



The microcopepod family Oncaeidae: state of knowledge and perspectives

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Abstract

Since the discovery of the first oncaeid copepod described by Philippi in 1843 as *Oncaea venusta*, great progress has been achieved regarding the morphological/descriptive taxonomy of the microcopepod family Oncaeidae, occurring in all great oceans and all depth layers of the ocean. The species diversity of this family is still underestimated and the ecological role of oncaeids within the marine ecosystem is not yet well understood, but the life strategy appears to be fundamentally different from most other pelagic microcopepod families. The present paper aims at a comprehensive review of the current state of knowledge of this microcopepod family, including taxonomic and phylogenetic issues, questions of species identification, specific morphological and molecular genetic characteristics, information on regional and vertical distribution and abundance, motion behaviour, feeding and food relationships, reproduction aspects, biomass and elemental composition, respiration and metabolic rates. Relevant open questions are highlighted, and examples are given of shortcomings and high uncertainties in results of current attempts to include oncaeid copepods in various aspects of global marine ecosystem studies. It is concluded that continued support of taxonomic research is required for Oncaeidae and other small copepod species, based on an integrated approach of morphological and molecular genetic methods and user-friendly regional identification keys, to allow an adequate consideration of oncaeids in advanced ecological studies and to achieve a better understanding of the ecological role of this abundant microcopepod family in marine ecosystems.

Keywords Taxonomy · Genetic · Distribution · Abundance · Biomass · Reproduction · Metabolism

Introduction

Research on marine copepod communities has for a long time been focused on the larger species, and the importance of small species has been largely neglected (see e.g., Hopcroft et al. 2001 and review by Gallienne and Robins 2001). Early community studies reporting on the use of small mesh sizes to collect small marine copepods quantitatively included e.g., Delalo (1966), LeBrasseur and Kennedy (1972), Gordeeva and Shmeleva (1973). Since the 1980s increasing effort has been made to also consider the small size fraction of copepods (less than 1 mm total body length) for a more complete understanding of marine pelagic

ecosystems (e.g., Böttger 1982; Paffenhöfer 1983; Paffenhöfer et al. 1984; Ueda 1987; Böttger-Schnack 1996; Yamaguchi et al. 2002a, b; Hopcroft et al. 2005; Hirai and Tsuda 2015; Bode et al. 2018; Tang et al. 2019; Koski et al. 2020). But even nowadays, marine community analyses on regional scale (e.g., Bode-Dalby et al. 2023) or global scale (e.g., Siviadan et al. 2022) are often conducted by using sampling nets with mesh sizes not suitable to capture smaller species. As pointed out by Roura et al. (2018), small copepods are not only unicellular feeders, but have to be considered as metazoan predators as well, when assessing biogenic carbon fluxes in the ocean.

This small size category, addressed as microcopepods in the present context, includes representatives of various taxa, such as calanoids (e.g., Paracalanidae, Stephidae, Spinocalanidae), harpacticoids (*Microsetella*) and cyclopoids (Oithonidae, Corycaeidae, and Oncaeidae). The family Oncaeidae is the most diverse taxon of microcopepods; over 80% of the ca. 114 described species have a body length of less than 1 mm in females, while males are mostly even smaller

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than females (Böttger-Schnack et al. 1989). Thus, regional data on species diversity, abundance, and biomass, as well as data on functional aspects like feeding, reproduction, and metabolism are rare for this family.

Consequently, in the various approaches assessing global rates and patterns for marine pelagic copepods, the significance of Oncaeidae is largely unknown. (e.g., Hirst and Kiørboe 2002; Hirst and Bunker 2003; Bunker and Hirst 2004; Hernandez-Leon and Ikeda 2005; Horn et al. 2016). Recently, Sun et al. (2022) provided a paper on “advances in the research of Oncaeidae”, which calls for substantial complementation and adjustments in several respects.

The present paper attempts to provide a comprehensive review of the current state of knowledge of the family Oncaeidae, including their taxonomy, morphology, phylogeny, molecular genetics, their abundance, regional and vertical distribution in various climates, biomass and elemental composition, metabolic rates (respiration), as well as their life strategies, such as movement, feeding and reproduction. Concurrently, open questions and research demands are highlighted, which restrict the possibility to assess the role of oncaeids in marine ecosystems, and examples are given of the shortcomings and substantial uncertainties in results of current attempts to include oncaeid copepods in various aspects of global marine ecosystem studies.

The aim is to provide a basis for and stimulate future studies for a more adequate consideration of Oncaeidae in the assessment of marine pelagic ecosystems.

Taxonomy and systematics

History of species descriptions

The first oncaeid copepod was reported in 1843 from the Mediterranean Sea, near Palermo, when Rudolph Amandus Philippi (1808–1904) described and figured the first specimen of this family, a male, which he called *Oncaea*

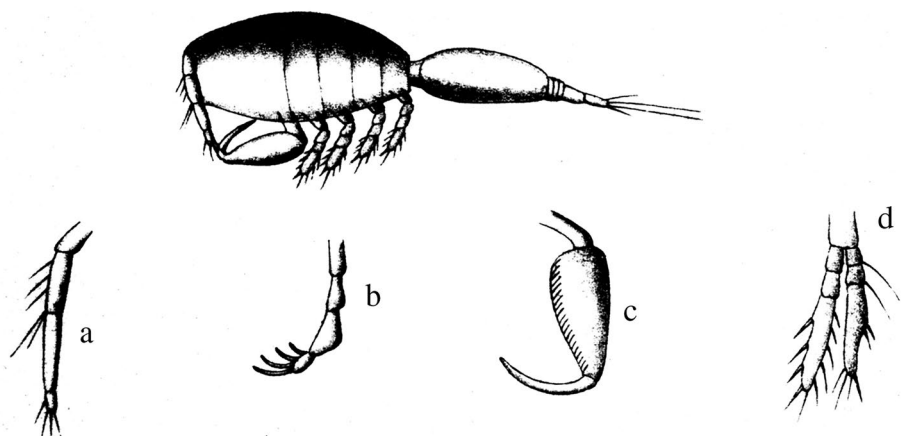
venusta (Fig. 1). The generic name *Oncaea* from Greek *onc-* meaning “hook”, was possibly directed to the distal endopod segment of the big maxilliped, which is drawn into a long-curved claw, which is typical for this family; Philippi 1843, p. 63: “...das Endglied ist eine sichelförmige Klaue.” Regrettably, Philippi dropped the specimen to the floor before he had been able to make drawings of the remaining mouthparts (Philippi 1843, p. 63).

Not until about half a century later, apart from another species described in 1863 (*Antaria mediterranea* Claus 1863), Wilhelm Giesbrecht (1854–1913) was the one, who made a (complete) description of both sexes of *O. venusta* from the Gulf of Naples and established the family name Oncaeidae, to include another 9 species of the genus *Oncaea* collected in the Mediterranean Sea and the tropical Pacific (Giesbrecht 1891, short Latin diagnosis) and established the genus *Conaea* Giesbrecht 1891 (Giesbrecht 1891, 1892, 1902). He also reported the genus *Oncaea* from the Red Sea but did not identify any species (Giesbrecht 1896). So, the cradle of Oncaeidae is in the Mediterranean Sea.

In the twentieth century, the continuation of species descriptions of Oncaeidae over time showed two main steps (Fig. 2): In the sixties and early seventies, Russian and Ukrainian taxonomists, namely Shmeleva (1966, 1967, 1968, 1969, 1979), Shmeleva and Delalo (1965), and Gordeeva (1972, 1973, 1975a, b) described a total of 21 species from the Mediterranean Sea and the tropical Atlantic. In the late seventies and afterwards, the very detailed taxonomic studies on Oncaeidae in Antarctic and Arctic waters by Heron (1977) and co-workers (Heron et al. 1984; Heron and Bradford-Grieve 1995) considerably raised the number of oncaeid species by over 30 species, thereby providing great progress in the morphological knowledge of the family (over 60 species described).

In the period following these two distinct steps, the increase in species descriptions over time was more continuous. Many new species were added from the Red and Northern Arabian Seas (Boxshall and Böttger 1987;

Fig. 1 First presentation of an oncaeid copepod “*Oncaea venusta*” by Philippi (1843). Original drawing from Philippi, body length given in his text as “eine Linie” = one line (without antennae and caudal setae)



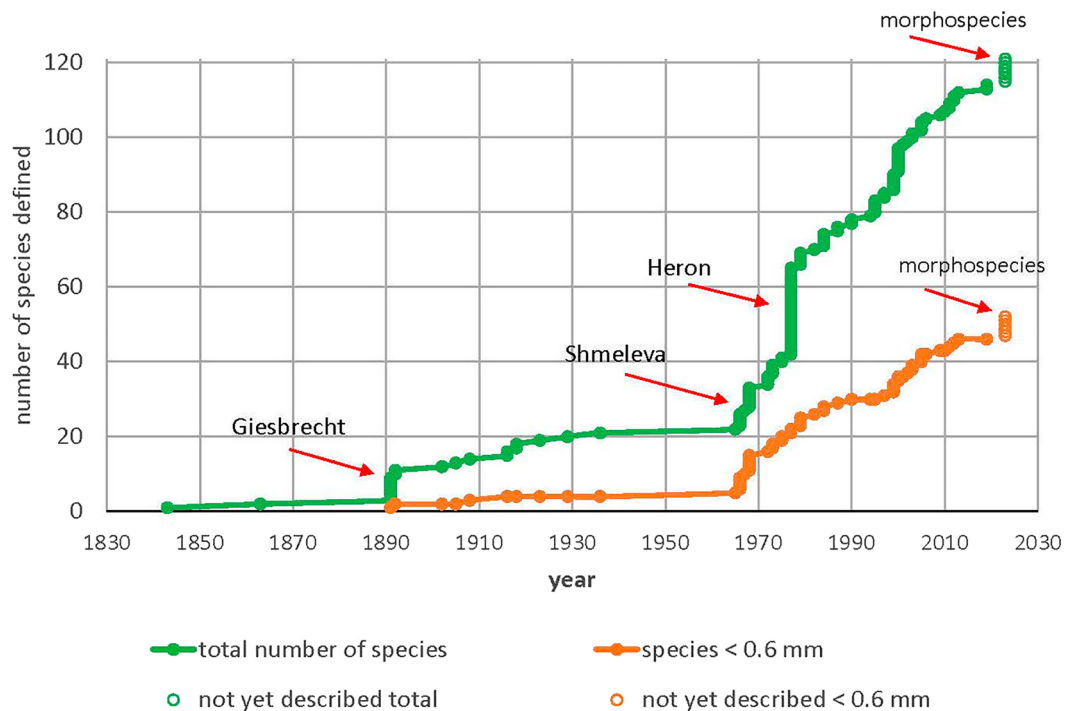


Fig. 2 Number of oncaeid species defined over time. Green line represents total number of species, orange line represents number of species < 0.6 mm total female length. Authors are indicated, who made

substantial contributions to the description of species. “Morphospecies” are clearly defined new species, not yet taxonomically described (see Böttger-Schnack and Schnack 2016–2022)

Böttger-Schnack and Boxshall 1990; Böttger-Schnack and Huys 1997a; Böttger-Schnack 1999, 2001, 2002, 2003, 2005, 2009, 2011), from the Mediterranean (Böttger-Schnack 2011), and from localities in the Atlantic (Boxshall 1977a; Malt 1982a; Bersano and Boxshall 1996 [“1994”]) and the Pacific (Heron and Frost 2000; Wi et al. 2010, 2011, 2012; Cho et al. 2013, 2019), resulting in a total number of 114 species of Oncaeidae described to date (see Walter and Boxshall 2023, at WoRMS <https://www.marinespecies.org/aphia.php?p=taxdetails&id=128586>). In Fig. 2, also seven yet undescribed morphospecies are included (shown separately), which are clearly identifiable, but still await description (see also identification key “OncIdent” at <https://rb-schnack.de/login-for-identification-key.html>).

Size of described species

The total body length of oncaeid species extends over a range of 0.17–1.5 mm (female size); males are usually smaller than females, but the sex-size difference diminishes with decreasing body size (cf. Böttger-Schnack et al. 1989). In small species, such as *Spinoncaea*, both sexes are almost equal in size (Böttger-Schnack 2003), whereas in large species (*Triconia antarctica*) males are only about half the size of their females (Heron 1977). The descriptive progress of small species less than 0.6 mm female body length (Fig. 2,

orange line) was mainly brought about by Shmeleva and/or Gordeeva, whereas Heron and her co-authors mainly considered species larger than 0.6 mm body length. In subsequent years, small oncaeid species were more frequently considered. At present, about 37% of all described oncaeids (female size) are smaller than 0.6 mm.

Completeness and quality of taxonomic descriptions

Giesbrecht’s detailed and profound taxonomic studies on oncaeid species set the basis for our general knowledge of the morphology of Oncaeidae, including also basic information about their mouthparts (except the labrum).

In the following decades, however, morphological descriptions usually concentrated on a limited number of characters (Table 1, column “prior to 1977”), such as body proportions, armature of swimming legs, antenna, antennule and the conspicuous, big maxilliped, but excluding the mouthparts (e.g., Farran 1908; Sars 1916; Früchtl 1923; all studies by Shmeleva and Gordeeva [as cited above]). Basically, discrete characters were described, which sometimes were incomplete or erroneous, esp. in the case of *setal* counts on the swimming legs, and the antennule or the antenna (e.g., Shmeleva 1969), which can be attributed to difficulties in dissecting and observing these small species.

Table 1 Body parts considered in taxonomic descriptions of oncaeid species

Body parts	Considered prior to 1977	Considered after 1977	Showing sexual dimorphism
Antennule A1	○	○○	+
Antenna A2	○	○○	(+)
Mouthparts			
Maxillule Mx1	–	●●	
Maxilla Mx2	–	●●	
Mandible Md	–	●●	
Labrum anterior	–	●●	
Labrum posterior	–	(●●)	
Maxilliped Mxp	○	○○	+
Swimming legs (P1-P4)	(leg armature)	○○	
Leg P5	○	○○	+
Habitus			
Genital (double-) somite + urosomites	○	○○	+
Caudal ramus	○	○○	(+)

○ = generally considered, but not in great detail; ○○ = considered in more detail, Heron's work provided a new standard for species descriptions; ●● = important for phylogenetic relationships, but hardly to be used in identification keys; (...) = not in all cases

Observation problems may also have led to some few invalid species descriptions, when late juvenile male stages were taken as females, although genital apertures were not present. The following species names had thus to be rejected: *O. obscura* Farran 1908, *O. neobscura* Razouls 1969, and *O. parobscura* Shmeleva 1979 (see WoRMS database).

Heron's excellent descriptions (Heron 1977; Heron et al. 1984; Heron and Bradford-Grieve 1995) set the standard for advanced taxonomic descriptions, as she figured and described each species in great detail, considering all the mouthparts, including for the first time the anterior side of the labrum (Table 1, column "after 1977") as well as ornamentation details (e.g., on the exoskeleton). She also pointed out the importance of continuous characters, such as the proportional spine lengths on the swimming legs, or the form of the female genital double-somite, which was useful for distinction of closely related species.

