversity, distribution and seasonality in the northern Barents Sea and Arctic Ocean. Tromsø: UiT The Arctic University of Norway, 2023. https://hdl.handle.net/10037/29453

Claus C. Die frei lebenden Copepoden mit besonderer berücksichtigung der Fauna Deutschlands, der Nordsee und des Mittelmeeres. Leipzig: W. Engelmann, 1863. https://www.biodiversitylibrary.org/bibliography/58676 (7 June 2024, date last accessed).

Cleary AC, Durbin EG, Rynearson TA *et al.* Feeding by *Pseudocalanus* copepods in the Bering Sea: trophic linkages and a potential mechanism of niche partitioning. *Deep Sea Res Part II Top Stud Oceanogra* 2016;**134**:181–9. https://doi.org/10.1016/j.dsr2.2015.04.001

Collins AG, Morandini AC. World List of Scyphozoa. In: *Cyanea Péron & Lesueur*. Paris: Annales du Muséum national d'histoire naturelle de Paris, 2025, p. 1810. https://www.marinespecies.org/aphia.php?p=taxdetails&id=135259 (4 March 2025, date last accessed).

Continuous Plankton Recorder Survey Team. Continuous plankton records. In: *Marine Ecology Progress series*. Oldendorf: Inter-Research Science Center, 2004, 11–75.

Corkett CJ, McLaren IA. The biology of *Pseudocalanus*. In: *Advances in Marine Biology*. Amsterdam: Elsevier, 1979, 1–231. https://linkinghub.elsevier.com/retrieve/pii/S0065288108604046 (15 March 2024, date last accessed).

Cornelius PFS. Evolution in leptolid life-cycles (Cnidaria: hydroida). *J Nat Hist* 1990;**24**:579–94. https://doi.org/10.1080/00222939000770391

Cornelius PFS. Hydroids and medusae of the family Companulariidae recorded from the eastern north Atlantic, with a world synopsis of genera. *Bull Brit Mus Zool* 1982;**42**:37–148.

Cornelius PFS. *North-West European Thecate Hydroids and Their Medusae. 1: Laodiceidae to Haleciidae. Synopses of the British Fauna*. Shrewsbury: Field Studies Council for Linnean Society of London and Estuarine and Coastal Services Association, 1995, p. 347.

Cornelius PFS. The hydroid species of *Obelia* (Coelenterata, Hydrozoa: campanulariidae), with notes on the medusa stage. *Bull Brit Mus Zool* 1975;**28**:249–93. https://doi.org/10.5962/p.314143

Cornils A, Blanco-Bercial L. Phylogeny of the Paracalanidae Giesbrecht, 1888 (Crustacea: copepoda: calanoida). *Mol Phylogenet Evol* 2013;**69**:861–72. https://doi.org/10.1016/j.ympev.2013.06.018

Cornils A, Held C. Evidence of cryptic and pseudocryptic speciation in the *Paracalanus parvus* species complex (Crustacea, Copepoda, Calanoida). *Front Zool* 2014;**11**:19. https://doi.org/10.1186/1742-9994-11-19

Cornils A, Wend-Heckmann B, Held C. Global phylogeography of *Oithona similis* s.l. (Crustacea, Copepoda, Oithonidae)—a cosmopolitan plankton species or a complex of cryptic lineages?. *Mol Phylogenet Evol* 2017;**107**:473–85. https://doi.org/10.1016/j.ympev.2016.12.019

Cornils A, Wend-Heckmann B. First report of the planktonic copepod *Oithona davisae* in the northern Wadden Sea (North Sea): evidence for recent invasion?. *Helgoland Mar Res* 2015;**69**:243–8. https://doi.org/10.1007/s10152-015-0426-7

Cracraft J. Species concepts and speciation analysis. In: RF Johnston (ed.), *Current Ornithology*. New York, NY: Springer, 1983, 159–87. http://link.springer.com/10.1007/978-1-4615-6781-3_6 (25 April 2024, date last accessed).

Crouch KE, Blanco-Bercial L, Richardson DE *et al.* Species-specific patterns of distribution and abundance of the cryptic copepods *Pseudocalanus moultoni* and *P. newmani* on Georges Bank (NW Atlantic Ocean) during spring 1995–2012. *Cont Shelf Res* 2020;**208**:104242. https://doi.org/10.1016/j.csr.2020.104242

da Costa KG, Vallinoto M, da Costa RM. Molecular identification of a new cryptic species of *Acartia tonsa* (Copepoda, Acartiidae) from the Northern coast of Brazil, based on mitochondrial COI gene sequences. *J Coast Res* 2011;**64**:359–63. http://www.jstor.org/stable/26482194

Darling JA, Carlton JT. A framework for understanding marine cosmopolitanism in the anthropocene. *Front Mar Sci* 2018;**5**:293. https://doi.org/10.3389/fmars.2018.00293

David M, Gollasch S, Cabrini M *et al.* Results from the first ballast water sampling study in the Mediterranean Sea—the Port of Koper study. *Mar Pollut Bull* 2007;**54**:53–65. https://doi.org/10.1016/j.marpolbul.2006.08.041

Dawson MN, Gupta AS, England MH. Coupled biophysical global ocean model and molecular genetic analyses identify multiple introductions of cryptogenic species. *Proc Natl Acad Sci* 2005;**102**:11968–73. https://doi.org/10.1073/pnas.0503811102

Dawson MN, Jacobs DK. Molecular evidence for cryptic species of *Aurelia aurita* (Cnidaria, Scyphozoa). *Biol Bull* 2001;**200**:92–6. https://doi.org/10.2307/1543089

Dawson MN. Macro-morphological variation among cryptic species of the moon jellyfish, *Aurelia* (Cnidaria: scyphozoa). *Mar Biol* 2003;**143**:369–79. https://doi.org/10.1007/s00227-003-1070-3

De Sousa LF, Marques D, Leandro SM *et al.* Description of the complete larval development of *Lysmata amboinensis* (De Man) (Decapoda: lysmatidae) reared under laboratory conditions. *Zootaxa* 2022;**5099**:501–26. https://doi.org/10.11646/zootaxa.5099.5.1

Della Croce N, Venugopal P. Distribution of marine cladocerans in the Indian Ocean. *Mar Biol* 1972;**15**:132–8. https://doi.org/10.1007/BF00353641

Di Capua I, Boxshall GA. Records of oncaeidae (Copepoda) from the Gulf of Naples, with new records of three species of *Triconia*. *J Mar Biol Assoc UK* 2008;**88**:1407–15. https://doi.org/10.1017/S002531540800194X

Di Capua I, D'Angiolo R, Piredda R *et al.* From phenotypes to genotypes and back: toward an integrated evaluation of biodiversity in calanoid copepods. *Front Mar Sci* 2022;**9**:833089. https://doi.org/10.3389/fmars.2022.833089

Di Capua I, Maffucci F, Pannone R *et al.* Molecular phylogeny of oncaeidae (Copepoda) using nuclear ribosomal internal transcribed spacer (ITS rDNA). *PLoS One* 2017;**12**:e0175662. https://doi.org/10.1371/journal.pone.0175662

Di Capua I, Piredda R, Mazzocchi MG *et al.* Metazoan diversity and seasonality through eDNA metabarcoding at a Mediterranean long-term ecological research site. *ICES J Mar Sci* 2021;**78**:3303–16. https://doi.org/10.1093/icesjms/fsab059

Di Capua I. *Temora* Baird, 1850. In: *ICES Identification Leaflets for Plankton*. Vol. **195**. Copenhagen: ICES, 2021, 1–17.