On this basis, Heron and her co-authors could clarify the importance of intraspecific differences in morphometric characters of "varieties" or "forms", which had been observed earlier in several oncaeid species, such as in *Triconia conifera*, *Oncaea media* and *Oncaea notopus*, and their results helped

to unravel the taxonomy of these allegedly cosmopolitan species. These advances have not been considered in Sun et al. (2022), instead earlier described "form"-names have been cited, which are not valid anymore. Examples for the current state of knowledge about *conifera*-variants/forms is given in Table 2. The taxonomic knowledge about species and forms of the *media*-complex was reviewed by Böttger-Schnack (2001, p. 56–58) including characters to separate *O. media* and related species (her Table 5). For species of the *notopus*-group (as defined by Böttger-Schnack and Huys 1998, their species group 7, and Böttger-Schnack and Schnack 2013, their Table 1 and 3) explanations are given in the "Marine Planktonic Copepods" (MPC) database (Razouls et al. 2005–2022, <https://copepodes.obs-banyuls.fr/en/fichesp.php?sp=2087>).

A yet unresolved taxonomic problem concerns the type-species of Oncaeidae *Oncaea venusta*, which is known for its great variability in total body length. Two forms, a large *O. venusta* f. *typica* and a small f. *venella*, were described by Farran (1929), but an intermediate size group has been recorded as well (see Böttger-Schnack 2001 for a review). Despite of detailed taxonomic studies, including morphological (e.g., Heron and Bradford-Grieve 1995; Böttger-Schnack

Table 2 Currently accepted names of earlier reported "form variants" of *Oncaea conifera* (now *Triconia conifera*)

Reported forms	Accepted names
"Form a" (Farran 1936)	<i>Triconia conifera</i> (Giesbrecht 1891)
"Stocky form" (Moulton 1973)	
"Variety III" (Giesbrecht 1902)	<i>Triconia antarctica</i> (Heron 1977)
"Form b" var. <i>furcula</i> (Farran 1936)	<i>Triconia furcula</i> (Farran 1936)
"Long form" (Moulton 1973)	
"Form c" (Farran 1936)	<i>Triconia redacta</i> (Heron and Bradford-Grieve 1995)
"Minus form" (Moulton 1973)	
"Bumped form" (Moulton 1973)	<i>Triconia derivata</i> (Heron and Bradford-Grieve 1995)

2001) and also molecular genetic analyses of sympatric size variants of *O. venusta* (Elvers et al. 2006), the actual status of medium-sized *venusta* form variants could not yet be clarified, and the decision of Heron (2002) to raise an Atlantic medium-sized variant to species rank appears to be inadequate (Böttger-Schnack and Huys 2004; see also WoRMS at <https://www.marinespecies.org/aphia.php?p=taxdetails&id=361949>). Medium-sized form variants of *O. venusta*, are composed of two different genetic clades, but could not yet be separated morphologically from large and small forms, which are genetically distinct (Elvers et al. 2006). For practical application use, the differentiation and enumeration of small, medium, and large size variants of *O. venusta* separately (e.g., Miyamoto et al. 2017) appears to be the best way of dealing with this problem at present.

In most subsequent descriptions of oncaeid species Heron's descriptive style was adopted and further improved by including (1) ornamentation details of the exoskeleton or the appendages (e.g. Malt 1983a), (2) analysis of the posterior side of the labrum, which was found to be important for the systematics of the family (see below under "Definition of generic composition"), and (3) the consideration of continuous characters, also providing more recently first information about their *intraspecific* variability (e.g., Wi et al. 2012; Cho et al. 2013, 2017, 2019, 2020, 2021).

Up to now, the knowledge about intraspecific variability of continuous characters is very limited—this is an important gap in the knowledge to be considered in future studies.

Redescriptions of several insufficiently described species of small size, based on type material and/or neotypes [from the type locality] supplemented and enhanced the original descriptions, and at the same time lead to discovery of new, closely related species representing sibling or sister species of those described earlier: e.g., *Oncaea zernovi* Shmeleva 1966, sister: *O. bispinosa* Böttger-Schnack 2002; *Spinoncaea ivlevi* (Shmeleva 1966), sisters: *S. tenuis* Böttger-Schnack 2003 and *S. humesi* Böttger-Schnack 2003; *Oncaea ovalis* Shmeleva 1966, sisters: *O. crypta* Böttger-Schnack 2005, *O. cristata* Böttger-Schnack 2005, and *O. parabathyalis* Böttger-Schnack 2005.

The time-consuming process of redescribing insufficiently described oncaeid species needs to be continued; especially smaller oncaeid species still await fundamental redescription.

An assessment of the quality state of morphological descriptions for species of Oncaidae is summarized in Fig. 3. Descriptions were grouped into 4 categories: 1 (dark green) completely (re)described, considering mouthparts incl. anterior and posterior view of labrum, 2 (green) almost completely (re)described, mouthparts excl. posterior view of labrum and other few details, 3 (orange) incompletely described, excluding mouthparts and other characters, but basic characters adequate and identifiable, 4 (red) insufficiently described, distinct

morphological errors, not clearly identifiable (incl. species inquirenda); this category also includes yet unknown males of described species and females of undescribed morphospecies. In this figure, the proportion of species less than 0.6 mm total body length is indicated for females, males are not differentiated according to their size.

To date, about two-thirds of all known females are completely or almost completely described. The generally more numerous small species of less than 0.6 mm are to a similar proportion incompletely and to a higher proportion insufficiently described as compared to larger ones. As for the males, only little more than half are completely or almost completely described, and for one third of all oncaeid species males are yet unknown.

The morphology of developmental stages (nauplii and juvenile copepodids) of oncaeid copepods is described for a few species living in coastal or near-shore areas, such as *O. mediterranea* (Hanaoka 1952), *O. venusta* (Björnberg 1972; Koga 1984), *Monothula subtilis* (Malt 1982a, as *Oncaea subtilis*), *O. media* (Björnberg 1972; Malt 1982a; Sazhina 1982) and *O. curta* (Kuei and Björnberg 2003 ["2002"]), based on net sampling and/or rearing experiments. For the latter two species the exact species identification remains uncertain, because *O. media* Giesbrecht 1891 was found to be a species complex (Heron and Bradford-Grieve 1995): e.g., Malt's *O. media* was re-assigned to *O. waldemari* by Böttger-Schnack (2001, p. 71) and *O. curta* may also have been *O. waldemari* Bersano and Boxshall 1996 ["1994"] provided they are two different species (Böttger-Schnack 1999). For oceanic deep-water species, some morphological details (urosome segmentation and body length) of copepodid stages of 4

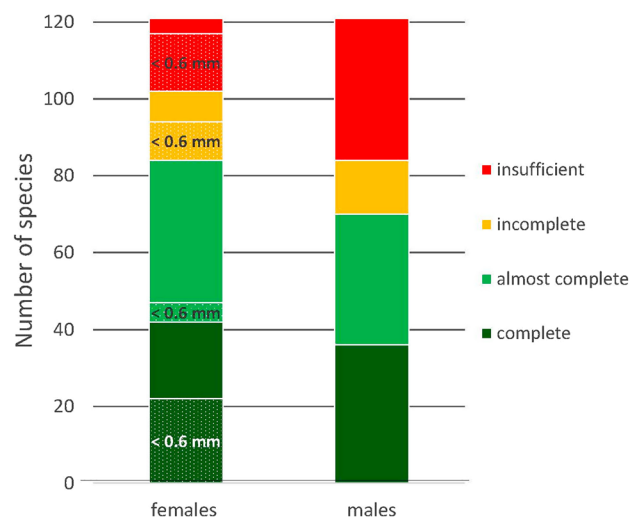


Fig. 3 Quality of taxonomic description of oncaeid species grouped into four categories: insufficient, sufficient but incomplete, almost complete, complete description. For females the portion of small species (<0.6 mm total length) is indicated for each category. (See text for details)

subarctic species (*Triconia borealis*, *T. canadensis*, *Oncaea grossa* and *O. parila*) were reported by Nishibe (2005, Tab. 3.2). He also documented the first nauplius stage of *Triconia canadensis* (Nishibe 2005, Fig. 3.22). For 3 Antarctic species early life stages (CI-CV) were considered in a study on the vertical distribution of the species by Metz (1996), however, no morphological information is provided besides body size.

As pointed out by Nishibe (2005) and Nishibe and Ikeda (2007a) there is uncertainty about the sequence of urosome segmentation from female CV to CVI in oncaeid copepods: According to Malt (1982b, Figs. 3o, 7e) and Nishibe (2005, Fig. 3.1), the female CV has a 4-segmented urosome developing into a female CVI (adult) with a 5-segmented urosome by adding one somite. Böttger-Schnack (2001) and Böttger-Schnack and Huys (2001), on the other hand, described the CV female with a 5-segmented urosome (Böttger-Schnack 2001, Fig. 28A, C) and the adult CVI female also with 5-segmented urosome (her Fig. 24 A, C). The view is that the newly added 6th segment in the last molt is compensated by the simultaneous fusion of the genital and the first abdominal somite, forming a double-somite, which is typical for the great majority of cyclopoid and poecilostome copepod taxa (Huys and Boxshall 1991). Due to the uncertainty of the number of urosomites in stage CV female, a distinction of this stage from CIV and CVI females can be made only by the presence or absence of the pre-cursors or spinulose elements on the second abdominal somite in combination with differences in body length (e.g., Nishibe 2005).

In summary, there is a serious lack of morphological descriptions especially for males and juvenile stages (including nauplii) of oncaeid species.

Definition of the generic composition of Oncaeidae

The family Oncaeidae belongs to the order Cyclopoida; it was formerly placed in the Poecilostomatoida, which is now accepted as suborder Ergasilida within the order Cyclopoida (Khodami et al. 2017, Khodami et al. 2018).

The history of defining the generic composition of the family Oncaeidae has been explained and the former, broad family concept of Oncaeidae has been revised in a phylogenetic study based on morphological characters (Huys and Böttger-Schnack 1996–1997). Nine out of 12 genera that had traditionally been subsumed under this family name were excluded and only three valid genera were retained in the family: *Conaea* Giesbrecht 1891, *Epicalymma* Heron 1977, and the very large type-genus *Oncaea* s.l., including more than 70 species. This type-genus is regarded as a paraphyletic (or possibly polyphyletic) taxon (Huys and Böttger-Schnack (1996–1997).

In a subsequent preliminary phylogenetic study, including information about the posterior side of the labrum (see under

“Feeding/food relationships”, Fig. 11), which had not been described before, the paraphyletic status of the *Oncaea* s.l. was confirmed and the genus was split up into 20 species groups, many of which may eventually be accorded generic status (Böttger-Schnack and Huys 1998).

In the following years, three of these species groups have been raised to generic level, namely *Triconia* Böttger-Schnack 1999, *Monothula* Böttger-Schnack and Huys 2001, and *Spinoncaea* Böttger-Schnack 2003. A new genus and species, *Archioncaea arabica* Böttger-Schnack and Huys 1997, representing the most primitive oncaeid copepod known to date, was added subsequently and discussed. The finding of this species supplemented our present phylogenetic knowledge of the family based on its unique plesiomorphic characters, such as a trisetose exopod on P5 and a long inner coxal seta on P1 (Böttger-Schnack and Huys 1997a).

The systematic status of the family Oncaeidae is summarized in Fig. 4, showing the presently defined genera (top) and the 17 species groups within *Oncaea* s.l. (bottom). The number of species included in each genus or group is indicated by the size of the block and noted inside. Most diverse to date is the genus *Triconia* (29 species), examples for monotypic genera are *Archioncaea* and the *curvata*-group. A summary of the morphological characters used for the identification of the oncaeid genera and the species groups within *Oncaea* s.l. is given by Böttger-Schnack and Schnack (2013, Tables 2, 3).

A resumption and finalization of the preliminary phylogenetic analysis of Oncaea s.l. is still urgently needed. The results achieved so far are used as basis for the identification of the numerous species in this genus and are considered in the construction of an identification key for the family Oncaeidae (see below under “Identification of species”).

Studies on the systematics of oncaeid copepods using molecular genetic data are rare, but first insights have been given allowing, (1) differentiation of sympatric size variants of *Oncaea venusta*, the type-species of the family, collected at different locations of the Indo-West Pacific Ocean (Elvers et al. 2006); (2) verification of new diagnostic morphological characters used for species distinction of 24 oncaeid species or forms in the Mediterranean Sea (Böttger-Schnack and Machida 2011); and (3) first phylogenetic analyses of Oncaeidae in the Mediterranean, leading to yet unresolved discrepancies in the generic status and sisterhood of *Triconia* and *Oncaea* s.str. (Di Capua et al. 2017).

Genetic information

Availability of data (GenBank, BOLD)

Molecular genetic data for taxa of Oncaeidae are rare, only 193 nucleotide sequences are listed in Genbank (at <https://www.ncbi.nlm.nih.gov/nucleotide/?term=Oncaeidae>, cited

end 2022), which is a small number in comparison to other widespread families such as the Oithonidae (5237 records) or Paracalanidae (1005 records). BOLD (http://www.boldsystems.org/index.php/Public_SearchTerms) provides 81 COI sequences, for 18 species of Oncaeidae. At present, nucleotid codes are available for 32 valid species out of the total of 114 oncaeid species, representing 4 genera (Fig. 5). 17 nucleotid records deposited in GenBank were not identified further than genus or family (= *Oncaea* sp., *Triconia* sp. or “Oncaeidae sp.”). The Mediterranean *Oncaea serrulata* Böttger-Schnack 2011 was originally submitted as “*Oncaea* sp. 7 Böttger-Schnack” to GenBank (cf. Böttger-Schnack and Machida 2011), and was subsequently described as a new species. For 3 genera, namely *Archioncaea*, *Epicalymma* and *Conaea*, and more than 80 species, no genetic information is known to date.

Within the large genus *Oncaea* s.l., species belonging to 7 out of 17 species groups as defined in Fig. 4 are represented in GenBank (Fig. 5), but most of them with very few numbers of sequences only. The genus *Oncaea* s.str. is best studied (6 out of 8 species), together their nucleotid codes make up half of all codes known to date (92 out of 193 codes). This is mainly due to the many dates for the type-species *Oncaea venusta*, representing more than 1/5 (22%) of all nucleotid codes of Oncaeidae analysed so far.

For several generally abundant and/or regionally important oncaeid species, representative also for different

species groups within *Oncaea* s.l., nucleotid sequences are not yet available. Regional examples are given in Table 3.

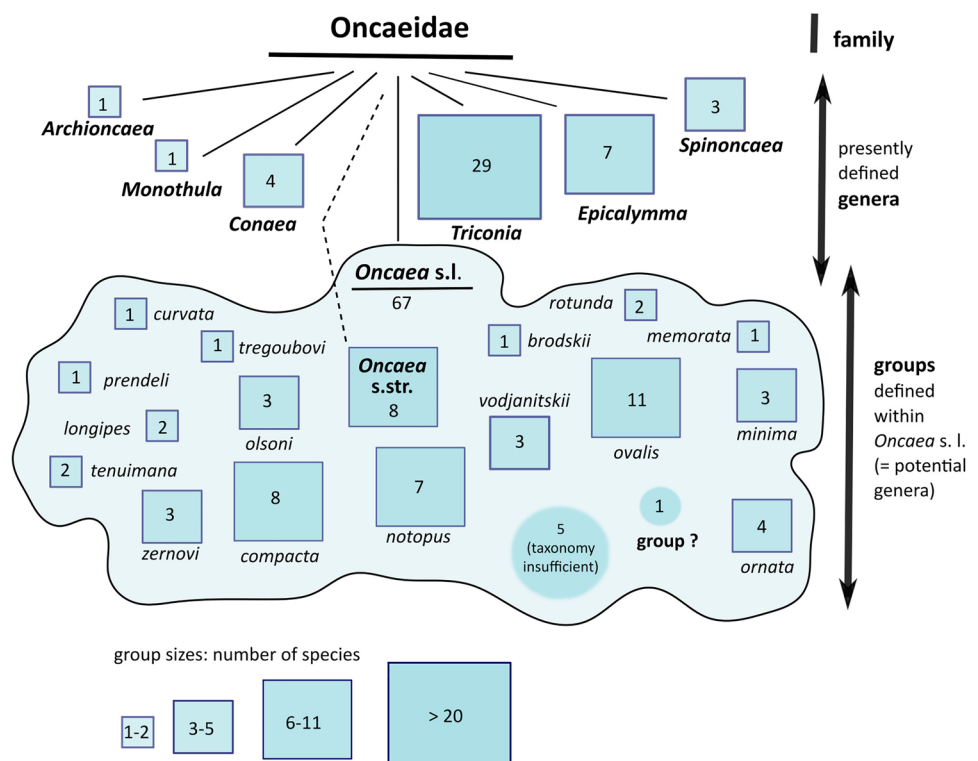
Usability of different genetic markers

DNA barcoding using the mitochondrial cytochrome c oxidase subunit I (COI) has widely been used for identification of marine planktonic species (cf. Bucklin et al. 2021 for review), but cannot be recommended for the family Oncaeidae, because amplification of the mitochondrial COI gene was found to be less successful for species of this family than amplifications of 12S srRNA or similar genes (e.g. Böttger-Schnack and Machida 2011; Cho et al. 2021). Of 106 mitochondrial nucleotids listed in Genbank only 29 were successfully analysed from the COI gene sequence.

Identification of species

The unequivocal identification of oncaeid species is very difficult due to their high morphological similarity and challenges in dissection techniques due to their small size. Identification keys for Oncaeidae available in the printed literature are all regionally limited: e.g., polar seas (e.g., Heron 1977; Heron et al. 1984; Heron and Bradford-Grieve 1995; Heron and Frost 2000); the South Atlantic (Boltovskoy 1999), the North Atlantic (Malt 1983b, ICES

Fig. 4 Generic structure of the family Oncaeidae and species groups defined within the genus *Oncaea* s.l., according to preliminary phylogenetic analysis (Huys and Böttger-Schnack 1996–1997). Each square represents a genus or group. Assignments of groups within the polyphyletic genus *Oncaea* s.l. is not yet solved. The number of species included in each genus and group is indicated by a digit and visualized by the size of the square



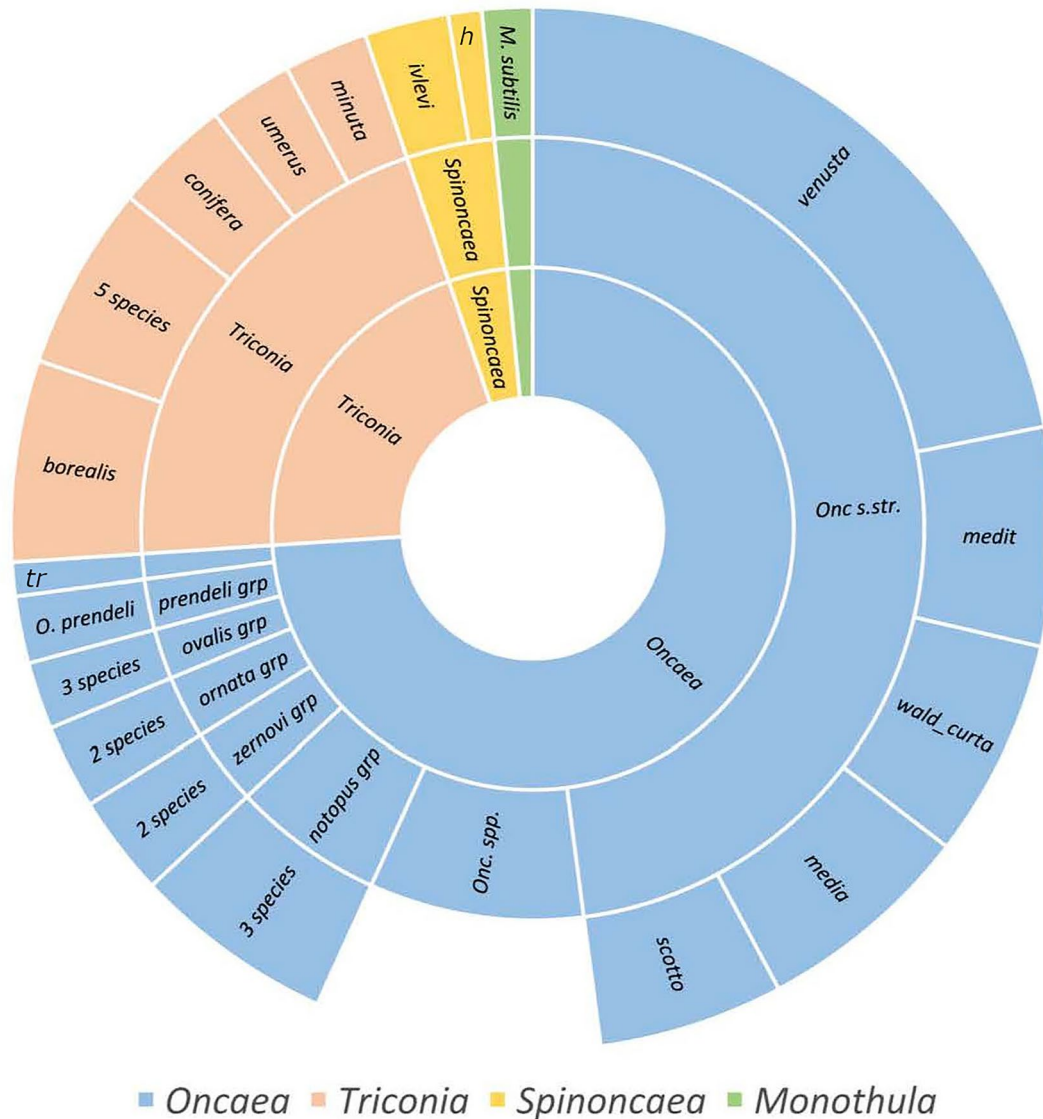


Fig. 5 Percentage distribution of individual genetic codes among species, groups, and genera of Oncaeidae as reported in GenBank (total number of codes=193). Abbreviated taxon names: *Onc.*

str.=*Oncaea* s.str., *Onc. spp.*=*Oncaea* spp., *medit*=*O. mediterranea*, *wald_curta*=*O. waldemari* and/or *curta*, *scotto*=*O. scottodicarloi*, *M*=*Monothula*, *h*=*Spinoncaea humesi*, *tr*=*O. tregoubovi*

Identification sheets) and the Mediterranean Sea (Rose 1933; Shmeleva 1969). These printed keys are generally outdated due to recent progress in taxonomy. The same applies to attempts in providing identification keys for copepod nauplii, including oncaeids (e.g. Björnberg et al. 1994) and also for online information systems such as the former Marine Species Identification Portal, now Linnaeus Project (https://sat-zooplankton.linnaeus.naturalis.nl/linnaeus_ng/app/views/key/index.php?step=4932&epi=23).

Since 2016, a global interactive identification key is available for female Oncaeidae, “OncIdent” (Böttger-Schnack and Schnack 2019), which can be accessed after

registration under the link: <https://rb-schnack.de/login-for-identification-key.html>. The key addresses all clearly identifiable oncaeid species in the world ocean, including several yet undescribed, but identifiable morphospecies (cf. Böttger-Schnack and Schnack 2013). A few described species could not be taken up, due to insufficiently clear definition/descriptions. Regional keys are included at present for the Mediterranean Sea and the North Atlantic. The key is regularly updated, and species names are linked to other databases such as WoRMS (World Register of Marine Species) or the MPC (Marine Planktonic Copepods) database. Taxonomic notes are provided for each species, explaining its taxonomic history, morphological

Table 3 Regionally important oncaeid species, for which nucleotide sequences are yet missing in data bases (GenBank, BOLD). *O.* = *Oncaea*

Region	Species	Area	References for distribution information
Polar Seas	<i>O. curvata</i> (<i>curvata</i> -group)	Antarctic and adjacent waters	Fransz (1988), Metz (1995, 1996); Takahashi et al. (2017); Tanimura et al. (2008)
	<i>O. lacinia</i> (<i>ovalis</i> -group)	Arctic Sea Subarctic areas	Heron et al. (1984) Nishibe (2005)
	<i>O. compacta</i> (<i>compacta</i> -group)	Arctic Sea	Heron et al. (1984)
Temperate or tropical climates	<i>O. longipes</i> (<i>longipes</i> -group)	Deep Arabian Sea Tosa Bay, southern Japan coast (mesopelagic layer)	Böttger-Schnack (1996) Nishibe et al. (2009)
	<i>O. clevei</i> , <i>O. paraclevei</i>	Indo-Pacific warm water	MPC data base; Rezai et al. (2004)
	<i>Conaea rapax</i>	Widespread in meso- and bathypelagic layers	McKinnon et al. (2013)

similarities with other species, denoting its type locality, and pointing to abnormalities in morphological characters.

In the key, species of the large genus *Oncaea* s.l. are grouped according to their respective species group (see above under “Definition of the generic composition”), which enables the user to identify at least the relevant group, in case that a specific ID would be too difficult or could not be achieved. It is recommended to use this “group specification” in doubtful cases, to avoid contributing to the many erroneous species names that can be found in the literature, which subsequently may have resulted in incorrect distribution data or other errors (Bortolus 2008).

No generally valid interactive identification key can yet be built for male Oncaeidae and for juvenile stages, due to missing or insufficient taxonomic descriptions as mentioned above.

A key to the genera of Oncaeidae has been published by Boxshall and Halsey (2004, page 615), which has been presented by Sun et al. (2022) in matrix form (their Table 2). This key, however, is not entirely correct at two steps of the dichotomic decisions. A corrective note is given in the “Introduction” to the OncIdent-Key mentioned above. Sun et al. introduced additional errors, as the matrix presentation would require more genera specific information, than given in the dichotomous key. Hence, the number of exopodal setae on P5 is not correctly presented for 6 of the 7 genera, when stating that these genera have 0–2 setae on P5. Correct numbers of exopodal setae are: *Monothula* 2, *Spinoncaea* 1, *Oncaea* 1–2, *Triconia* 2, *Epicalymma* 1, *Conaea* 1.

A specific problem arises from incorrect spelling of the name *Oncaea* (as “*Oncea*”), which sometimes occurs in the literature, e.g., Eslake et al. (1991) [*Oncaea curvata* as “*Oncea curvata*”], Plounevez et al. (1999), Harris et al. (2000) [A Methodology Manual] or Tande et al.

(2000). This complicates the discovery and interpretation of the results presented in these studies. In the latter work also an invalid species name is apparent: Tande et al. (2000) refer to “*Oncea borealis*” in their abstract but to “*Oncea glacialis*” throughout the text. *Oncaea borealis* is a synonym of *Triconia borealis*, while the specific name *glacialis* does not exist as a valid species name in the family Oncaeidae (cf. WoRMS-database).

Distribution and abundance

Oncaeid copepods are distributed worldwide in oceanic areas of all climates and in all depth layers, reaching from the epi-, meso- and bathypelagic zone down to even benthopelagic layers (Wishner 1979 [Appendix p. 144]; Guidi-Guilvard et al. 2009; Kersten 2015). They occur in coastal and shelf areas and are also found in estuaries (Favareto et al. 2009; Bollens et al. 2011), in fjords (e.g., Vargas et al. 2002; Weydmann et al. 2013) and in enclosed marine lakes in (sub)temperate regions (Lučić et al. 2019) as well as in polar regions (Eslake et al. 1991, Antarctic hypersaline lakes). The occurrence of oncaeids in antarctic sea-ice cores, (Swadling et al. 1997a; Schnack-Schiel et al. 2008) may be an accidental or temporary effect (Hoshiai and Tanimura 1986); they are not regarded as sympagic copepods (Kiko et al. 2008).

Sampling methods

The family Oncaeidae is part of the small meso- or microzooplankton community, and their actual abundance can only be reasonably estimated by the use of very fine mesh gauze in plankton nets or when filtering water obtained with other sampling devices, such as pumps (e.g. Star and Mulin 1981; Paffenhöfer et al. 1984; Thor et al. 2005; Kersten

2015), or sampling bottles (e.g. LeBrasseur and Kennedy 1972; Vinogradov et al. 1987; Hopkins and Torres 1988; Takahashi and Uchima 2008).

In near-shore or coastal areas with high plankton densities, the content of water bottles (e.g., 5 l-Niskin) was also obtained from the original sample volume by the sedimentation method (Kršinić and Viličić 1989; Kršinić et al. 2007).

Before 1985, oncaeid copepods were rarely caught (semi-)quantitatively because the mesh size of the filtration devices was too large; records up to this date were summarized by Böttger (1985, Table 53). In the following years, the more frequent use of finer mesh sizes led to a better assessment of the quantitative numerical importance of microcopepods in general and oncaeids in particular.

Comparative studies using small and larger mesh sizes demonstrated that the traditionally used nets of 300 µm or 200 µm mesh size (e.g., WP2 net) would only collect a small insignificant part of the microcopepod community (Calbet et al. 2001; Gallienne and Robins 2001; Munk et al. 2003; Paffenhöfer and Mazzocchi 2003; Zervoudaki et al. 2006; Miyashita et al. 2009; Makabe et al. 2012; Ward et al. 2012). Zervoudaki et al. (2006) recorded that even abundances of a large species like *Oncaea mediterranea* (adults) were underestimated by a factor of ~2 when comparing 200 µm and 45 µm mesh nets, and this factor strongly increased when medium-sized species like *O. media* (factor 20) and smaller species and juvenile copepodids (*Oncaea* spp., factor 70–80) were considered. Miyashita et al. (2009, Fig. 3) showed that the abundance of copepods with a prosome length of less than ca 600–700 µm was underestimated by more than one order of magnitude and their biomass (dry weight) by a factor of 1.6 in 300 µm as compared to 64 µm mesh size. About two thirds of all described oncaeid species have a prosome length of less than 600–700 µm (equivalent to a total body length of approx. 850–950 µm in the adult female), so even adult female oncaeids are not adequately represented in the traditionally used mesh nets, not to mention their smaller males and juvenile stages. For an adequate consideration of oncaeid species a mesh size of 100 µm or less is required; it should be no larger than about 50 µm when the smallest species are to be sampled quantitatively (see also next paragraph).

Enumeration methods

Estimation of microcopepod abundances is usually based on samples or subsamples, which are examined and counted in a counting chamber (Bogorov or else) under a dissecting microscope, thereby enabling detailed examination of morphology (Habitus), as well as measures of individual body length, often used for calculating biomass values and derived measures (see under “**Biomass and chemical composition**”).