Dittrich B. Studies on the life cycle and reproduction of the parasitic amphipod *Hyperia galba* in the North Sea. *Helgoländer Meeresuntersuchungen* 1988;**42**:79–98. https://doi.org/10.1007/BF02364205

Dobzhansky T. Anthropology and the natural sciences-the problem of human evolution. *Curr Anthropol* 1963;**4**:138–48. https://doi.org/10.1086/200354

Dos Santos A, González-Gordillo JI. Illustrated keys for the identification of the Pleocyemata (Crustacea: Decapoda) zoeal stages, from the coastal region of south-western Europe. *J Mar Biol Assoc UK* 2004;**84**:205–27. https://doi.org/10.1017/S0025315404009075h

Dufresnes C, Poyarkov N, Jablonski D. Acknowledging more biodiversity without more species. *Proc Natl Acad Sci* 2023;**120**:e2302424120. https://doi.org/10.1073/pnas.2302424120

Durbin A, Hebert PDN, Cristescu MEA. Comparative phylogeography of marine cladocerans. *Mar Biol* 2008;**155**:1–10. https://doi.org/10.1007/s00227-008-0996-x

Dutz J, Christensen AM. Broad plasticity in the salinity tolerance of a marine copepod species, *Acartia longiremis*, in the Baltic Sea. *J Plankton Res* 2018;**40**:342–55. https://doi.org/10.1093/plankt/fby013

Egloff DA, Fofonoff PW, Onbé T. Reproductive biology of marine cladocerans. In: *Advances in Marine Biology*. Amsterdam: Elsevier, 1997, 79–167. https://linkinghub.elsevier.com/retrieve/pii/S0065288108602229 (15 March 2024, date last accessed).

Elliott A, Hobson V, Tang KW. Balancing fishery and conservation: a case study of the barrel jellyfish *Rhizostoma octopus* in South Wales. *ICES J Mar Sci* 2017;**74**:234–41. https://doi.org/10.1093/icesjms/fsw157

Eloire D, Somerfield PJ, Conway DVP *et al.* Temporal variability and community composition of zooplankton at station L4 in the Western Channel: 20 years of sampling. *J Plankton Res* 2010;**32**:657–79. https://doi.org/10.1093/plankt/fbq009

Elvers D, Böttger-Schnack R, Blohm D *et al.* Sympatric size variants of the microcopepod *Oncaea venusta* exhibit distinct lineages in DNA sequences. *Mar Biol* 2006;**149**:503–13. https://doi.org/10.1007/s00227-005-0234-8

Ershova EA, Nyeggen MU, Yurikova DA *et al.* Seasonal dynamics and life histories of three sympatric species of *Pseudocalanus* in two Svalbard fjords. *J Plankton Res* 2021;**43**:209–23. https://doi.org/10.1093/plankt/fbab007

Farran GP. Crustacea. Part X.-copepoda. Natural History Report of the British Museum, British Antarctic ('Terra Nova') Expedition 1910. *Zoology* 1929;**8**:203–306.

Favier J-B, Winkler G. Coexistence, distribution patterns and habitat utilization of the sibling species complex *Eurytemora affinis* in the St Lawrence estuarine transition zone. *J Plankton Res* 2014;**36**:1247–61. https://doi.org/10.1093/plankt/fbu063

Ferrari FD, Orsi J. *Oithona davisae*, new species, and *Limnoithona sinensis* (Burckhardt, 1912) (Copepoda: oithonidae) from the Sacramento-San Joaquin Estuary, California. *J Crust Biol* 1984;**4**:106–26. https://doi.org/10.2307/1547900

Fewkes JW. Studies of the jelly-fishes of Narragansett Bay. *Bull Mus Comp Zool Harvard Coll* 1881;**8**:141–82.

Figueroa NJ, Figueroa DF, Hicks D. Phylogeography of *Acartia tonsa* Dana, 1849 (Calanoida: copepoda) and phylogenetic reconstruction of the genus *Acartia* Dana, 1846. *Mar Biodiver* 2020;**50**:23. https://doi.org/10.1007/s12526-020-01043-1

Fleminger A, Hulsemann K. Geographical range and taxonomic divergence in North Atlantic *Calanus* (*C. helgolandicus, C. finmarchicus and C. glacialis*). *Mar Biol* 1977;**40**:233–48. https://doi.org/10.1007/BF00390879

Flood PR. Toward a photographic atlas on special taxonomic characters of oikopleurid Appendicularia (Tunicata). In: G Gorsky, M Youngbluth, D Deibel (eds), *Response of Marine Ecosystems to Global Change: Ecological Impact of Appendicularians*. Paris: Archives contemporaines, 2005, 59–85.

Fragopoulu N, Siokou-Frangou I, Christou ED *et al.* Patterns of vertical distribution of pseudocalanidae and paracalanidae (Copepoda) in pelagic waters (0 to 300 M) of the Eastern Mediterranean Sea. *Crustaceana* 2001;**74**:49–68. https://doi.org/10.1163/156854001505433

Frost B, Fleminger A. A revision of the genus *Clausocalanus*: (Copepoda: calanoida) with remarks on distributional patterns in diagnostic characters. In: *Bulletin of the Scripps Institution of Oceanography*, La Jolla, CA. University of California Press, 1968.p. 235.

Frost BW. A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. *Can J Zool* 1989;**67**:525–51. https://doi.org/10.1139/z89-077

Gabrielsen TM, Merkel B, Søreide JE *et al.* Potential misidentifications of two climate indicator species of the marine Arctic ecosystem: *Calanus glacialis* and *C. finmarchicus*. *Pol Biol* 2012;**35**:1621–8. https://doi.org/10.1007/s00300-012-1202-7

Gallienne CP, Robins DB. Is *Oithona* the most important copepod in the world's oceans?. *J Plankton Res* 2001;**23**:1421–32. https://doi.org/10.1093/plankt/23.12.1421

Garić R, Batistić M *Fritillaria ragusina* sp. nov., a new species of Appendicularia (Tunicata) from the Adriatic Sea. *J Mar Biol Assoc UK* 2011;**91**:555–9. https://doi.org/10.1017/S0025315409991627

Garić R, Batistić M. Description of *Aurelia pseudosolida* sp. nov. (Scyphozoa, Ulmaridae) From the Adriatic Sea. *Water* 2022;**14**:135. https://doi.org/10.3390/w14020135

Garić R, Pfannkuchen M, Denes M *et al.* Challenges in appendicularian integrative taxonomy and barcoding. In: *Proceedings of the ICES Annual Science Conference*. Copenhagen, Denmark: International Council for the Exploration of the Sea (ICES), 2018.

Gittenberger A, Rensing M, Faasse M *et al.* Non-indigenous species dynamics in time and space within the coastal waters of the netherlands. *Diversity* 2023;**15**:719. https://doi.org/10.3390/d15060719

Glynn F, Houghton JDR, Provan J. Population genetic analyses reveal distinct geographical blooms of the jellyfish *Rhizostoma octopus* (Scyphozoa). *Biol J Linnean Soc* 2015;**116**:582–92. https://doi.org/10.1111/bij.12614

Goldstein J, Javidpour J. Selective feeding protects moon jellyfish (*Aurelia aurita s.l*) from overloading with microplastics. *Mar Pollut Bull* 2023;**188**:114702. https://doi.org/10.1016/j.marpolbul.2023.114702

Govindarajan AF, Halanych KM, Cunningham CW. Mitochondrial evolution and phylogeography in the hydrozoan *Obelia geniculata* (Cnidaria). *Mar Biol* 2005;**146**:213–22. https://doi.org/10.1007/s00227-004-1434-3

Grabbert S, Renz J, Hirche H-J *et al.* Species-specific PCR discrimination of species of the calanoid copepod *Pseudocalanus*, *P. acuspes* and *P. elongatus*, in the Baltic and North Seas. *Hydrobiologia* 2010;**652**:289–97. https://doi.org/10.1007/s10750-010-0360-2

Hahn A, Brennan RS. Phenotypic plasticity drives seasonal thermal tolerance in a Baltic copepod. *J Exp Mar Biol Ecol* 2024;**576**:152014. https://doi.org/10.1016/j.jembe.2024.152014

Haq SM. Breeding of *Euterpina acutifrons*, a harpacticid copepod, with special reference to dimorphic males. *Mar Biol* 1972;**15**:221–35. https://doi.org/10.1007/BF00383552

Haq SM. Development of the copepod *Euterpina acutifrons* with special reference to dimorphism in the male. *Proc Zool Soc Lond* 1965;**144**:175–201. https://doi.org/10.1111/j.1469-7998.1965.tb05172.x

Hazerli D, Höpel CG, Richter S. New insights into the evolution of portunoid swimming crabs (Portunoidea, Heterotremata, Brachyura) and the brachyuran axial skeleton. *Front Zool* 2022;**19**:24. https://doi.org/10.1186/s12983-022-00467-8

Heimeier D, Lavery S, Sewell MA. Using DNA barcoding and phylogenetics to identify Antarctic invertebrate larvae: lessons from a large scale study. *Mar Genomics* 2010;**3**:165–77. https://doi.org/10.1016/j.margen.2010.09.004

Heron GA, Frost BW. Copepods of the family Oncaeidae (Crustacea: poecilostomatoida) in the Northeast Pacific Ocean and inland coastal waters of Washington State. *Proc Biol Soc Wash* 2000;**113**:1015–63. Biological Society of Washington, Washington.