Not so common is the use of an inverted microscope [Utermöhl-Chamber] (e.g., Kršinić et al. 2007, 2016), which includes the problem that individual specimens cannot be viewed from different angles, thus calling for a researcher highly experienced in the identification of the species in the area investigated. Kršinić et al. (2007) avoided mesh size selection by using large bottle samples and concentrating the plankton material by sedimentation. A detailed comparison of methods using sedimented and filtered plankton samples in microzooplankton research is given by Kršinić (1980).

More recently also automated image analysis (e.g., Zooscan) has been used for abundance estimates of net samples (e.g., Saviadan et al. 2022) and/or in situ observations using a video plankton recorder (VPR) (e.g., Beroujon et al. 2022). This very time saving approach has, however, limited identification power, especially for the very small copepod species, as demonstrated for comparative investigations using VPR and fine mesh net samples (Beroujon et al. 2022).

Carcasses

Differentiation of the live/dead status (=carcasses) of microcopepods during enumeration of samples has rarely been conducted in marine ecological studies, although carcasses were found to represent a considerable portion of copepod material in the water column (Yamaguchi et al. 2002a) and may contribute to passive carbon sinking flux (Tang et al. 2019).

For poecilostomatoid copepods (mainly oncaeids), Yamaguchi et al. (2002a) reported a percentage higher than 50% among total carcass numbers in the subarctic Pacific in the 4000 m water column.

For individual oncaeid species, percentages of carcasses may vary widely, from zero to 100% as shown in the Arabian Sea for the water column 0–1850 m (Böttger-Schnack 1996). In the Red Sea, smaller oncaeid species had much higher relative abundances of carcasses (20–40% of total standing stock in the upper 450 m) than larger ones (usually <5%), and the greatest relative abundance of carcasses for a single species was always outside the mode depth of living specimens, either below or above the mode depth (Böttger-Schnack 1990a, b).

Consideration of oncaeids in copepod community analysis

A summary of locality records of quantitative plankton studies in marine areas, based on sampling devices using 0.1 mm mesh size (or less) and considering Oncaeidae at least at the family level (as “*Oncaea* spp.” or “Oncaeidae”) is depicted in Fig. 6a. In total, 120 studies are included, most of which were recorded over the past 4 decades, only very few studies

were taken before 1980. References to the studies included in Fig. 6 are given in the appendix.

Most studies were taken at or near coastal areas, including all continental zones, except the west and southeast coast of Africa and south-eastern Asian provinces. In central oceanic areas, few studies have been made, mostly restricted to the Pacific (Fig. 6a). Only early Russian studies covered a wide area in the central Atlantic (Gordeeva and Shmeleva 1973).

The depth range sampled is indicated by different symbols. Of the 120 studies, about half (59 studies) were confined to the upper 100 m, and less than one quarter covered ranges deeper than 500 m (26 studies). The black square in the eastern North Pacific denotes a study in the benthopelagic layer at 4000 m depth (Kersten 2015).

Ecological studies including species identification of Oncaeidae—at least for dominant species—are geographically less widespread (Fig. 6b), being (almost) absent from the sampling indicated in Fig. 6a in the waters off the North- and South American coasts.

Complete community analyses of oncaeid copepods, including also very small species less than 0.5 mm in body length, are rare (Fig. 6c, 33 studies). They are situated in (1) the Mediterranean Sea, where a “hotspot” of information is available for the Adriatic Sea, (2) the Red Sea and adjacent northern Arabian Sea as well as the Eastern Indian Ocean, near Australia, (3) the western Pacific, both subarctic and temperate, and (4) two areas each of the Arctic and the Antarctic (Fig. 6c).

Abundance of oncaeid copepods

The numerical abundance of oncaeid copepods, sampled with mesh sizes of 0.1 mm or less, varies considerably depending on oceanic region and depth range sampled. Examples for observed maximum abundance values are given in Table 4.

Within the total copepod community sampled with small mesh sizes (0.1 mm or less), the relative numerical abundance of oncaeid copepods (adult and juvenile copepodids) differs also largely among regions and depth ranges:

In coastal areas and epipelagic layers of the ocean their numerical abundance is usually smaller than or at most equivalent to that of small calanoids, oithonids, and sometimes corycaeids and harpacticoids, as has been shown for

- (1) tropical and temperate climates (LeBrasseur and Kennedy 1972; Paffenhöfer 1980; Star and Mullin 1981; Chojnacki and Węgleńska 1984; Valentin et al. 1987; Roman et al. 1995; Böttger-Schnack 1995, 1996, 1997; Paffenhöfer and Mazzocchi 2003; Böttger-Schnack et al. 2008; Munk et al. 2018),
- (2) Subarctic/Arctic regions (Yamaguchi et al. 2002a; Hopcroft et al. 2005), and
- (3) Antarctic areas (Makabe et al. 2017).

Sometimes, however, oncaeid copepods even outnumber the other copepod taxa in these upper/shallow depth layers (e.g., Judkins 1980; Paffenhöfer 1983; Groendahl and Hernroth 1986; Miyashita et al. 2009; Ojima et al. 2013, 2015).

In deep oceanic meso- and bathypelagic zones between 200 and 4000 m depth, the Oncaeidae always represent the most important copepod group in terms of numerical abundance, accounting for 60–80% of all copepods as reported for areas of very different hydrographic conditions (Böttger-Schnack 1994, 1995, 1996, 1997; Yamaguchi et al. 2002a; McKinnon et al. 2013; Makabe et al. 2017; Takahashi et al. 2017; Abe et al. 2020). Only in some deep-water zones of the Mediterranean Sea, harpacticoid copepods have been found to be equally abundant to oncaeids (Böttger-Schnack 1994, 1997; Kršinić et al. 2020).

The contribution of oncaeids to total copepod biomass is generally much lower due to their small size, and calanoid copepods are usually dominant (e.g., Yamaguchi et al. 2002a; Fig. 4b; Ward et al. 2012; Fig. 4).

Species diversity and composition of oncaeid communities

The total number of oncaeid species reported for different oceanic regions, based on small mesh net samples, are not directly comparable and not necessarily representative, because different depth ranges were sampled (min. 0–200 m and max. 0–2000 resp. 3000 m). In general, the following picture has so far been obtained:

I- In tropical and warm temperate regions, the maximum number of oncaeid species was about 70, reported for open waters in the Indo-Pacific region, over the depth range of 0–2000 m (Böttger-Schnack 1996); within the upper 200 or 500 m, 35–50 species were found (Nishibe et al. 2009; McKinnon et al. 2013; Itoh et al. 2014). Comparably low numbers of about 30 species were reported for the Red Sea in the 0–> 1050 m depth range (Böttger-Schnack 1994, 1995), where the unusually high temperatures and salinities in subsurface waters of this enclosed area, coupled with a depleted oxygen content in the mesopelagic zone and lack of food in the bathypelagic zone causes an absence of typical deep-water communities (e.g., Weikert 1982). In the Mediterranean Sea, the number of oncaeid species (max. 40) is similarly influenced by unusual hydrographical conditions in the deep zone (e.g., Böttger-Schnack 1994, 1997). For the central Atlantic, Gordeeva and Shmeleva (1973) recorded 33 oncaeid species in the upper 1000 m of the water column.

II- In a subarctic region of the NW Pacific, a maximum of 38 species of Oncaeidae was reported, including some influence of warm water communities (Nishibe and Ikeda 2004).

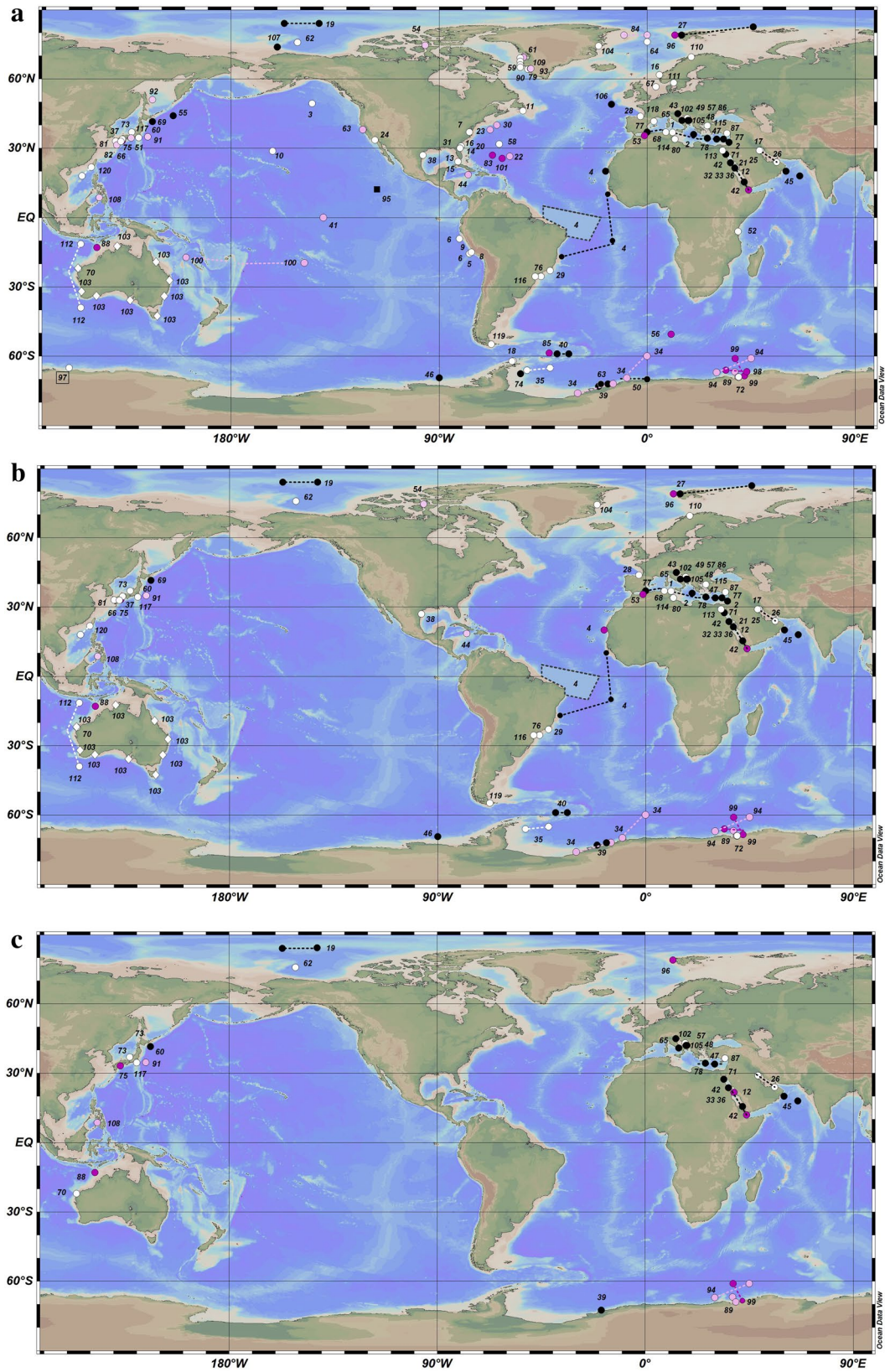


Fig. 6 **a** Geographical distribution of quantitative zooplankton studies considering Oncaeidae at least on family level, based on small mesh net samples (100 μm or less). Numbers refer to references given in the appendix, listed (with few exceptions) in a time sequence from 1964 – 2022. White dots = samples ranging from 0 to 100 m, pink dots = samples ranging down to 200 m, red dots = samples ranging down to 500 m, black dots = samples ranging deeper than 500 m. Diamond symbols indicate monitoring stations; square symbol indicates deep sea benthopelagic samples. **b** Geographical distribution of quantitative zooplankton studies including at least some species identification for Oncaeidae, based on small mesh net samples (100 μm or less). See Fig. 6a for further explanations. **c** Geographical distribution of quantitative zooplankton studies including an analysis of the local species composition of Oncaeidae, based on small mesh net samples (100 μm or less). See Fig. 6a for further explanations

III-In polar seas, species numbers of oncaeids may be minor, but small oncaeid species less than 0.5 mm body length have not yet been adequately studied: In the high Arctic, a total of 12 species were recorded in small mesh nets sampled at 0–90 m and between 300 and 3000 m depth (Heron et al. 1984, Table 2). In Antarctic waters, little more than 4 species were recorded in the epi- and upper mesopelagic zone (Metz 1993, 0–1000 m; Takahashi et al.

2017, 0–500 m). The comprehensive study of Heron (1977), however, indicated a comparably speciose deep-water community of Oncaeidae (20 species) in the deep SW Pacific Antarctic area at 1000–2000 m depth sampled with nets of 0.2 mm mesh size.

Table 5 presents the most typical species for different climate zones by three size groups according to female body length.

Vertical distribution of oncaeid species

The vertical distribution of species numbers of Oncaeidae (adult specimens only) in different climatic regimes down to a maximum depth of 2000 m or even below is shown in Fig. 7 for a-High Arctic, b- Subarctic, and c-Tropical seas (data taken from Heron et al. 1984; Nishibe and Ikeda 2004; Böttger-Schnack 1996, respectively). Generally, species numbers increase with depth to maximum values in the meso- and bathypelagic zones. In the upper layers, a distinct difference in species numbers becomes apparent between the Arctic zone, inhabited by very few or even a single species

Table 4 Observed maximum abundance values for oncaeid copepods sampled with mesh sizes of 0.1 mm or less

General area	Specific zone	Abundance (max. ind. m^{-3})	References
Coastal areas		$> 10^4$	Paffenhöfer et al. (1987), Valentin et al. (1987)
	Semi-enclosed bay	10^5	Lučić et al. (2019)
Offshore areas	Epipelagic zone, tropical and temperate climates	10^2 – 10^3	Roman et al. (1995), Nishibe et al. (2009), Böttger-Schnack (1996), Paffenhöfer and Mazzocchi (2003)
	(Sub)polar seas	10^2 – 10^3	Lischka and Hagen (2016), Thor et al. (2005), Yamaguchi et al. (2002a)
	Bathy- and mesopelagic layers	0.01–10	Böttger-Schnack and Schnack (2009), Makabe et al. (2017), Kršinić et al. (2020)
	Deep sea benthopelagic layers	1.0–3.5	Kersten (2015)

Table 5 Typical oncaeid species per climate zone by size group according to female body length

Climate zone	Size groups		
	< 0.5 mm	0.5–1.0 mm	> 1.0 mm
Arctic	<i>O. lacinia</i> ** <i>O. pumilis</i> **	<i>T. borealis</i> * <i>O. parila</i> * <i>Epicalymma</i> spp.**	<i>T. canadensis</i> ** <i>O. englishi</i> **
Antarctic	?	<i>O. curvata</i> * <i>Epicalymma</i> spp.**	<i>T. antarctica</i> ** <i>O. englishi</i> **
Tropical and temperate	<i>Spinoncaea</i> spp.* <i>O. zernovi</i> -group* <i>Epicalymma</i> spp.** <i>O. longipes</i> ** <i>O. tregoubovi</i> **	<i>O. scottodicarloi</i> * <i>O. media</i> * <i>T. similis</i> -group* <i>O. ovalis</i> -group** <i>O. notopus</i> -group**	<i>O. venusta</i> * <i>O. mediterranea</i> * <i>T. conifera</i> -group** <i>O. ornata</i> -group** <i>Conaea rapax</i> **

O. = *Oncaea*, *T.* = *Triconia*

*Mainly epi- to mesopelagic

**Mainly meso- to bathypelagic zone.

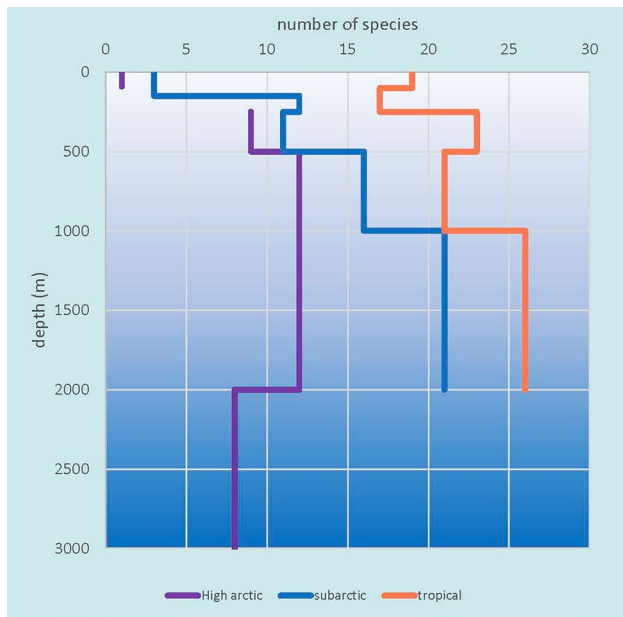


Fig. 7 Number of oncaeid species encountered per depth zone in three different climatic regions; data taken from Heron et al. (1984) for High arctic, Nishibe and Ikeda (2004) for subarctic, and Böttger-Schnack (1996) for tropical (Arabian Sea) region

only, and the tropical zone, where up to or more than 20 different oncaeid species are found (Fig. 7).

Vertical differences in the species composition of oncaeid communities is largely depending on the vertical structure of the hydrographic conditions. Paffenhöfer (1983) compared two size groups of Oncaeidae showing that in a stratified water column, the group of small

specimens (passing 100 µm and kept by 30 µm mesh) were more abundant in the upper warmer layer and the group of larger specimens (kept by 100 µm mesh) were more abundant in the lower colder intrusion water. It remains open, though, whether this was mainly a species- or a stage-related difference. The intrusion water may have contained species of a quite different size composition as the coastal species community. Considering adult specimens only, data from the Oyashio region of the western subarctic Pacific down to a depth of 2000 m, presented by Nishibe and Ikeda (2004, Table 4), show a clear species-specific difference between two alternative hydrographical regimes encountered in this area. The results are visualized in Fig. 8:

- (1) In September 1996, a typical situation of the subarctic Oyashio water was observed, with a clear dominance of a single species (*Triconia borealis*) in the upper 250 m, whereas in deeper layers mesopelagic and deep-water species, e.g., *Oncaea lacinia* and *O. parila*, are dominating. In the deepest layer – below 1000 m – several typical deep-water species occur, such as *Epicalymma* species, which are similarly abundant.
- (2) In December 1996, the hydrographic situation in the upper 250 m had changed due to the influence of the warmer Kuroshio current, reflected by an obvious change in the community structure of oncaeids in the upper layers, which are now dominated by warm-temperate or tropical species, such as *Oncaea scottodicalroi*, *O. media*, or the very small *Spinoncaea* species. The community composition below 250 m depth did not show such a dramatic change but remained similar to the September situation,

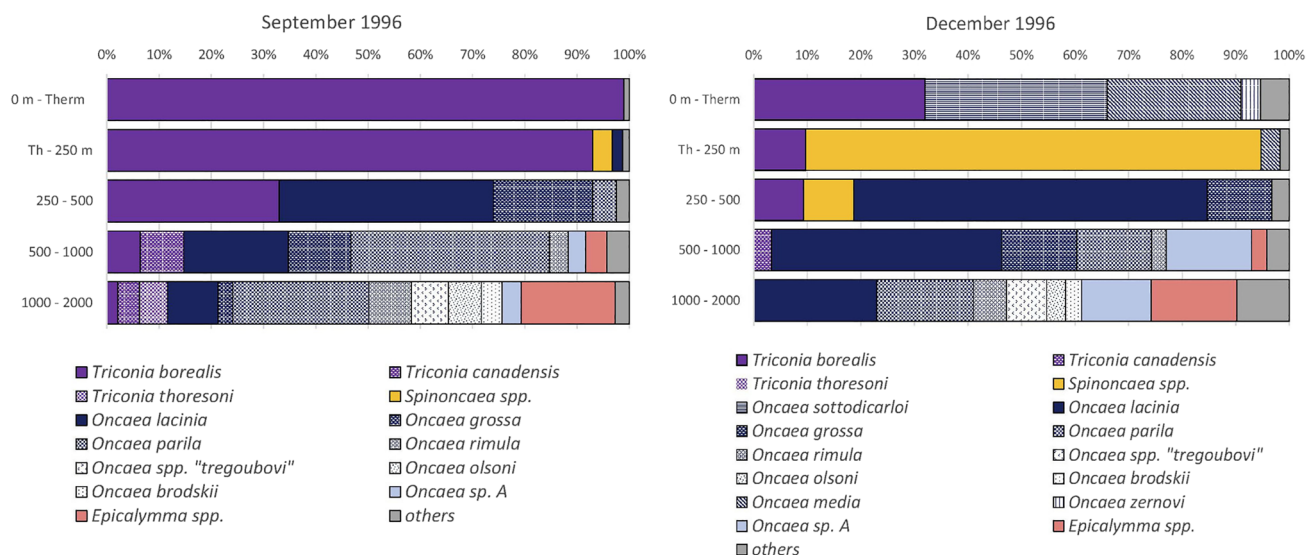


Fig. 8 Example for differences in the vertical structure of oncaeid communities at the same station, depending on the hydrographic condition. Data from Nishibe and Ikeda (2004, Table 4). Th = Therm = Thermocline

indicating a fairly stable deep-water community in this area (Nishibe and Ikeda 2004).

A more comprehensive regional comparison of oncaeid communities requires more extended studies using comparable methodological approaches.

Biology and ecology of Oncaeidae

Motion behaviour

Compared to other pelagic copepod taxa (calanoids, oithonids), little is known about the individual motion behaviour of oncaeid species. Björnberg (1972) observed active swimming movements of *Oncaea media* in lab aquaria and measured the velocity of its upward movement (0.57–0.75 cm sec⁻¹) in the morning “under direct sunlight” and downward sinking (0.12–0.22 cm sec⁻¹) around noon. Observations of the individual swimming behaviour of oncaeid copepods using video recording indicated a non-continuous swimming with small hops and/or a complex swimming pattern for adults of *O. venusta* (Hwang and Turner 1995; Seuront et al. 2004). For nauplii of *O. mediterranea* a rare activity, but very fastmoving swimming behaviour was observed by Paffenhöfer et al. (1996).

At sea, vertical movements of oncaeid species have been observed in the water column during day and night [= diurnal vertical migration (DVM)], among different seasons [= seasonal migration] and among ontogenetic stages [ontogenetic vertical migration (OVM)] and have been investigated in various climate zones, e.g. tropical/subtropical/temperate regions (Tsalkina 1970, 1972, 1977; Boxshall 1977b; Böttger-Schnack 1990a, b, 1997; Checkley et al. 1992; Itoh et al. 2014), in Arctic and subarctic waters (Groendahl and Hernroth 1986; Richter 1994; Fortier et al. 2001; Nishibe 2005; Darnis and Fortier 2014) and the Antarctic (Metz 1993, 1995, 1996; Bielecka and Żmijewska 1997; Tanimura et al. 1997, 2008). [*Note that the elements of Fig. 5 in Böttger-Schnack (1997) have been mixed up during the printing process; a corrected version of this figure is included as Online Resource_1].

Observations of species-specific DVM are very variable and range—depending on area and hydrographic conditions—from strong DVM for some large species in tropical and temperate regions with a vertical amplitude of up to 100 m or even 200 m between day and night (e.g. *Triconia conifera*) to minor DVM for others (e.g. epipelagic *Oncaea venusta*, *O. media* or mesopelagic *O. ornata*, *Conaea gracilis*) (Tsalkina papers; Boxshall 1977b; Böttger-Schnack 1990a; Checkley et al. 1992; Brugnano et al. 2012; Itoh et al. 2014). Female *T. conifera* showed bimodal vertical distribution patterns during the night, indicating that only part of

the population migrated upwards (Boxshall 1977b; Böttger-Schnack 1990a, b); for this species, no DVM was observed in a shallow continental shelf area off Mexico by Checkley et al. (1992). Some data are available for small *Spinoncaea* species and *O. zernovi*, suggesting that their DVM is weak or absent (Böttger-Schnack 1990a, Tab. 3; 1990b, Tab. 3; Itoh et al. 2014); but the data base is yet insufficient for any definite conclusion.

In polar seas, the large Antarctic mesopelagic *Oncaea antarctica* (now *Triconia antarctica*) showed no DVM during winter (darkness) and an inverse DVM during summer, moving upwards during the day and being more dispersed in the 1000 m water column (Bielecka and Żmijewska 1997). Similarly, the medium-sized *O. curvata* (CI–CVI) did not show DVM under sea ice during winter (Tanimura et al. 1997), while an inverse DVM was observed during summer, where the entire population (CIII – CVI) moved to deeper layers during the night (Tanimura et al. 2008). In subarctic waters, the population of the large mesopelagic *T. canadensis* did not show significant day-night differences in vertical distribution, as only a part of the population (CV stage) moved upwards during the night (Nishibe 2005). The medium-sized *T. borealis* showed an insignificant DVM in subarctic waters (Nishibe 2005), and a small or even inverse DVM in the high Arctic under sea ice (Fortier et al. 2001); no or insignificant DVM was reported for its developmental stages (nauplii and copepodids) in a Swedish fjord (Titelman and Fiksen 2004).

Ontogenetic vertical migration (OVM) has been observed by Metz (1996) for the epipelagic Antarctic species *O. curvata*; adult and CI stages showed a tendency for a deeper occurrence compared to later juvenile copepodid stages. For two mesopelagic species, *O. antarctica* (now *T. antarctica*) and *O. parila*, a systematic difference in the depth distribution of developmental stages was not obvious. In the subarctic Pacific, Nishibe and Ikeda (2007a) observed OVM for two mesopelagic species, *T. canadensis* and *O. parila*, characterized by deeper occurrence of early and late developmental stages as compared to a shallower occurrence of middle stages.

Observed differences in vertical distribution patterns of oncaeid species are difficult to interpret because of two major problems: unequivocal taxonomic identification and adequate sampling strategy.

(1) Taxonomic identification problems are due to the potential existence of sister and/or sibling species in the material examined. Earlier ecological studies on *Oncaea conifera* (e.g., Tsalkina 1970, 1972, 1977) and on *Oncaea media* (e.g., Checkley et al. 1992) may have included several sister species of the *Triconia conifera*-complex and the *Oncaea media*-complex, respectively [see above under “Taxonomy”]. The species *Spinoncaea ivlevi*,

reported under the name *Oncaea ivlevi* Shmeleva in the Eastern Mediterranean Sea (Böttger-Schnack 1997, Fig. 5 [corrected version of this figure see Online Resource_1]), may have included the sister species *S. humesi* Böttger-Schnack 2003, which was unknown at that time. This became obvious from later taxonomic analyses (Böttger-Schnack 2003, Table 3b). Especially for small species the identification is often too difficult and time-consuming, so that even known sister species have not been differentiated in studies on vertical distribution (e.g., *O. zernovi* and its sister taxon *O. bispinosa* were combined in the study by Itoh et al. 2014).

(2) The sampling strategy may not be adequately adjusted, e.g., if the vertical resolution of samples is not sufficient for detecting vertical movements of small amplitudes (e.g., Böttger-Schnack 1990b) or if day and nighttime samples were taken at different stations (e.g., Groendahl and Hernroth 1986). Also, the sampling variability among individual vertical series at the same station and daytime may be a problem. Replicate sampling in a fairly stable environment of the central Red Sea (Böttger-Schnack 1990a, Fig. 4) provided some first impression of the short-term variability among individual vertical profiles, exemplified for the species *O. media* f. *minor*, later defined as *O. scottodicaloi*. Such information is usually not available so that the interpretation of day-night differences remains uncertain.

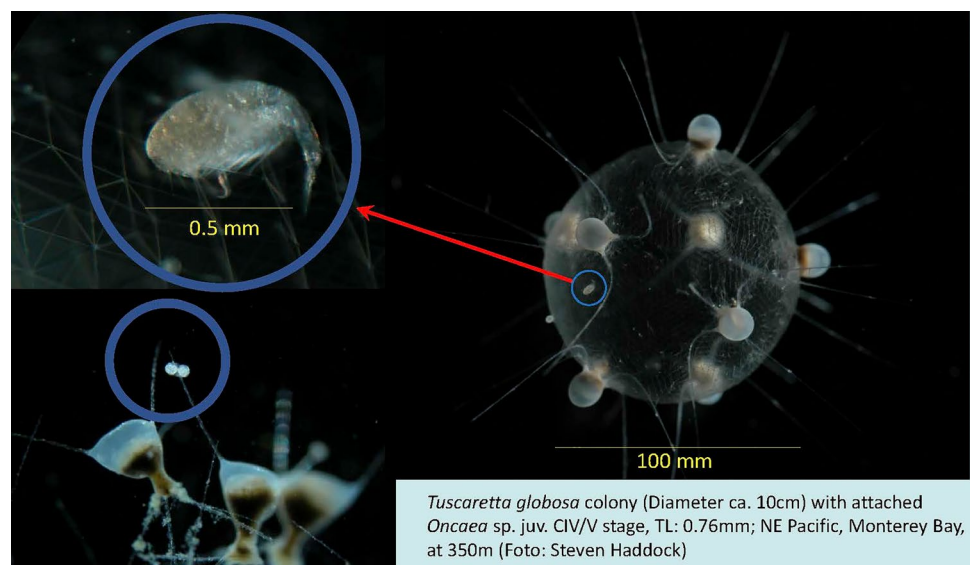
Association with substrates

Besides swimming freely, oncaeid copepods of warm climates have been observed in situ in association with various aggregates or substrates in the pelagic environment, such as (1) “marine snow” (= macroscopic aggregates of

detrital material) (Lampitt 1993; Green and Dagg 1997, see also literature review of Kiørboe 2000), also indicated by gene sequencing (Lundgreen et al. 2019, Sargasso Sea), (2) discarded appendicularian houses in epipelagic layers (Alldredge 1972; Ohtsuka and Kubo 1991, 1993; Nishibe et al. 2015) or in the mesopelagic zone (Steinberg et al. 1994), (3) gelatinous organisms, such as salps (Alldredge 1972) and (4) phaeodarian (radiolarian) colonies in the deep sea (Fig. 9). For polar seas, no in situ observations are available, but the observed food relationships of polar species of Oncaeidae (see under “Feeding/food relationships”) may point to an associative behaviour in this region/climate zone as well. The association with a fish host, as reported for a single male of *O. philippinensis* on the gills of deep-sea myctophids (Kazatchenko and Avdeev 1977), and the record of *O. venusta* on hydroid colonies (Ho 1984) must be regarded as accidental rather than obligatory (Huys and Böttger-Schnack 1996–1997).