Hidalgo M, Reglero P, Álvarez-Berastegui D *et al.* Hydrographic and biological components of the seascape structure the meroplankton community in a frontal system. *Mar Ecol Progr Ser* 2014;**505**:65–80. https://doi.org/10.3354/meps10763

Highfield JM, Eloire D, Conway DVP *et al.* Seasonal dynamics of meroplankton assemblages at station L4. *J Plankton Res* 2010;**32**:681–91. https://doi.org/10.1093/plankt/fbp139

Hill R, Allen L, Bucklin A. Multiplexed species-specific PCR protocol to discriminate four N. Atlantic Calanus species, with an mtCOI gene tree for ten *Calanus species*. *Mar Biol* 2001;**139**:279–87.

Hirai J, Chen F, Itoh H *et al.* Molecular and morphological analyses to improve taxonomic classification of *Metridia lucens/pacifica* in the North Pacific. *J Plankton Res* 2022;**44**:454–63. https://doi.org/10.1093/plankt/fbac020

Hirai J, Katakura S, Kasai H *et al.* Cryptic zooplankton diversity revealed by a metagenetic approach to monitoring metazoan communities in the coastal waters of the Okhotsk Sea, northeastern Hokkaido. *Front Mar Sci* 2017;**4**:379. https://doi.org/10.3389/fmars.2017.00379

Hirst AG, Castro-Longoria E. *Acartia bifilosa* (Copepoda: calanoida): a clarification of the species and its varieties *inermis* and *intermedia*. *J Plankton Res* 1998;**20**:1119–30. https://doi.org/10.1093/plankt/20.6.1119

Hofmann Elizondo U, Vogt M, Bednaršek N *et al.* The impact of aragonite saturation variability on shelled pteropods: an attribution study in the California Current System. *Glob Change Biol* 2024;**30**:e17345. https://doi.org/10.1111/gcb.17345

Holmborn T, Goetze E, Pollupuu M *et al.* Genetic species identification and low genetic diversity in *Pseudocalanus acuspes* of the Baltic Sea. *J Plankton Res* 2011;**33**:507–15. https://doi.org/10.1093/plankt/fbq113

Holst S, Laakmann S. Morphological and molecular discrimination of two closely related jellyfish species, *Cyanea capillata* and *C. lamarckii* (Cnidaria, Scyphozoa), from the northeast Atlantic. *J Plankton Res* 2014;**36**:48–63. https://doi.org/10.1093/plankt/fbt093

Hopcroft RR, Robison BH. New mesopelagic larvaceans in the genus *Fritillaria* from Monterey Bay, California. *J Mar Biol Assoc UK* 2005;**85**:665–78. https://doi.org/10.1017/S0025315405011598

Hopcroft RR. Diversity in larvaceans: how many species?. In: G Gorsky, M Youngbluth, D Deibel (eds), *Response of Marine Ecosystems to Global Change: Ecological Impact of Appendicularians*. Paris: Ed. Scientifiques Gb, 2005, 45–57.

Hosia A, Stemmann L, Youngbluth M. Distribution of net-collected planktonic cnidarians along the northern Mid-Atlantic Ridge and their associations with the main water masses. *Deep Sea Res Part II Top Stud Oceanogr* 2008;**55**:106–18. https://doi.org/10.1016/j.dsr2.2007.09.007

Hotke K. *DNA Barcode Variability in Canadian Cnidaria*. M.Sc. Thesis. University of Guelph, 2015.

Hunt B, Strugnell J, Bednarsek N *et al.* Poles apart: the “bipolar” pteropod species *Limacina helicina* is genetically distinct between the Arctic and Antarctic Oceans. *PLoS One* 2010;**5**:e9835. https://doi.org/10.1371/journal.pone.0009835

ICES. Working Group on Zooplankton Ecology (WGZE; outputs from 2020 meeting). *ICES Sci Rep* 2021;**3**:52. https://doi.org/10.17895/ices.pub.7689

Isinibilir M, Svetlichny L, Hubareva E. Competitive advantage of the invasive copepod *Oithona davisae* over the indigenous copepod *Oithona nana* in the Marmara Sea and Golden Horn Estuary. *Mar Freshwater Behav Physiol* 2016;**49**:391–405. https://doi.org/10.1080/10236244.2016.1236528

Janssen AW. Late quaternary to recent holoplanktonic mollusca (Gastropoda) from bottom samples of the eastern Mediterranean Sea: systematics, morphology. *Bollettino Malacologico* 2012;**48**: 1–105.

Jarms G, Morandini AC. World atlas of jellyfish: scyphozoa except Stauromedusae. In: *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (N.F.)*. München: Dölling und Galitz Verlag, 2019.

Jennings RM, Bucklin A, Pierrot-Bults A. Barcoding of arrow worms (phylum Chaetognatha) from three oceans: genetic diversity and evolution within an enigmatic phylum. *PLoS One* 2010;**5**:e9949. https://doi.org/10.1371/journal.pone.0009949

Johansson ML, Shiganova TA, Ringvold H *et al.* Molecular insights into the ctenophore Genus *Beroe* in Europe: new species, spreading invaders. *J Hered* 2018;**109**:520–9. https://doi.org/10.1093/jhered/esy026

John EH, Batten SD, Harris RP *et al.* Comparison between zooplankton data collected by the Continuous Plankton Recorder survey in the English Channel and by WP-2 nets at station L4, Plymouth (UK). *J Sea Res* 2001;**46**:223–32. https://doi.org/10.1016/S1385-1101(01)00085-5

Kasapidis P, Siokou I, Khelifi-Touhami M *et al.* Revising the taxonomic status and distribution of the *Paracalanus parvus* species complex (Copepoda, Calanoida) in the Mediterranean and Black Seas through an integrated analysis of morphology and molecular taxonomy. *J Plankton Res* 2018;**40**:595–605. https://doi.org/10.1093/plankt/fby036

Khelifi-Touhami M, Ounissi M. *Paracalanus* Boeck, 1864. In: *ICES Identification Leaflets for Plankton*. Vol. **199**. Copengagen: ICES, 2023, 1–22.

Khelifi-Touhami M, Semroud R, Hamdi EH *et al.* The planktonic copepod communities from the southern Mediterranean Sea (Algeria, Tunisia) with a re-description of *Paracalanus indicus*Wolfenden 1905 (Copepoda: calanoida). *Cahiers de Biologie Marine* 2007;**48**:327–37.