The species identity of associated Oncaeidae is little known. In epipelagic layers, adult species of *Oncaea* s.str. (*O. mediterranea*, *O. venusta*, *O. media*, and *O. scottodicaloi*) and of *Triconia* (*T. conifera* as *Oncaea conifera*) (Alldredge 1972; Ohtsuka and Kubo 1991; Nishibe et al. 2015) as well as unidentified juveniles (Ohtsuka and Kubo 1991) were found on discarded appendicularian houses. In mesopelagic layers, species of *Triconia* (recorded as *O. conifera* and *O. similis* [= *similis*? probably misspelled]) were identified after collection on giant appendicularian houses (Steinberg et al. 1994); since both species belong to a species complex within *Triconia*, namely the *conifera*- and *similis*-subgroup, respectively, they might have been confounded with similar-looking but different species in this case. In other studies, cited above (e.g., marine snow), the species identity of oncaeids was not determined.

Fig. 9 *Oncaea* sp. juvenile stage attached to a phaeodarian (radiolarian) colony. (Foto Steven Haddock)



Thus, open questions remain about possible differences in associative behaviour between: (1) species of different size—such as the abundant small species *Spinoncaea* and/or *O. zernovi* in warm climates, (2) species in different climate zones, (3) developmental stages, and (4) deep-sea species, e.g., species of *Epicalymma*. Further, the potential use of substrates other than those named above need to be investigated, e.g., the large mucous feeding webs produced by pteropod molluscs (Gilmer and Harbison 1986).

Feeding/food relationships

Feeding behaviour and food relationships of oncaeid copepods have been studied by various methods, including direct observations in the field and in the lab, feeding experiments, analysis of gut contents and faecal pellets, and studies on the elemental composition of species. A listing of methods employed for oncaeids, and corresponding references is given in Table 6.

Most of the studies were conducted in warm temperate and tropical climates and included species of *Oncaea* s.str. (*O. venusta*, *O. media*, *O. mediterranea*, *O. scottodicarloi* (as *O. media* f. *minor* in Ohtsuka et al. 1996) and of *Triconia* (mainly *T. conifera*, rarely *T. umerus*, *T. minuta*, *T. hawaii* and *T. dentipes*) as well as unidentified oncaeids. For polar seas, investigations included *O. curvata* and *T. antarctica* in the Antarctic (Hopkins 1985, 1987; Metz 1996, 1998; Swadling et al. 1997b; Kattner et al. 2003) and *T. borealis* in arctic waters (Kattner et al. 2003).

All investigated species represent medium-sized and large species of the family occurring in the epipelagic zone, and some vertically migrating mesopelagic species. In most cases, only adult females were considered, rarely males and/

or juvenile copepodid stages (Ohtsuka et al. 1996; Nishibe et al. 2015) or nauplii (Roff et al. 1995).

Food items consumed by oncaeid copepods as reported in studies cited in Table 6 included bacteria and a wide variety of phyto- and zooplankton, namely various diatoms, *Phaeocystis*, dinoflagellates, tintinnids, radiolarians, picoplankton, silicoflagellates, nematocysts of cnidarians, fish larvae, chaetognaths, calanoid copepods (pieces), unidentified crustacean remains, appendicularians: (house membranes, outer incurrent filters and inner food-concentrating filter fibres, copepod carcasses, sediment particles (Turner 1986a), and probably faecal strings of krill (Gonzalez et al. 1994; Suzuki et al. 2003).

The food composition appears to be rather variable, appendicularian houses and filters were frequently observed and recognized as important part of food but may sometimes be less used (Ohtsuka and Kubo 1991; Koski et al. 2007). In guts of vertically migrating mesopelagic species, a lower percentage of appendicularian houses was found in specimens from the deeper layers compared to those from the upper (epipelagic) zone, indicating a reduced feeding incidence at depth on this particular item (Ohtsuka et al. 1996).

In general, oncaeid copepods seem to prefer aggregated food to motile food (Metz 1996, 1998; Koski et al. 2017), but Kosikhina (1980) reported also about carnivorous feeding mode, with preference on chaetognaths, presenting even details of the feeding process.

Some authors assume that phytoplankton cells and other unicellular organisms may have been only indirectly ingested by feeding on appendicularian filters or on marine snow with the attached microorganisms (Turner 1986b; Ohtsuka and Kubo 1991). Similarly, bacterivory of oncaeid nauplii reported by Roff et al. (1995) may have been the result of indirect feeding (Turner and Tester 1992). But feeding

Table 6 Methods used in feeding studies with oncaeid copepods

Methods	References
Direct observations in situ: SCUBA diving, video recording; in the lab: video recording	Wickstead (1962), Ohtsuka and Kubo (1991), Ohtsuka et al. (1993), Go et al. (1998), Nishibe et al. (2015)
Feeding experiments	Allredge (1972), Pasternak (1984), Paffenhöfer (1993), Lampitt et al. (1993), Roff et al. (1995), Metz (1996), Swadling et al. (1997b), Go et al. (1998), Kosikhina, (1980), Nishibe et al. (2015), Koski et al. (2017), Koski and Lombard (2022)
Gut content analysis:	
Microscope	Pasternak (1984), Hopkins (1985, 1987), Ohtsuka and Kubo (1991), Ohtsuka et al. (1996), Go et al. (1998), Nakata et al. (2001a), Wu et al. (2004)
Gut-Chla	Koski et al. (2020)
Metabarcoding	Kobari et al. (2021)
Faecal pellet analysis	Pasternak (1984), Turner (1986a)
Body elemental composition:	
Fatty acid and alcohol	Kattner et al. (2003)
Stable isotopes $\delta^{15}\text{N}$	Aberle et al. (2010), Albuquerque et al. (2021)

experiments with the Antarctic species *Oncaea curvata* by Swadling et al. (1997b) resulted in a high clearance rate (263% body carbon ingestion per day) on pure phytoplankton food.

The feeding mechanism of oncaeids has not yet been fully investigated. Based on observations of adults of *Oncaea* s.str. and *Triconia*, it appears to be a combination of raptorial and surface behaviour, using different appendages as summarized by Ohtsuka and Kubo (1991 and literature cited therein) and supported by subsequent studies:

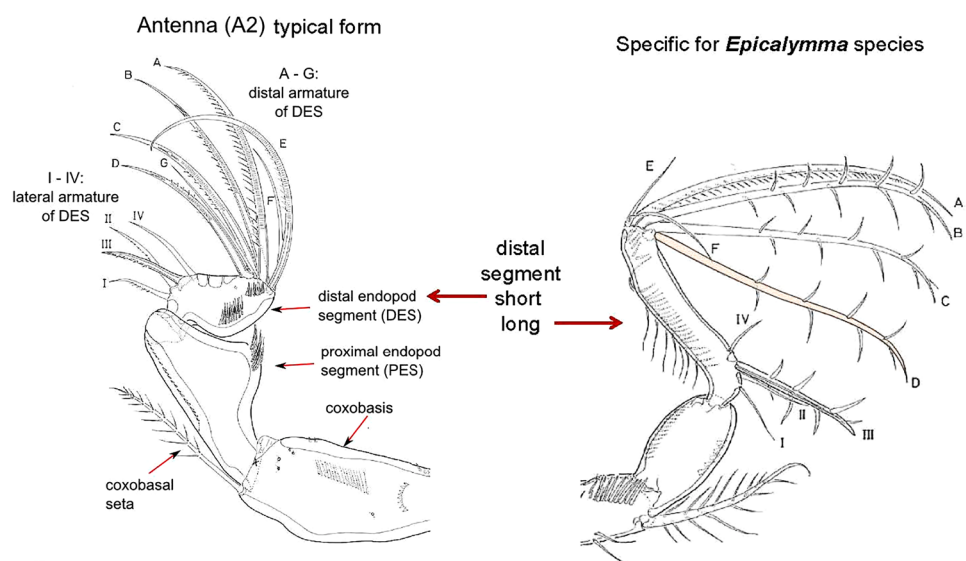
- 1- The antennules (A1) are comparably short and suitable for folding backwards to creep into appendicularian houses for feeding on the inner food-concentrating filter, which the copepods tend to prefer to the outer incurrent filters (cf. Ohtsuka and Kubo 1991)
- 2- The strong terminal setae of the antenna (A2) (Fig. 10) are used for attachment on gelatinous material or organisms (e.g., appendicularian houses, salps, marine snow) (Ohtsuka et al. 1993; Nishibe et al. 2015)
- 3- The mouthparts, i.e. mandible (Md) (Fig. 11), maxillule (M1) and maxilla (M2), are suitable for scraping food particles (Ohtsuka and Kubo 1991), and oncaeids were indeed observed to feed by “touching their mouthparts to the surface of the houses” (Nishibe et al. 2015), but also to apply the mouth to the “antennary joint” of copepod prey (Wickstead 1962, Pl.1, Fig. H) [possibly indicating some kind of suction (?)]
- 4- The large maxilliped (Mxp) of oncaeids, consisting of a robust basis and a distal endopod segment drawn out into a long-curved claw (Fig. 12) is regarded as a raptorial appendage for capturing macrozooplankters (e.g., fish larvae, chaetognaths, large copepods), large-sized phytoplankters and mucous materials like larvacean

houses, thecosome feeding webs and detrital matter. Within larvacean houses, the maxillipeds were also used for “... grasping food-concentrating filters...” (Ohtsuka and Kubo 1991).

The classification of the feeding mode of oncaeids in the literature ranges from omnivorous, or detritivorous to opportunistic feeding or possible coprophagous behaviour (Suzuki et al. 2003). Elemental compositions of polar species from the Arctic and Antarctic led to the conclusion that their feeding behaviour was omnivorous and/or carnivorous (Kattner et al. 2003). Stable isotope analyses ($\delta^{15}\text{N}$) of species of Oncaeidae in the Red Sea pointed to a low trophic position in the food web (Aberle et al. 2010). The possible use of faecal material as food was inferred from negative in situ correlations between krill faecal strings and cyclopoid copepods (*Oncaea* and *Oithona* combined) in the Antarctic, however, without considering the two families separately (Gonzalez et al. 1994; Suzuki et al. 2003). A possible feeding of *T. borealis* on carcasses of large calanoids in the Arctic under sea ice was assumed by Fortier et al. (2001) from observation that the deep living oncaeids show a low extent of DVM, related to the vertical distribution of potential food.

The general feeding habit shows that an allometric predator—prey rule cannot be applied for Oncaeidae. Within this family, species specific differences in the feeding types are not known and the assumed position in the food web appears to be largely speculative. Genera or species groups other than *Oncaea* s. str. and/or *Triconia* may have different preferences of food organisms or feeding habits. Species of smaller size, gender related differences and the feeding behaviour of mesopelagic and deep-sea species from different climatic regions have not yet

Fig. 10 Antenna (A2) morphology of Oncaeidae. Left: *Oncaea venusta typica* (after Böttger-Schnack 2001, Fig. 3A); right: *Epicalymma bulbosa* (after Böttger-Schnack 2009, Fig. 2A)



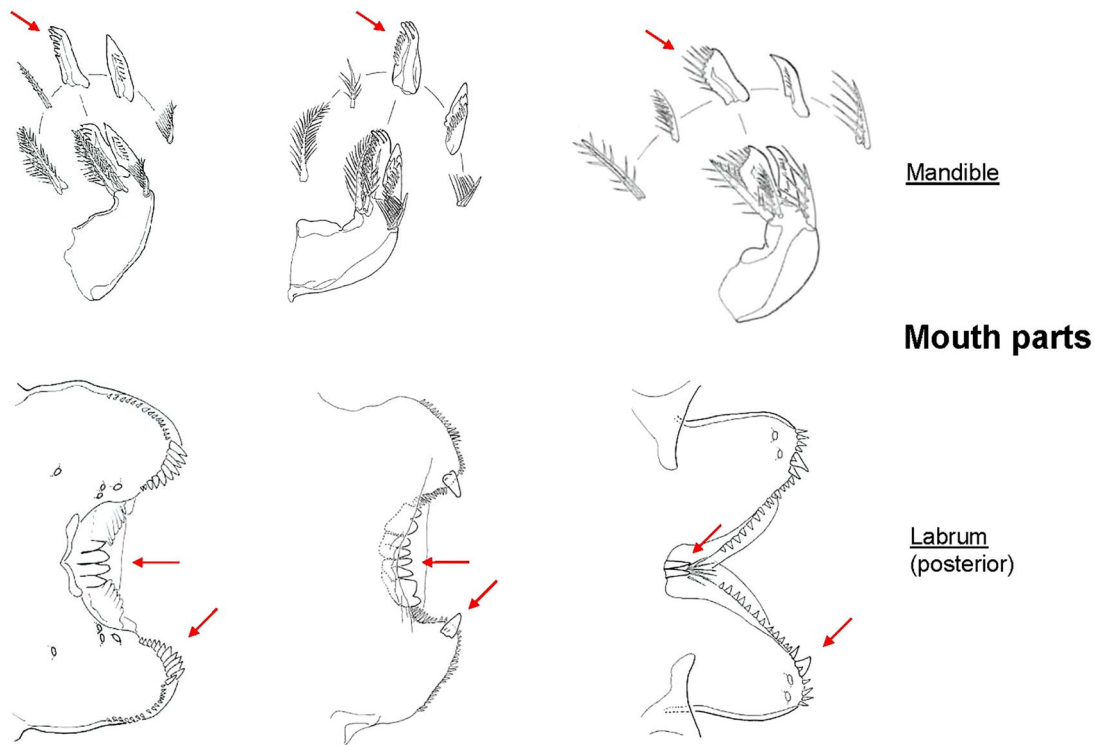
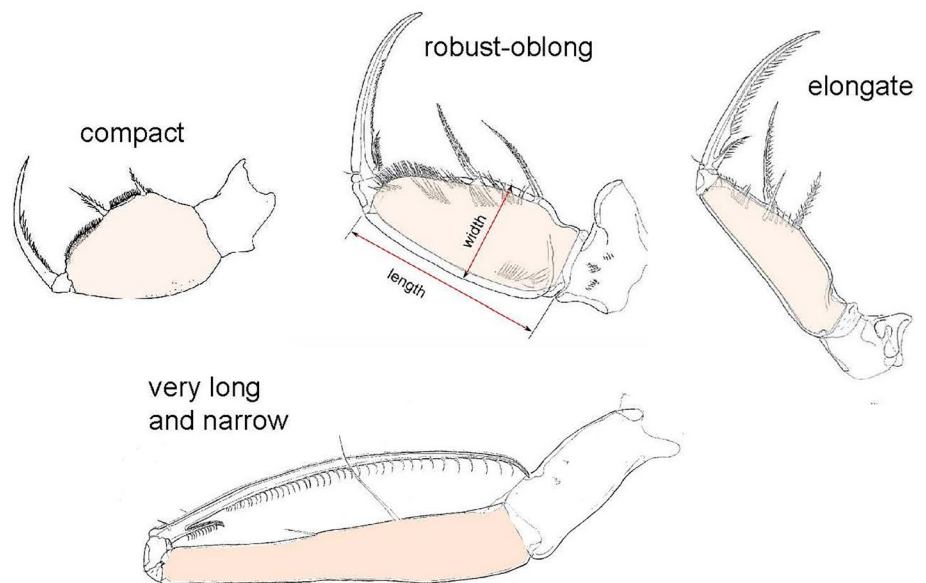


Fig. 11 Mouth parts of Oncaeidae. Left: *Triconia similis* (Böttger-Schnack 1999, Fig. 3C, D; middle: *Oncaea serrulata* (Böttger-Schnack 2011, Fig. 2C, D); right: *Oncaea bispinosa* (Böttger-Schnack 2002, Fig. 3C, D)

Fig. 12 Variation of maxiliped basis in oncaeid copepod species. Left: *Oncaea bowmani* (Heron 1977, Fig. 13d); middle: *Oncaea venusta typica* (Böttger-Schnack 2001, Fig. 3G); right: *Oncaea bispinosa* (Böttger-Schnack 2002, Fig. 3G); bottom: *Oncaea tenuimana* (Böttger-Schnack original)



been investigated, just as little as juvenile stages, including nauplii. For the latter, feeding demands have been investigated only for a single species (*O. mediterranea*) in experimental work using motile food (dinoflagellates, *Gymnodinium splendens*, and flagellates, *Rhodomonas*

sp.) which was successfully taken by nauplii and smaller copepodid stages, but declined in pre-adult CV (Paffenhöfer 1993). Differences in the construction and ornamentation of the cephalic appendages / mouthparts among genera or species groups of Oncaeidae and their juveniles may indicate different food preferences, which needs to

be investigated. Examples for such differences are given in Figs. 10, 11, 12 for the antenna, the mandible, and the maxilliped of adult females.