Kienberger K, Prieto L. The jellyfish *Rhizostoma luteum* (Quoy & Gaimard, 1827): not such a rare species after all. *Mar Biodiver* 2018;**48**:1455–62. https://doi.org/10.1007/s12526-017-0637-z

Kienberger K, Riera-Buch M, Schönemann AM *et al.* First description of the life cycle of the jellyfish *Rhizostoma luteum* (Scyphozoa: rhizostomeae). *PLoS One* 2018;**13**:e0202093. https://doi.org/10.1371/journal.pone.0202093

Køhler LG, Huwer B, Pujolar JM *et al.* Gelatinous macrozooplankton diversity and distribution dataset for the North Sea and Skagerrak/Kattegat during January-February 2021. *Data Brief* 2022;**44**:108493. https://doi.org/10.1016/j.dib.2022.108493

Kohnert PC, Cerwenka AF, Brandt A *et al.* Pteropods from the Kuril-Kamchatka Trench and the sea of Okhotsk (Euopisthobranchia; Gastropoda). *Progr Oceanogr* 2020;**181**:102259. https://doi.org/10.1016/j.pocean.2019.102259

Kolbasova GD, Zalevsky AO, Gafurov AR *et al.* A new species of *Cyanea* jellyfish sympatric to *C. capillata* in the White Sea. *Pol Biol* 2015;**38**:1439–51. https://doi.org/10.1007/s00300-015-1707-y

Korshunova T, Martynov A, Bakken T *et al.* External diversity is restrained by internal conservatism: new nudibranch mollusc contributes to the cryptic species problem. *Zool Script* 2017;**46**:683–92. https://doi.org/10.1111/zsc.12253

Korshunova T, Picton B, Furfaro G *et al.* Multilevel fine-scale diversity challenges the ‘cryptic species’ concept. *Sci Rep* 2019;**9**:6732. https://doi.org/10.1038/s41598-019-42297-5

Kosobokova KN, Hopcroft RR, Hirche H-J. Patterns of zooplankton diversity through the depths of the Arctic’s central basins. *Mar Biodiver* 2011;**41**:29–50. https://doi.org/10.1007/s12526-010-0057-9

Kramp PL. Some medusae (mainly scyphomedusae) from Australian coastal waters. *Trans R Soc South Austr Inc* 1965;**89**:257–73.

Kramp PL. Synopsis of the medusae of the world. *J Mar Biol Assoc UK* 1961;**40**:7. https://doi.org/10.1017/S0025315400007347

Kramp PL. The hydromedusae of the Atlantic Ocean and adjacent waters. Carlsberg Foundation's Oceanographical Expedition round the world and previous 'Dana'- Expeditions, 1928-30. Dana-report ; no. 46.Copenhagen: Carlsberg Foundation, 1959.

Kulagin DN, Stupnikova AN, Neretina TV *et al.* Spatial genetic heterogeneity of the cosmopolitan chaetognath *Eukrohnia hamata* (Möbius, 1875) revealed by mitochondrial DNA. *Hydrobiologia* 2014;**721**:197–207. https://doi.org/10.1007/s10750-013-1661-z

Laakmann S, Blanco-Bercial L, Cornils A. The crossover from microscopy to genes in marine diversity: from species to assemblages in marine pelagic copepods. *Philos Trans R Soc B Biol Sci* 2020;**375**:20190446. https://doi.org/10.1098/rstb.2019.0446

Laakmann S, Gerdts G, Erler R *et al.* Comparison of molecular species identification for North Sea calanoid copepods (Crustacea) using proteome fingerprints and DNA sequences. *Mol Ecol Resour* 2013;**13**:862–76. https://doi.org/10.1111/1755-0998.12139

Laakmann S, Holst S. Emphasizing the diversity of North Sea hydromedusae by combined morphological and molecular methods. *J Plankton Res* 2014;**36**:64–76. https://doi.org/10.1093/plankt/fbt078

Labuce A, Anda I, Solvita S *et al.* Survey of presence of non-indigenous *Eurytemora carolleeae* in the Gulf of Riga (Baltic Sea) five years after its first discovery. *Proc Latvian Acad Sci Sect B Nat Exact Appl Sci* 2018;**72**:230–35. https://doi.org/10.2478/prolas-2018-0032

Labuce A, Strake S, Dimante-Deimantovica I. *Eurytemora affinis* (Poppe, 1880) (Copepoda, Calanoida) in the Gulf of Riga, Baltic Sea—Elemental composition and diurnal vertical migration. *Crustaceana* 2020;**93**:447–66. https://doi.org/10.1163/15685403-00003977

Lajus D, Sukhikh N, Alekseev V. Cryptic or pseudocryptic: can morphological methods inform copepod taxonomy? An analysis of publications and a case study of the *Eurytemora affinis* species complex. *Ecol Evol* 2015;**5**:2374–85. https://doi.org/10.1002/ece3.1521

Lajus D, Sukhikh N, Alekseev V. Stochastic phenotypic variation: empirical results and potential use in *Eurytemora* research (Copepoda, Calanoida). *Crustaceana* 2020;**93**:317–36. https://doi.org/10.1163/15685403-00003983

Lang K. Monographie der Harpacticiden. In: *Hakan Ohlsson's Boktryckeri*. Vol. **1**. Stockholm: Nordiska Bokhandeln, 1948. https://www.marinespecies.org/aphia.php?p=sourcedetails&id=401 (26 April 2024, date last accessed).

Lawley JW, Gamero-Mora E, Maronna MM *et al.* Morphology is not always useful for diagnosis, and that's ok: species hypotheses should not be bound to a class of data. *South Afr J Sci* 2022;**118**:1–3. https://sajs.co.za/article/view/14495 (6 June 2024, date last accessed).

Lawley JW, Gamero-Mora E, Maronna MM *et al.* The importance of molecular characters when morphological variability hinders diagnosability: systematics of the moon jellyfish genus *Aurelia* (Cnidaria: scyphozoa). *PeerJ* 2021;**9**:e11954. https://doi.org/10.7717/peerj.11954

Lee CE, Frost BW. Morphological stasis in the *Eurytemora affinis* species complex (Copepoda: temoridae). *Hydrobiologia* 2002;**480**:111–28. https://doi.org/10.1023/A:1021293203512

Lee CE. Evolutionary mechanisms of habitat invasions, using the copepod *Eurytemora affinis* as a model system. *Evol Appl* 2016;**9**:248–70. https://doi.org/10.1111/eva.12334

Lee CE. Global phylogeography of a cryptic copepod species complex and reproductive isolation between genetically proximate 'populations'. *Evolution* 2000;**54**:2014–27. https://doi.org/10.1111/j.0014-3820.2000.tb01245.x

Lee CE. Rapid and repeated invasions of fresh water by the copepod *Eurytemora affinis*. *Evolution* 1999;**53**:1423. https://doi.org/10.2307/2640889

Lee PLM, Dawson MN, Neill SP *et al.* Identification of genetically and oceanographically distinct blooms of jellyfish. *J R Soc Interface* 2013;**10**:20120920. https://doi.org/10.1098/rsif.2012.0920

Leoni V, Bonnet D, Ramírez-Romero E *et al.* Biogeography and phenology of the jellyfish *Rhizostoma pulmo* (Cnidaria: scyphozoa) in southern European seas. *Glob Ecol Biogeogr* 2021;**30**:622–39. https://doi.org/10.1111/geb.13241

Levin DA. The nature of plant species. *Science* 1979;**204**:381–4. https://doi.org/10.1126/science.204.4391.381

Licandro P, Blackett M, Fischer A *et al.* Biogeography of jellyfish in the North Atlantic, by traditional and genomic methods. *Earth Syst Sci Data* 2015;**7**:173–91. https://doi.org/10.5194/essd-7-173-2015

Licandro P, Conversi A, Ibanez F *et al.* Time series analysis of interrupted long-term data set (1961-1991) of zooplankton abundance in Gulf of Maine (northern Atlantic, USA). *Oceanol Acta* 2001;**24**:453–66. https://doi.org/10.1016/S0399-1784(01)01169-0

Licandro P, Icardi P. Basin scale distribution of zooplankton in the Ligurian Sea (north-western Mediterranean) in late autumn. *Hydrobiologia* 2009;**617**:17–40. https://doi.org/10.1007/s10750-008-9523-9

Licandro P, Souissi S, Ibanez F *et al.* Long-term variability and environmental preferences of calycophoran siphonophores in the Bay of Villefranche (north-western Mediterranean). *Progr Oceanogr* 2012;**97-100**:152–63. https://doi.org/10.1016/j.pocean.2011.11.004

Lilley MKS, Houghton JDR, Hays GC. Distribution, extent of interannual variability and diet of the bloom-forming jellyfish *Rhizostoma* in European waters. *J Mar Biol Assoc UK* 2009;**89**:39–48. https://doi.org/10.1017/S0025315408002439

Lindegren M, Thomas MK, Jónasdóttir SH *et al.* Environmental niche separation promotes coexistence among ecologically similar zooplankton species—North Sea copepods as a case study. *Limnol Oceanogr* 2020;**65**:545–56. https://doi.org/10.1002/lno.11322

Lindeque PK, Hay SJ, Heath MR *et al.* Integrating conventional microscopy and molecular analysis to analyse the abundance and distribution of four *Calanus* congeners in the North Atlantic. *J Plankton Res* 2006;**28**:221–38. https://doi.org/10.1093/plankt/fbi115

Lindeque PK, Parry HE, Harmer RA *et al.* Next generation sequencing reveals the hidden diversity of zooplankton assemblages. *PLoS One* 2013;**8**:e81327. https://doi.org/10.1371/journal.pone.0081327

Linné CV. *Caroli Linnaei, Sveci, Doctoris Medicinae systema naturae, sive, Regna tria naturae systematice proposita per classes, ordines, genera, & species. Apud Theodorum Haak*. Leiden: Typographia Joannis Wilhelmi de Groot, Lugduni Batavorum, 1735, https://www.biodiversitylibrary.org/bibliography/877 (11 June 2024, date last accessed).

Lukhtanov VA. Polytypic species concept and subspecies in the genomic era. *Proc Natl Acad Sci* 2024;**121**:e2317038121. https://doi.org/10.1073/pnas.2317038121

Mackie GO, Pugh PR, Purcell JE. Siphonophore biology. In: *Advances in Marine Biology*. Amsterdam: Elsevier, 1988, 97–262. https://linkinghub.elsevier.com/retrieve/pii/S0065288108600747 (11 June 2024, date last accessed).

Mariottini GL, Pane L. Mediterranean jellyfish venoms: a review on scyphomedusae. *Mar Drugs* 2010;**8**:1122–52. https://doi.org/10.3390/md8041122

Markhaseva EL, Abramova AA, Mingazov N. *Pseudocalanus acuspes* (Crustacea: copepoda) from the White Sea. *Proc Zool Inst RAS* 2012;**316**:57–70. https://doi.org/10.31610/trudyzin/2012.316.1.57

Marlétaz F, Le Parco Y, Liu S *et al.* Extreme mitogenomic variation in natural populations of chaetognaths. *Genome Biol Evol* 2017;**9**:1374–84. https://doi.org/10.1093/gbe/evx090

JW Martin, J Olesen, J Høeg (eds). *Atlas of Crustacean Larvae*. Baltimore, MD: Johns Hopkins University Press, 2014. 370. https://doi.org/10.1353/book.31448

Masunaga A, Mansfield MJ, Tan Y *et al.* The cosmopolitan appendicularian *Oikopleura dioica* reveals hidden genetic diversity around the globe. *Mar Biol* 2022;**169**:157. https://doi.org/10.1007/s00227-022-04145-5

Matzen Da Silva J, Creer S, Dos Santos A *et al.* Systematic and evolutionary insights derived from mtDNA COI barcode diversity in the Decapoda (Crustacea: malacostraca). *PLoS One* 2011;**6**:e19449. https://doi.org/10.1371/journal.pone.0019449

Mayer AG. *Ctenophores of the Atlantic coast of North America*. Washington, DC: Carnegie Institution of Washington, 1912. https://www.biodiversitylibrary.org/bibliography/5968 (6 June 2024, date last accessed).

Mayer AG. *Medusae of the World. III the Scyphomedusae*. Washington, DC: Carnegie institution of Washington, 1910. https://www.biodiversitylibrary.org/bibliography/5996 (6 June 2024, date last accessed).

Mayr E. *Systematics and Origin of Species*. New York, NY: Columbia University Press, 1942. p. 334.

Mazzocchi MG, Licandro P, Dubroca L *et al.* Zooplankton associations in a Mediterranean long-term time-series. *J Plankton Res* 2011;**33**:1163–81. https://doi.org/10.1093/plankt/fbr017

Mazzocchi MG, Ribera d'Alcalà M. Recurrent patterns in zooplankton structure and succession in a variable coastal environment. *ICES J Mar Sci* 1995;**52**:679–91. https://doi.org/10.1016/1054-3139(95)80081-6

Mazzocchi MG, Siokou I, Tirelli V *et al.* Regional and seasonal characteristics of epipelagic mesozooplankton in the Mediterranean Sea based on an artificial neural network analysis. *J Mar Syst* 2014;**135**:64–80. https://doi.org/10.1016/j.jmarsys.2013.04.009

Mazzocchi MG, Zagami G, Ianora A *et al. Atlas of Marine Zooplankton Straits of Magellan*. Berlin, Heidelberg: Springer, 1995. 1–27. http://link.springer.com/10.1007/978-3-642-79139-0 (6 June 2024, date last accessed).

Mazzocchi MG. *Clausocalanus* Giesbrecht, 1888. In: *ICES Identification Leaflets for Plankton*. Vol. **189**. Copenhagen: ICES, 2020, 1–19.

Mazzocchi MG. *Oithona* Baird, 1843. In: *ICES Identification Leaflets for Plankton*. Vol. **188**. Copenhagen: ICES, 2019, 1–16. https://doi.org/10.17895/ices.pub.5254

Mekkes L, Sepúlveda-Rodríguez G, Bielkinaitė G *et al.* Effects of ocean acidification on calcification of the sub-antarctic pteropod *Limacina retroversa*. *Front Mar Sci* 2021;**8**:581432. https://doi.org/10.3389/fmars.2021.581432

Michelsen HK, Svensen C, Reigstad M *et al.* Seasonal dynamics of meroplankton in a high-latitude fjord. *J Mar Syst* 2017;**168**:17–30. https://doi.org/10.1016/j.jmarsys.2016.12.001

Miglietta MP, Pruski S. Cryptic species in time and space: an assessment of cryptic diversity within eight nominal species of hydrozoa (Cnidaria). *Proc R Soc B Biol Sci* 2023;**290**:20230851. https://doi.org/10.1098/rspb.2023.0851

Mills CE, Phylum ctenophora: list of all valid species names. Habor, WA: University of Washington, 2024, 1756. https://www.marinespecies.org/aphia.php?p=taxdetails&id=106331 (26 April 2024, date last accessed).

Miyamoto H, Machida RJ, Nishida S. Global phylogeography of the deep-sea pelagic chaetognath *Eukrohnia hamata*. *Progr Oceanogr* 2012;**104**:99–109. https://doi.org/10.1016/j.pocean.2012.06.003

Möllmann C, Köster F, Kornilovs G *et al.* Long-term trends in abundance of cladocerans in the Central Baltic Sea. *Mar Biol* 2002;**141**:343–52.

MolluscaBase. MolluscaBase. 2024. Accessed through: World Register of Marine Species at. https://www.marinespecies.org/aphia.php?p=taxdetails&id=138122 on 2024-07-12. https://www.marinespecies.org/imis.php?dasid=3104&doiid=356 (6 June 2024, date last accessed).

Mordukhai-Boltovskoi FD, Rivier IK. Predatory cladocerans (Podonodae, Polyphemoidae, Cercopagidae and Leptodoridae) of the world's fauna. Leningrad: Nauka, 1987, 182.

Moura CJ, Magalhães BI, Gonçalves JM. DNA barcoding of moon jellyfish (Cnidaria, Scyphozoa, Ulmaridae, *Aurelia*): two cryptic species from the Azores (NE Atlantic, Macaronesia), and evaluation of the non-indigenous species (NIS). *Diversity* 2023;**15**:323. https://doi.org/10.3390/d15030323

Musialik-Koszarowska M, Dzierzbicka-Głowacka L, Weydmann A. Influence of environmental factors on the population dynamics of key zooplankton species in the Gulf of Gdańsk (southern Baltic Sea). *Oceanologia* 2019;**61**:17–25. https://doi.org/10.1016/j.oceano.2018.06.001

Neitzel P, Hosia A, Piatkowski U *et al.* Pelagic deep-sea fauna observed on video transects in the southern Norwegian Sea. *Pol Biol* 2021;**44**:887–98. https://doi.org/10.1007/s00300-021-02840-5

Nishida S. Taxonomy and distribution of the family Oithonidae. *Bull Ocean Res Inst Univ Tokyo* 1985;**20**:1–167.

O'Brien TD, Blanco-Bercial L, Questel JM *et al.* MetaZooGene atlas and database: reference sequences for marine ecosystems. In: R DeSalle (ed.), *DNA Barcoding*. New York, NY: Springer, 2024, 475–89. https://link.springer.com/10.1007/978-1-0716-3581-0_28 (17 June 2024, date last accessed).