Reproduction aspects

Spawning type

Oncaeidae are egg-bearing copepods, carrying dorsal egg-sacs, which are usually paired or sometimes unpaired (*Monothula* (name-giving!), *Epicalymma*). In some small species (*Spinoncaea*) loose egg aggregations are found. A compilation of literature records for various reproductive parameters of oncaeids was provided by Böttger-Schnack and Schnack (2005, Table 1), including 33 species of all sizes (female total length, range 0.24–1.56 mm), all climates and various depth layers (incl. the deep sea), shortly summarized as follows:

Egg nos. per clutch vary from 2 to > 100 eggs for individual species, a single extreme value of 288 eggs per clutch was reported for a medium sized form of *O. venusta* (Nakata et al. 2004, as *Oncaea* f-1, not included in the compilation of Böttger-Schnack and Schnack 2005).

The egg size of individual species measures from 37–140 µm in diameter (mean values), with most egg sizes between 40 and 60 µm, rarely 90—> 100 µm. Species with very large eggs are *Triconia canadensis* (egg sac), and *O. englishi* and *O. shmelevi* (both species with paired single eggs).

Clutch type, number and sizes of the eggs are not generally dependent on female body length: Small species of less than 0.4 mm total body length have been found to carry two single large eggs (e.g., *O. vodjanitskii*) or specific egg sacs containing 5–8 eggs each (*O. bispinosa*, cf. Böttger-Schnack and Schnack 2005, Fig. 2). Large species of > 1 mm may carry single large eggs as well (*O. englishi*, cf. Heron 1977, Fig. 25n) or typical multi-layered egg sacs (e.g., *T. conifera*, or *T. canadensis*, cf. Nishibe 2005, Fig. 3.12.B). Egg sac morphology appears to be species specific as discussed by Böttger-Schnack and Schnack (2005) and the egg size does not increase in proportion to female size (body length), though some trend to larger eggs in larger species is apparent. An earlier assumption by Böttger-Schnack et al. (1989), that small species generally carry few large eggs has not been confirmed.

Fecundity and reproduction rate

Experimental studies on the fecundity of oncaeids (egg production, development time, egg mortality) are restricted to a few comparably large species from warm-temperate or tropical climates, such as *O. venusta*, *O. mediterranea*,

species of the *media*-group of *Oncaea* s.str. (*O. media*, *O. scottodicarloi*) and representatives of the *Triconia conifera*-subgroup. For polar regions, the only information available is from a detailed experimental study on the reproduction of the large mesopelagic *Triconia canadensis* from Pacific subarctic waters (Nishibe 2005; Nishibe and Ikeda 2007b).

Information on egg production rates and development times are summarized in Table 7. Egg production rates of species in warm-temperate/ tropical climates ranged from 3 to 15 eggs (or nauplii) per female per day at temperatures between 20 and 30 °C and egg development times ranged between 4.3 and 8.0 days in most cases; Melo Júnior et al. (2021) observed a minimum egg development time of 3.3 days for *O. venusta* and Webber and Roff (1995) reported a value of < 3.8 for *O. mediterranea*. The egg production rate could not be determined for the subarctic *T. canadensis*, and the development time of eggs (at 3 °C) was found to be exceptionally long, ranging from 74.7 to 84.5 days as mean values per clutch(?) from individual females. For this species also the hatching success was calculated, ranging from 50 to 100% (Nishibe 2005; Nishibe and Ikeda 2007b).

The developmental time of juveniles (nauplii to adults) is little known, single lab studies for (sub)tropical species at 20–22 °C reported 20–30 days (*O. mediterranea*, Paffenhöfer 1993; Webber and Roff 1995) or ca 35 days (*O. curta*, Kuei and Björnberg 2003), respectively. No corresponding data are available for polar species; in these areas, field data, following cohorts of juvenile stages in the water column over time, were used to estimate developmental times of juveniles for Antarctic (Metz 1996) and subarctic (Nishibe 2005; Nishibe and Ikeda 2007a) species. From these studies, generation times have been estimated as 1–1.5 years for *O. curvata* and about 1 year for *O. antarctica* (now *T. antarctica*) (Metz 1996); for *Triconia canadensis* and *O. grossa* also a 1-year generation time was implied from stage-to-stage development (Nishibe and Ikeda 2007a). For other species no clear results have been obtained.

Sex ratio and mating behaviour

Other aspects that need to be considered as parameters of reproduction biology are (1) proportion of males and females in the environment (sex ratio) as well as (2) mating behaviour (cf. Titelman et al. 2007). For oncaeid copepods, the sex ratio is often not reliably documented, due to the smaller size of the males, which may not have been quantitatively sampled and the difficulties in the identification of males, many of which are not yet described (see above: Taxonomy). It remains unclear, to which extent the sex ratio differs among oncaeid species and how this influences the reproduction success of this copepod family. In plankton samples, males have been observed clasping to a female urosome with their large maxillipeds (cf. Giesbrecht 1892, plate

Table 7 Egg production rates and development times for oncaeid copepod species

Region	Species	Clutch size (n F ⁻¹)	Egg diameter (µm)	Fecundity (Eggs F ⁻¹ day ⁻¹)	Egg development time (days)	References
Subarctic (T=3 °C)	<i>Triconia canadensis</i>	8–54	100	–	74.7–84.5	Nishibe and Ikeda (2007b)
Warm-temperate/tropic (T=20–30 °C)	<i>Oncaea venusta</i> or <i>venusta</i> -group	18—> 100	50–60	3–12	(3.3) 4.3–8	Sazhina (1985); Hirakawa (1995); Dagg and Govoni (1996); Satapoomin et al. (2004); Nakata et al. (2004); Melo Júnior et al. (2021)
	<i>Oncaea media</i> or <i>media</i> -group	20–68	40–46	3.4–15	4.7–8	Sazhina (1985); Nakata et al. (2004); Zervoudaki et al. (2007); Fyttis et al. (2015)
	<i>O. scottodicarloi</i>	14–32	–	6.15	8	Fyttis et al. (2015)
	<i>O. mediterranea</i>	–	50–65	5.3–13.3	–	Paffenhöfer (1993)
	–	–	–	–	< 3.8	Webber and Roff (1995)
	<i>Triconia conifera</i> or <i>conifera</i> -group	54	75–88	–	–	Sazhina (1985)

F female

2, Fig. 10; also, Böttger-Schnack 2001, Fig. 21A), which is regarded as the mating position of oncaeids. These observations refer to large and medium-sized species, males of which are smaller than females. No corresponding observation was made for smaller species, e.g., *Spinoncaea*, where males and females are of similar size. Regardless of their size, females have regularly been observed with spermatophores attached dorsally to the genital double-somite (e.g., Metz 1996; Böttger-Schnack and Schnack 2005). Experimental results on mating behaviour have been reported for *Oncaea venusta* by Melo Júnior et al. (2021) providing information about the sequence and percentage of time spent in mating and non-mating position, and in carrying egg sacs. Individual couples were observed in copulation position for periods of less than a day up to 3.5 days. Periods carrying eggs sacs lasted about 4 days.

The main open questions regarding the reproduction of oncaeid copepods are (1) seasonality of egg production, like the results presented by Melo Júnior et al. (2021) for *O. venusta* in a subtropical coastal area, (2) mortality of juveniles during development and – very important – (3) differences between species. Recent attempts to include Arctic oncaeid copepods in the estimations of reproduction, growth and mortality of small copepods in a Greenland fjord (Koski et al. 2021) remain uncertain as the data basis used was calculated from equations not established for Oncaeidae. (see under “Role of Oncaeidae in marine Ecosystems”).

Biomass and chemical composition

The level of knowledge about biomass values of oncaeid copepods is very limited, because there are few direct measurements on dry weight (DW), ash-free dry weight (AFDW) and elemental composition (Carbon = C, Nitrogen = N). Often, these data are presented without definition of the species and/or stage(s) analysed, just referring to *Oncaea* spp., such as data by Nassogne (1972, DW), Hopcroft and Roff (1998, AFDW), Satapoomin (1999, C), and Paffenhöfer (2006, AFDW) for warm-temperate/tropical areas, or Mizdalski (1988, DW, AFDW) for the Antarctic.

The most comprehensive set of data on species specific dry weight—length relations has been provided for 12 species from the NW subarctic Pacific (separately for female, male and late juvenile stages) by Nishibe (2005, Tab. 2.2). The female lengths covered range from 330–1560 µm total body length (TL), resp. 208–1066 µm prosome length (PL). The resulting regression for weight on prosome length is presented in Table 8. Corresponding regressions, based on less comprehensive data sets, have been published for juvenile and adult stages of a single species, *O. mediterranea*, from the tropical Atlantic (Webber and Roff 1995), for *Oncaea* spp. from the Mediterranean Sea (Nassogne 1972), and for *Oncaea* spp. from the tropical Indian Ocean (Satapoomin 1999). These equations lead to substantial differences when used to calculate weight from length measurements, as will

Table 8 Length and weight data for oncaeid copepods

Length—weight regressions				
Region	Number of species or name of taxon	Stages or range of prosome length, PL (µm)	Regression function DW (µg), PL (µm)	References
NW subarctic Pacific	12 oncaeid species	208–1066	$\text{Log}_{10}\text{DW} = 2.875 \text{ log}_{10}\text{PL} - 7.458$	Nishibe (2005)
Tropical Atlantic	<i>O. mediterranea</i>	C1–C6	$\text{Log}_{10}\text{DW} = 2.1 \text{ log}_{10}\text{PL} - 5.05$	Webber and Roff (1995)
Mediterranean Sea	<i>Oncaea</i> spp.	200–600	$\text{Log}_{10}\text{DW} = 3.11 \text{ log}_{10}\text{PL} - 7.68^{(1)}$	Nassogne (1972)
Trop. Indian Ocean	<i>Oncaea</i> spp.	300–740	$\text{Log}_{10}\text{DW} = 2.9 \text{ log}_{10}\text{PL} - 7.6^{(2)}$	Satapoomin (1999)
Mean weight data				
Region	Taxon	Total length (µm)	AFDW (µg Ind ⁻¹)	References
Tropical Atlantic	<i>Oncaea</i> spp.	–	5.9	Hopcroft and Roff (1998)
Tropical Atlantic	<i>Oncaea</i> spp.	–	7.4/7.1	Paffenhöfer (2006)
Weddell Sea	<i>Oncaea</i> spp.	350–1150	3.7 (15.2 DW)	Mizdalski (1988)

DW dry weight, AFDW ash free dry weight, PL prosome length, C1–C6 copepodid stages 1 to 6

¹Converted from original regression equation: $\log \text{DW} (\mu\text{g } 10^{-1}) = 3.106 \log \text{PL} (\text{mm } 10^{-1}) - 0.466$ (Nassogne 1972, TabXIV)

²DW value based on carbon (C) values measured, assuming $\text{DW} = 2\text{C}$

be exemplified below under “[Uncertainties in calculated biomass values](#)”.

In addition to weight—length relations, Table 8 also includes some mean values for ash free dry weight (AFDW) published for oncaeid taxa, though at low taxonomic resolution only. For *Oncaea* spp. from the tropical Atlantic, AFDW-values range from 5.9 to 7.4 µg per female. The substantially lower mean AFDW-value (3.7 µg) reported for the Weddell Sea remains questionable, as it does not correspond to the DW-value, given as 15.2 µg.

Information on the elemental composition (C, N) of oncaeids is summarized in Table 9. C and N values were measured separately for the adults of 4 species in the NW Pacific subarctic area (Nishibe 2005; Nishibe and Ikeda 2008, C and N per DW), including numerous data on seasonal differences, and for *O. venusta* females on one season from the subtropical domain of the NW Pacific (Nishibe 2005, Tab. 4.4, 5.74 µg C per female). Petipa and Borichenko (1985) provided a single carbon value of *O. venusta* females from the equatorial Indian Ocean (TL 1.27 mm, 6.26 µg C ind.⁻¹). Metz (1996, Tab. 4.13) reported data on carbon

Table 9 Elemental composition of oncaeid copepods: amount of Carbon (C) and Nitrogen (N)

Region	Taxon	C & N values	References
<u>Length regressions</u>			
Tropical Indian Ocean	<i>Oncaea</i> spp.	$\text{C}(\mu\text{g}) = 2.51 * 10^{-8} \text{ PL}(\mu\text{m})^{2.9}$	Satapoomin (1999)*
Pacific, off Okinawa Island	<i>Oncaea</i> spp.	$\text{C}(\mu\text{g}) = 5.34 * 10^{-9} \text{ PL}(\mu\text{m})^{3.16}$	Nakata et al. (2001b)
Pacific, Kuroshio Extension	3 oncaeid species**)	$\text{N}(\mu\text{g}) = 2.49 * 10^{-8} \text{ PL}(\mu\text{m})^{2.67}$	Nakata et al. (2004)
<u>Mean values per Indiv</u>			
Subtropical NW Pacific	<i>Oncaea venusta</i> F	5.74 µg C	Nishibe (2005)
Equatorial Indian Ocean	<i>Oncaea venusta</i> F	6.26 µg C	Petipa and Borichenko (1985)
Antarctic	<i>Oncaea curvata</i> F	0.72, 1.55 µg C	Metz (1996)
	<i>Oncaea curvata</i> M	0.54, 0.71 µg C	
Western subarctic Pacific	<i>Oncaea grossa</i> F	2.2 µg C	0.422 µg N
	<i>Oncaea grossa</i> M	1.4 µg C	0.288 µg N
	<i>Oncaea parila</i> F	1.2 µg C	0.204 µg N
	<i>Triconia borealis</i> F	0.97 µg C	0.198 µg N
	<i>Triconia canadensis</i> F	16.7 µg C	2.058 µg N
	<i>Triconia canadensis</i> M	7.9 µg C	1.086 µg N

*Converted from original regression function: $\ln \text{C} (\mu\text{g}) = 2.9 \ln \text{PL} (\mu\text{m}) - 17.5$

***Oncaea media* and two variants of *Oncaea venusta*

content of *O. curvata* females and males from 2 stations in the Antarctic. For females the data differed substantially between the two stations by a factor of about two (0.72 and 1.55 $\mu\text{g C}/\text{ind.}^{-1}$). Satapoomin (1999) analysed the carbon content (C; μg) for *Oncaea* spp. of various body lengths (PL; μm) from a coastal area in the Andaman Sea, tropical Indian Ocean, and provided the following regression: $\ln C = 2.9 \ln \text{PL} - 17.5$; the author also converted the equation to DW assuming a conversion factor of 0.5 (see Table 8). It should be noted that Satapoomin's data showed (1) a high variance of individual values, (2) irregular distribution of data over the length range (her Fig. 2), (3) included various seasons, and (4) did not provide an identification of species and/or stages included in the analysis. Thus, using these equations for an estimate of C or DW based on length measurements of any oncaeid species or group should include a very high degree of uncertainty.