OBIS. Distribution records for Acartia (Acartiura) hudsonica Pinhey, 1926. Paris: Ocean Biodiversity Information System. Intergovernmental Oceanographic Commission of UNESCO. 2024a. www.obis.org. https://obis.org/taxon/104196 (6 June 2024, date last accessed).

OBIS. Distribution records for Paracalanus Boeck, 1865. Paris: Ocean Biodiversity Information System. Intergovernmental Oceanographic Commission of UNESCO. 2024b. www.obis.org. https://obis.org/taxon/104196 (6 June 2024, date last accessed).

OBIS. Distribution records for Temora turbinata Dana, 1849. Paris: Ocean Biodiversity Information System. Intergovernmental Oceanographic Commission of UNESCO, 2024c. www.obis.org. https://obis.org/taxon/104196 (6 June 2024, date last accessed).

Ohnesorge A, John U, Kuczynski L *et al.* Roaming the seas—assessing marine invertebrate biodiversity along salinity gradients with zooplankton and eDNA metabarcoding. *Environ DNA* 2024;**6**:e70037. https://doi.org/10.1002/edn3.70037

Ohnesorge A, John U, Taudien S *et al.* Capturing drifting species and molecules—lessons learned from integrated approaches to assess marine metazoan diversity in highly dynamic waters. *Environ DNA* 2023;**5**:1541–56. https://doi.org/10.1002/edn3.478

Onbé T. Ctenopoda and Onychopoda (Cladocera). In: D Boltovskoy. *South Atlantic Zooplankton*. Leiden: Backhuys, 1999, 797–814.

Pansera M, Camatti E, Schroeder A *et al.* The non-indigenous *Oithona davisae* in a Mediterranean transitional environment: coexistence patterns with competing species. *Sci Rep* 2021;**11**:8341. https://doi.org/10.1038/s41598-021-87662-5

Papadopoulos LN, Peijnenburg KTCA, Luttikhuizen PC. Phylogeography of the calanoid copepods *Calanus helgolandicus and C. euxinus* suggests pleistocene divergences between Atlantic, Mediterranean, and Black Sea populations. *Mar Biol* 2005;**147**:1353–65. https://doi.org/10.1007/s00227-005-0038-x

Parent GJ, Plourde S, Browman HI *et al.* Defining what constitutes a reliable dataset to test for hybridization and introgression in marine zooplankton: comment on Choquet et al. 2020 "No evidence for hybridization between Calanus finmarchicus and *C. glacialis* in a subarctic area of sympatry. *Limnol Oceanogr* 2021;**66**:3597–602. https://doi.org/10.1002/lno.11725

Parent GJ, Plourde S, Turgeon J. Natural hybridization between *Calanus finmarchicus* and *C. glacialis* (Copepoda) in the Arctic and Northwest Atlantic. *Limnol Oceanogr* 2012;**57**:1057–66. https://doi.org/10.4319/lo.2012.57.4.1057

Paula J, Dos Santos A. Larval and early post-larval stages of the crab, *Xantho pilipes* A. Milne-Edwards, 1867 (Crustacea, Decapoda, Xanthidae), reared under laboratory conditions. *Invert Reprod Dev* 2000;**38**:253–64. https://doi.org/10.1080/07924259.2000.9652458

Peijnenburg KTCA, Breeuwer JAJ, Pierrot-Bults AC *et al.* Phylogeography of the planktonic chaetognath *Sagitta setosa* reveals isolation in European seas. *Evolution* 2004;**58**:1472–87. https://doi.org/10.1111/j.0014-3820.2004.tb01728.x

Peijnenburg KTCA, Fauvelot C, Breeuwer JAJ *et al.* Spatial and temporal genetic structure of the planktonic *Sagitta setosa* (Chaetognatha) in European seas as revealed by mitochondrial and nuclear DNA markers. *Mol Ecol* 2006;**15**:3319–38. https://doi.org/10.1111/j.1365-294X.2006.03002.x

Peijnenburg KTCA, Van Haastrecht EK, Fauvelot C. Present-day genetic composition suggests contrasting demographic histories of two dominant chaetognaths of the North-East Atlantic, *Sagitta elegans* and *S. setosa*. *Mar Biol* 2005;**147**:1279–89. https://doi.org/10.1007/s00227-005-0041-2

Peralba À, Mazzocchi MG, Harris RP. Niche separation and reproduction of *Clausocalanus* species (Copepoda, Calanoida) in the Atlantic Ocean. *Progr Oceanogr* 2017;**158**:185–202. https://doi.org/10.1016/j.pocean.2016.08.002

Peralba À, Mazzocchi MG. Vertical and seasonal distribution of eight *Clausocalanus* species (Copepoda: calanoida) in oligotrophic waters. *ICES J Mar Sci* 2004;**61**:645–53. https://doi.org/10.1016/j.icesjms.2004.03.019

Pierrot-Bults AC. Chaetognatha. In: *ICES Identification Leaflets for Plankton*. Vol. **193**. Copenhagen: ICES, 2020, 1–16.

Plagge C, Son NT, Ng PLK *et al. Liocarcinus corrugatus* (Pennant, 1777) (Crustacea: brachyura: portunidae): a cosmopolitan brachyuran species?. *Raffles Bull Zool* 2016;**64**:374–88. http://zoobank.org/urn:lsid:zoobank.org:pub:73BA15E0-882D-432B-A097-C12C911609CF

Plough L, Fitzgerald C, Plummer A *et al.* Reproductive isolation and morphological divergence between cryptic lineages of the copepod *Acartia tonsa* in Chesapeake Bay. *Mar Ecol Progr Ser* 2018;**597**:99–113. https://doi.org/10.3354/meps12569

Prieto L, Armani A, Macías D. Recent strandings of the giant jellyfish *Rhizostoma luteum* Quoy and Gaimard, 1827 (Cnidaria: scyphozoa: rhizostomeae) on the Atlantic and Mediterranean coasts. *Mar Biol* 2013;**160**:3241–7. https://doi.org/10.1007/s00227-013-2293-6

Questel JM, Blanco-Bercial L, Hopcroft RR *et al.* Phylogeography and connectivity of the *Pseudocalanus* (Copepoda: calanoida) species complex in the eastern North Pacific and the Pacific Arctic Region. *J Plankton Res* 2016;**38**:610–23. https://doi.org/10.1093/plankt/fbw025

Ratnarajah L, Abu-Alhaija R, Atkinson A *et al.* Monitoring and modelling marine zooplankton in a changing climate. *Nat Commun* 2023;**14**:564. https://doi.org/10.1038/s41467-023-36241-5

Razouls C, Desreumaux N, Kouwenberg J *et al. Biodiversity of Marine Planktonic Copepods (morphology, geographical distribution and biological data)*. Paris: Sorbonne University, CNRS, 2024. http://copepodes.obs-banyuls.fr/en (19 May 2024, date last accessed).

Rodionova NV, Panov VE., Establishment of the Ponto-Caspian predatory cladoceran *Evadne anonyx* in the eastern Gulf of Finland, Baltic Sea. *Aqu Invas* 2006;**1**:7–12. https://doi.org/10.3391/ai.2006.1.1.3

Russell FS. Pelagic Scyphozoa with a supplement to the first volume on Hydromedusae. In: *The Medusae of the British Isles*. Cambridge: Cambridge University Press, 1970, p. 283.

Saiz E, Calbet A, Broglio E. Effects of small-scale turbulence on copepods: the case of *Oithona davisae*. *Limnol Oceanogr* 2003;**48**:1304–11. https://doi.org/10.4319/lo.2003.48.3.1304

Sars GO. *An Account of the Crustacea of Norway, With Short Descriptions and Figures of all the Species*. New York, NY: Creative Media Partners, 1918, p. 776. https://www.biodiversitylibrary.org/item/67639

Sasaki MC, Dam HG. Integrating patterns of thermal tolerance and phenotypic plasticity with population genetics to improve understanding of vulnerability to warming in a widespread copepod. *Glob Change Biol* 2019;**25**:4147–64. https://doi.org/10.1111/gcb.14811

Schnack-Schiel SB, Mizdalski E, Cornils A. Copepod abundance and species composition in the eastern subtropical/tropical Atlantic. *Deep Sea Res Part II Top Stud Oceanogr* 2010;**57**:2064–75. https://doi.org/10.1016/j.dsr2.2010.09.010

Schroeder A, Stanković D, Pallavicini A *et al.* DNA metabarcoding and morphological analysis—assessment of zooplankton biodiversity in transitional waters. *Mar Environ Res* 2020;**160**:104946. https://doi.org/10.1016/j.marenvres.2020.104946

Schroth W, Jarms G, Streit B *et al.* Speciation and phylogeography in the cosmopolitan marine moon jelly, *Aurelia* sp. *BMC Evol Biol* 2002;**2**:1. https://doi.org/10.1186/1471-2148-2-1

Schuchert P. World Hydrozoa Database. 2024. https://www.marinespecies.org/hydrozoa on yyyy-mm-dd. https://www.marinespecies.org/imis.php?dasid=1464&doiid=357 (14 March 2024, date last accessed).

Scorrano S, Aglieri G, Boero F *et al.* Unmasking *Aurelia* species in the Mediterranean Sea: an integrative morphometric and molecular approach. *Zool J Linnean Soc* 2016; **180**: 243–67. http://doi.wiley.com/10.1111/zoj.12494 (6 June 2024, date last accessed).

ScottoDi Carlo B, Ianora A, Fresi E *et al.* Vertical zonation patterns for Mediterranean copepods from the surface to 3000 m at a fixed station in the Tyrrhenian Sea. *J Plankton Res* 1984;**6**: 1031–56.

Sei S, Rossetti G, Villa F *et al.* Zooplankton variability related to environmental changes in a eutrophic coastal lagoon in the Po Delta. *Hydrobiologia* 1996;**329**:45–55. https://doi.org/10.1007/BF00034546

Semmouri I, De Schamphelaere KAC, Willemse S *et al.* Metabarcoding reveals hidden species and improves identification of marine zooplankton communities in the North Sea. *ICES J Mar Sci* 2021;**78**:3411–27. https://doi.org/10.1093/icesjms/fsaa256

Sewell RBS. *The Copepoda of Indian Seas: Calanoida. Memoirs of the Indian Museum*. Kolkata: Zoological Survey of India, 1929, p. 407. https://books.google.de/books?id=2XsCtgEACAAJ

Sherlock RE, Walz KR, Schlining KL *et al.* Morphology, ecology, and molecular biology of a new species of giant larvacean in the eastern North Pacific: *B athochordaeus mcnutti* sp. nov. *Mar Biol* 2017;**164**:20. https://doi.org/10.1007/s00227-016-3046-0

Shiganova TA, Abyzova GA. Revision of Beroidae (Ctenophora) in the southern seas of Europe: systematics and distribution based on genetics and morphology. *Zool J Linnean Soc* 2022;**194**:297–322. https://doi.org/10.1093/zoolinnean/zlab021

Shimizu K, Noshita K, Kimoto K *et al.* Phylogeography and shell morphology of the pelagic snail *Limacina helicina* in the Okhotsk Sea and western North Pacific. *Mar Biodiver* 2021;**51**:22. https://doi.org/10.1007/s12526-021-01166-z

Shin CP, Allmon WD. How we study cryptic species and their biological implications: a case study from marine shelled gastropods. *Ecol Evol* 2023;**13**:e10360. https://doi.org/10.1002/ece3.10360

Shuvalov VS. Geographical variability of some species of the family Oithonidae (Copepoda, Cyclopoida). *Stud Mar Fauna* 1972;**12**:169–86.

Siokou-Frangou I. Zooplankton annual cycle in a Mediterranean coastal area. *J Plankton Res* 1996;**18**:203–23. https://doi.org/10.1093/plankt/18.2.203

Soares MDO, Campos CC, Santos NMO *et al.* Marine bioinvasions: differences in tropical copepod communities between inside and outside a port. *J Sea Res* 2018;**134**:42–8. https://doi.org/10.1016/j.seares.2018.01.002

Sokal RR, Sneath PH. *Principles of Numerical Taxonomy*. New York, NY: W.H. Freeman and Company, 1963, p. 359.

Sromek L, Lasota R, Wolowicz M. Impact of glaciations on genetic diversity of pelagic mollusks: antarctic *Limacina antarctica* and Arctic *Limacina helicina*. *Mar Ecol Progr Ser* 2015;**525**:143–52. https://doi.org/10.3354/meps11237

Stancyk SE, Moreira GS. Inheritance of male dimorphism in Brazilian populations of *Euterpina acutifrons* (Dana) (Copepoda: harpacticoida). *J Exp Mar Biol Ecol* 1988;**120**:125–44. https://doi.org/10.1016/0022-0981(88)90084-6

Starko S, Fifer JE, Claar DC *et al.* Marine heatwaves threaten cryptic coral diversity and erode associations among coevolving partners. *Sci Adv* 2023;**9**:eadf0954. https://doi.org/10.1126/sciadv.adf0954

Stiasny G, van der Maaden H. Über Scyphomedusen aus dem Ochotskischen und Kamtschatka Meer nebst einer kritik der Genera *Cyanea* und *Desmonema*. *Zoologische Jahrbucher, Abteilung fur Systematik, Geographie und Biologie der Tiere*, 1943;**76**:227–66.

Stupnikova AN, Molodtsova TN, Mugue NS *et al.* Genetic variability of the *Metridia lucens* complex (Copepoda) in the Southern Ocean.

J Mar Syst 2013;**128**:175–84. https://doi.org/10.1016/j.jmarsys.2013.04.016

Sukhikh N, Souissi A, Souissi S *et al*. Genetic and morphological heterogeneity among populations of *Eurytemora affinis* (Crustacea: copepoda: temoridae) in European waters. *CR Biol* 2016;**339**:197–206. https://doi.org/10.1016/j.crvi.2016.03.004

Sukhikh N, Souissi A, Souissi S *et al*. Invasion of *Eurytemora* sibling species (Copepoda: temoridae) from North America into the Baltic Sea and European Atlantic coast estuaries. *J Nat Hist* 2013;**47**:753–67. https://doi.org/10.1080/00222933.2012.716865

Sukhikh N, Souissi A, Souissi S *et al*. Life in sympatry: coexistence of native *Eurytemora affinis* and invasive *Eurytemora carolleeae* in the Gulf of Finland (Baltic Sea). *Oceanologia* 2019;**61**:227–38. https://doi.org/10.1016/j.oceano.2018.11.002

Sukhikh NM, Alekseev VR. *Eurytemora caspica* sp. nov. from the Caspian Sea—one more new species within the *E. affinis* complex (Copepoda: calanoida: temoridae). *Proc Zool Instit RAS* 2013;**317**:85–100. https://doi.org/10.31610/trudyzin/2013.317.1.85

Suzuki K, Niida Y, Tsubono T *et al*. Mechanisms underlying heterogeneous distribution of moon jellyfish *Aurelia aurita* s.l. across a sharp pycnocline. *Mar Ecol Progr Ser* 2018;**591**:229–39. https://doi.org/10.3354/meps12357

Takahashi M, DiBattista JD, Jarman S *et al*. Partitioning of diet between species and life history stages of sympatric and cryptic snappers (Lutjanidae) based on DNA metabarcoding. *Sci Rep* 2020;**10**:4319. https://doi.org/10.1038/s41598-020-60779-9

Telesh I, Postel L, Heerkloss R *et al*. Zooplankton of the Open Baltic Sea: atlas. *Mar Sci Rep* 2008;**73**:1–262.

Telesh IV, Ojaveer H. The predatory water flea *Cercopagis pengoi* in the Baltic Sea: invasion history, distribution and implications to ecosystem dynamics. In: E Leppäkoski, S Gollasch, S Olenin (eds), *Invasive Aquatic Species of Europe. Distribution, Impacts and Management*. Dordrecht: Springer, 2002, 62–5. http://link.springer.com/10.1007/978-94-015-9956-6_7 (15 March 2024, date last accessed).

Temnykh A, Nishida S. New record of the planktonic copepod *Oithona davisae* Ferrari and Orsi in the Black Sea with notes on the identity of *Oithona brevicornis*. *Aqu Invas* 2012;**7**:425–31. https://doi.org/10.3391/ai.2012.7.3.013

Terbiyik Kurt T, Polat S. Introduction of a new Indo-Pacific marine cladoceran to the Mediterranean Sea. *Mediter Mar Sci* 2018;**18**:517–523.https://doi.org/10.12681/mms.13885

Terbıyık Kurt T, Beşiktepe Ş. First distribution record of the invasive copepod *Oithona davisae* ferrari and Orsi, 1984, in the coastal waters of the Aegean Sea. *Mar Ecol* 2019;**40**:e12548. https://doi.org/10.1111/maec.12548

Tokioka T. The taxonomical outline of chaetognatha. *Public Seto Mar Biol Lab* 1965;**12**:335–57. https://doi.org/10.5134/175381

Torres AP, Palero F, Dos Santos A *et al*. Larval stages of the deep-sea lobster *Polycheles typhlops* (Decapoda, Polychelida) identified by DNA analysis: morphology, systematic, distribution and ecology. *Helgoland Mar Res* 2014;**68**:379–97. https://doi.org/10.1007/s10152-014-0397-0

Totton AK *A Synopsis of the Siphonophora*. London: British Museum (Natural History), 1965.

Trudnowska E, Balazy K, Stoń-Egiert J *et al*. In a comfort zone and beyond—ecological plasticity of key marine mediators. *Ecol Evol* 2020;**10**:14067–81. https://doi.org/10.1002/ece3.6997

Ueda H. Redescription of the planktonic calanoid copepod *Acartia hudsonica* from Atlantic and Pacific waters: a new record from Japanese waters. *J Oceanogr Soc Jpn* 1986;**42**:124–33. https://doi.org/10.1007/BF02109099

Unal E, Frost BW, Armbrust V *et al*. Phylogeography of *Calanus helgolandicus* and the Black Sea copepod *Calanus euxinus*, with notes on *Pseudocalanus elongatus* (Copepoda, Calanoida). *Deep Sea Res Part II Top Stud Oceanogr* 2006;**53**:1961–75. https://doi.org/10.1016/j.dsr2.2006.03.017

Uriarte I, Villate F, Iriarte A. Zooplankton recolonization of the inner estuary of Bilbao: influence of pollution abatement, climate and non-indigenous species. *J Plankton Res* 2016;**38**:718–31. https://doi.org/10.1093/plankt/fbv060

Uye S, Sano K. Seasonal variations in biomass, growth rate and production rate of the small cyclopoid copepod *Oithona davisae* in a temperate eutrophic inlet. *Mar Ecol Progr Ser* 1998;**163**:37–44. https://doi.org/10.3354/meps163037

Van Den Heuvel-Greve MJ, Van Den Brink AM, Glorius ST *et al*. Early detection of marine non-indigenous species on Svalbard by DNA metabarcoding of sediment. *Pol Biol* 2021;**44**:653–65. https://doi.org/10.1007/s00300-021-02822-7

Vasquez AA, Hudson PL, Fujimoto M *et al*. *Eurytemora carolleeae*in the Laurentian Great Lakes revealed by phylogenetic and morphological analysis. *J Great Lakes Res* 2016;**42**:802–11. https://doi.org/10.1016/j.jglr.2016.04.001

Vidjak O, Bojanić N, De Olazabal A *et al*. Zooplankton in Adriatic port environments: indigenous communities and non-indigenous species. *Mar Pollut Bull* 2019;**147**:133–49. https://doi.org/10.1016/j.marpolbul.2018.06.055

Walczyńska KS, Søreide JE, Weydmann-Zwolicka A *et al*. DNA barcoding of Cirripedia larvae reveals new knowledge on their biology in Arctic coastal ecosystems. *Hydrobiologia* 2019;**837**:149–59. https://doi.org/10.1007/s10750-019-3967-y

Walter TC, Boxshall G. World of Copepods Database. 2024. https://www.marinespecies.org/copepoda on 2024-06-06, https://www.marinespecies.org/imis.php?dasid=3104&doiid=356 (6 June 2024, date last accessed).

Watson JD, Crick FHC. Molecular structure of nucleic acids: a structure for deoxyribose nucleic acid. *Nature* 1953;**171**:737–8. https://doi.org/10.1038/171737a0

Weydmann A, Carstensen J, Goszczko I *et al*. Shift towards the dominance of boreal species in the Arctic: inter-annual and spatial zooplankton variability in the West Spitsbergen Current. *Mar Ecol Progr Ser* 2014;**501**:41–52. https://doi.org/10.3354/meps10694

Weydmann A, Coelho NC, Ramos AA *et al*. Microsatellite markers for the Arctic copepod *Calanus glacialis* and cross-amplification with *C. finmarchicus*. *Conser Genet Resour* 2014;**6**:1003–5. https://doi.org/10.1007/s12686-014-0269-6

Weydmann A, Kwasniewski S. Distribution of *Calanus* populations in a glaciated fjord in the Arctic (Hornsund, Spitsbergen)—the interplay between biological and physical factors. *Pol Biol* 2008;**31**:1023–35. https://doi.org/10.1007/s00300-008-0441-0

Weydmann A, Przyłucka A, Lubośny M *et al*. Mitochondrial genomes of the key zooplankton copepods Arctic *Calanus glacialis* and North Atlantic *Calanus finmarchicus* with the longest crustacean noncoding regions. *Sci Rep* 2017;**7**:13702. https://doi.org/10.1038/s41598-017-13807-0

Weydmann-Zwolicka A, Balazy P, Kuklinski P *et al*. Meroplankton seasonal dynamics in the high Arctic fjord: comparison of different sampling methods. *Progr Oceanogr* 2021;**190**:102484. https://doi.org/10.1016/j.pocean.2020.102484

Williams R, Wallace MA. Continuous plankton records: a plankton atlas of the North Atlantic and North Sea: supplement the genus *Clausocalanus* (Crustacea: copepoda. Calanoida) in 1965. *Bull Mar Ecol* 1975;**83**:167–84.

Wilson RJ, Speirs DC, Heath MR. On the surprising lack of differences between two congeneric calanoid copepod species, *Calanus finmarchicus* and *C. helgolandicus*. *Progr Oceanogr* 2015;**134**:413–31. https://doi.org/10.1016/j.pocean.2014.12.008

Winkler G, Dodson JJ, Lee CE. Heterogeneity within the native range: population genetic analyses of sympatric invasive and noninvasive clades of the freshwater invading copepod *Eurytemora affinis*. *Mol Ecol* 2008;**17**:415–30. https://doi.org/10.1111/j.1365-294X.2007.03480.x

Winkler G, Souissi S, Poux C *et al*. Genetic heterogeneity among *Eurytemora affinis* populations in Western Europe. *Mar Biol* 2011;**158**:1841–56. https://doi.org/10.1007/s00227-011-1696-5

Wootton M, Castellani C. Crustacea: copepoda. In: C Castellani, M Edwards (eds), *Marine Plankton: A Practical Guide to Ecology,* *Methodology, and Taxonomy*, 1st edn. Oxford: Oxford University Press, 2017.

Yebra L, Bonnet D, Harris R *et al*. Barriers in the pelagic: population structuring of *Calanus helgolandicus* and *C. euxinus* in European waters. *Mar Ecol Progr Ser* 2011;**428**:135–49. https://doi.org/10.3354/meps09056

Yebra L, García-Gómez C, Valcárcel-Pérez N *et al*. Assessment of short-term spatio-temporal variability in the structure of mesozooplankton communities integrating microscopy and multigene high-throughput sequencing. *Estuar Coast Shelf Sci* 2022;**276**:108038. https://doi.org/10.1016/j.ecss.2022.108038

Zenetos A, Cinar ME, Pancucci-Papadopoulou MA *et al*. Annotated list of marine alien species in the Mediterranean with records of the worst invasive species. *Mediter Mar Sci* 2005;**6**:63. https://doi.org/10.12681/mms.186

Handling editor: Francis Juanes