Nakata et al. (2001b) reported on the carbon content of *Oncaea* spp. in the Pacific off Okinawa Island and provided the following relation of prosomal length (PL; μm) to carbon mass (C; μg) for this group: $C = 5.34 * 10^{-9} \text{PL}^{3.16}$ (data unpubl.). Later, Nakata et al. (2004) analysed the nitrogen content (N; $\mu\text{g ind.}^{-1}$) of 3 oncaeid species from the Pacific Kuroshio Extension, resulting in the regression equation: $N = 2.49 * 10^{-8} \text{PL}^{2.67}$.

Many open questions remain regarding the effect of differences in species composition in those studies having analysed "*Oncaea* spp.", which hamper the comparability of results on biomass and chemical composition. A distinct difference was determined e.g., in the C/N ratio of the large mesopelagic *T. canadensis* compared to the other (smaller) mesopelagic oncaeid species in the same area by Nishibe (2005), resp. Nishibe and Ikeda (2008). They suspect a corresponding difference in the food composition utilized by these species.

Uncertainties in calculated biomass values

Calculations of biomass data of oncaeid copepods in ecological studies are often based on published information not suitable for the respective scope of application. In the following a few examples are given:

For calculating the DW of the Antarctic *O. curvata*, Metz (1996) used the length/weight (DW) relationship for *Oncaea* spp. from the Mediterranean Sea presented by Nassogne (1972), cited after Frasz (1988), resulting in a DW value of 6.8 μg for the female and 4.3 μg for the male. Due to a citation error by Frasz (see below), these values are, however, by about a factor 3 too high; they should read 2.2 μg and 1.4 μg , respectively, according to the original regression provided by Nassogne. Mayzaud et al. (2002), on the other hand, used for *O. curvata* the length to weight relationship of *O. mediterranea* from the tropical Atlantic by Webber and Roff (1995, see above), resulting in DW values of 2.5 μg for

the female and 1.5 μg for the male. These values are very different to those published by Metz, but well comparable to the corrected values of Metz.

Hopcroft et al. (2005) calculated the biomass of arctic *Oncaea* spp. (mainly *Triconia borealis*) by applying a regression of AFDW on body length established for *Oithona nana* from the tropical Atlantic by Hopcroft et al. (1998). In subsequent arctic studies this equation was continued to be used (e.g., Hopcroft et al. 2010; Questel et al. 2013, Ershova et al. 2015, 2021) leading to error propagation. Using results obtained for different climate zones and species or even families as in this case, includes a high degree of uncertainty, which needs to be considered.

The part of uncertainty related to the applied length–weight regressions is illustrated in Fig. 13A, B.

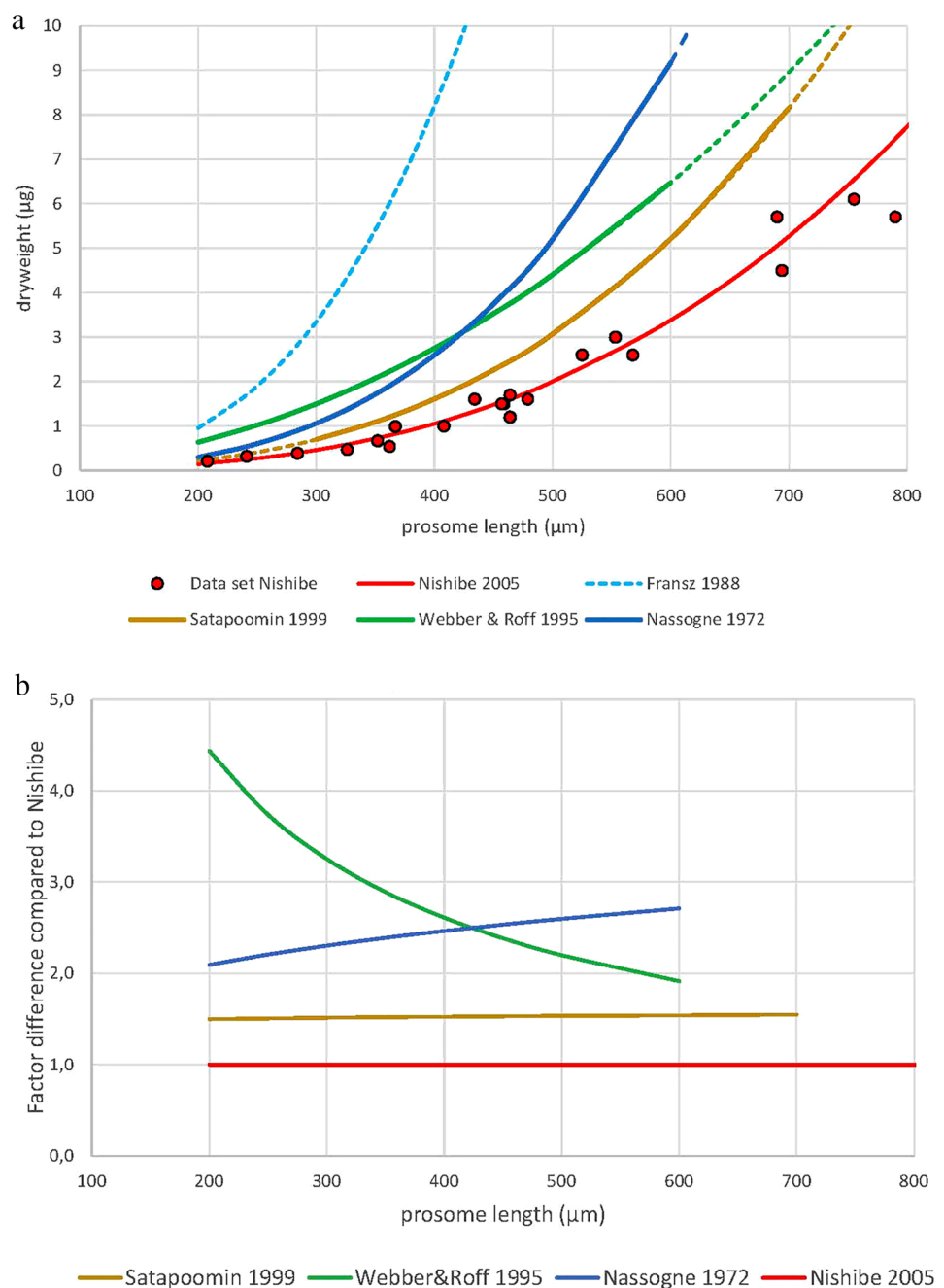
Part A of the figure shows the different length–weight regressions so far established for oncaeid copepods by Nassogne (1972), Webber and Roff (1995), and Satapoomin (1999) from warm-temperate/tropical areas and those established for subarctic waters by Nishibe (2005). Dashed lines denote extrapolated parts of the regression lines, which exceed the length ranges considered in the respective paper. Webber and Roff did not provide length data of the developmental stages examined; in their case we assumed the maximum PL of female to be ca 670 μm (cf. Böttger-Schnack and Huys 1997b). The dotted line denotes a relationship used by Frasz (1988) and Metz (1996), not included in the further comparison (see below).

In Fig. 13B, the relative differences are indicated between the dry weights per length obtained from the three regressions of warm-temperate or tropical regions in comparison to the regression of the subarctic species from Nishibe, which indicates generally lowest values per length. The regression from Satapoomin has an almost identical rate of increase of weight per length, differing by a constant factor of about 1.5 from that of Nishibe. It should be noted, however, that the dry weights reported from Satapoomin have not been measured directly but have been calculated from carbon measurements, applying a ratio of 0.5 for C/DW. Thus, the difference between both regressions is depending on this ratio, which appears to be rather variable (Nishibe 2005, Tab 4.4).

The other two regressions from warm-temperate or tropical regions indicate substantially higher weight values than obtained for the subarctic zone and a pronounced size dependent difference. From small to large specimens the relative difference in weight compared to Nishibe's relation changes from about the factor 4–2 for the relation of Webber & Roff and from about 2–3 for the relation of Nassogne.

The regression published by Nassogne (1972) from the Mediterranean Sea has been cited and utilized in later publications dealing with the Antarctic region by Frasz (1988) and Metz (1996). Unfortunately, the regression equation has

Fig. 13 **A** Length weight regressions for Oncaeidae from different publications for comparison. Individual data points are available for the regression of Nishibe (2005). **B** Relative distance of weight value per length from different regressions compared to the regression from Nishibe (2005)



been used without considering that it is based on length values given in 0.1 μg units; instead, the equation was applied assuming a μg unit for the length values. In addition, some other conversion error is obviously included. The corresponding relationship is included in Fig. 13A for comparison, to show the degree of overestimation of the biomass values for this copepod family in the mentioned publications.

In general, higher dry weight values per size are indicated for oncaeids in tropical/temperate areas as compared to cold regions, and the relative differences may be substantially size dependent. Thus, a high degree of uncertainty

is included, when using such relations to calculate weight values from length measurements.

More recently, Koski et al. (2021) tried to overcome the difficulties of direct biomass measurements for oncaeid copepods (*Oncaea* spp.) in a Greenland fjord by using averages of carbon estimations based on Satapoomin (1999) for juvenile stages and the “average length to weight ratios” for adult females “... of three similar-sized *Oncaea* species in sub-Arctic Sea of Japan (Nishibe and Ikeda 2007a, b, 2008).” [Koski et al. 2021, p. 3]. These estimates include two sources of uncertainty:

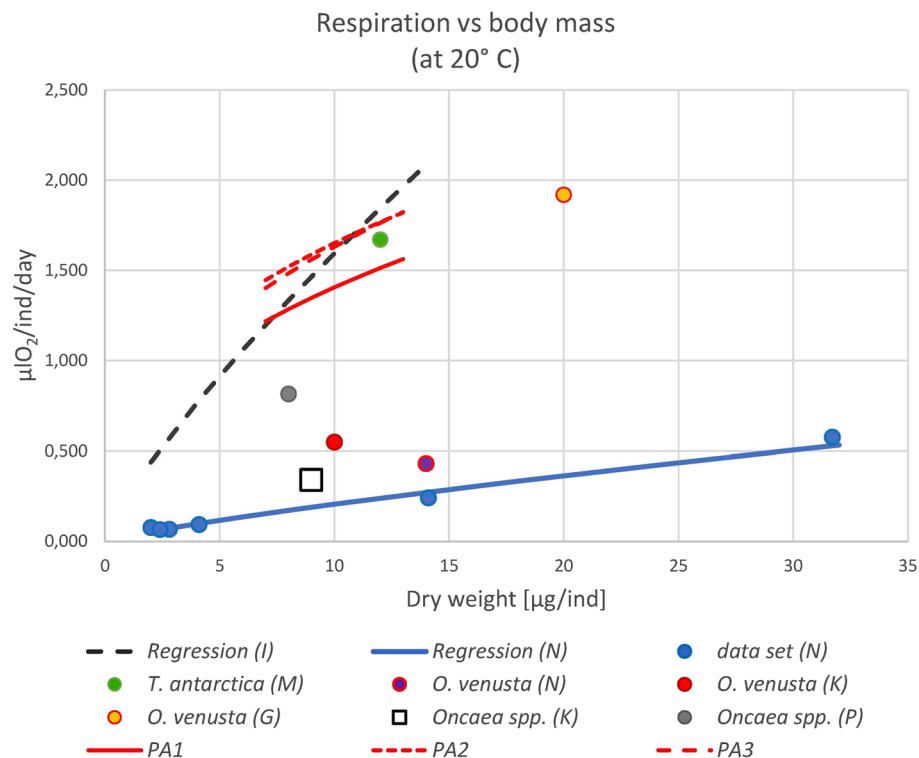


Fig. 14 Compilation of information about respiration rates of Oncaeidae in relation to body mass. For comparability, all values measured at different temperatures are adapted to 20 °C using $Q_{10}=2.0$ (Ikeda et al. 2001). **Individual data points:** (1) *T. antarctica* (M)=Mayzaud et al. 2002, measured at 2 °C; (2) *O. venusta* (N)=Nishibe 2005, measured at 20 °C; (3) *O. venusta* (K)=Klekowski et al. 1977, measured at 25.5 °C; (4) *O. venusta* (G)=Gaudy and Boucher 1983, measured at 20 °C; (5) *Oncaea* spp. (K)=Klekowski et al. 1977, temperature range 18° – 26 °C, median given from 47 highly varied values published as adapted to 20 °C; (6) *Oncaea* spp. (P)=Paffenhöfer 2006, measured at 20 °C, body mass given as AFDW, here converted to DW using factor 1.1. **Regressions:** (1) “Regression (N)”: based on

data set (N) of 4 subarctic oncaeid species: mean values given per species and sex of *T. borealis* (F), *T. canadensis* (F,M), *O. grossa* (F,M), *O. parila* (F) (Nishibe 2005; Nishibe and Ikeda 2008); (2) “Regressions PA1—PA3”: *O. venusta*, three groups measured at 20°, 23°–24°, 26°–28 °C respectively (Pasternak and Averianov 1980), values recalculated to transfer dimensions from mcal to $\mu\text{l O}_2$ and $\mu\text{g DW}$ using 4.86 mcal/ $\mu\text{l O}_2$ and 3.5 mcal/ $\mu\text{g DW}$ respectively, based on values used by the authors and assuming 80% water content in body wet weight; (3) “Regression (I)” for comparison: global respiration model for epipelagic calanoid copepods related to dry weight and temperature (Ikeda et al. 2001), applied here to 20 °C

- The length to weight data by Nishibe and Ikeda (2008) refer to meso- and bathypelagic species (*O. parila*, *O. grossa*) besides *Triconia borealis*, which may be different to those of the unspecified species in the Greenland fjord.
- For subarctic species Nishibe and Ikeda (2008) reported significant seasonal differences in carbon weight: e.g., for *O. parila* female carbon weight was found to vary between 0.85 and 1.65 $\mu\text{g ind.}^{-1}$ in 4 months (March, June, Oct, Dec.), resulting in a relative difference of about the factor 2 for carbon estimations.

Respiration

A substantial number of direct measurements of respiration rates of oncaeid copepods have already been made since the late 1970s, though for few species only and mostly for undefined oncaeid species. The early

measurements by Klekowski et al. (1977) for *Oncaea* spp. from tropical Atlantic and Pacific areas, and those by Pasternak and Averianov (1980) for *Oncaea venusta* showed a high degree of variation (0.003–0.075 $\mu\text{lO}_2 \text{ ind}^{-1} \text{ h}^{-1}$); at the restricted size range of *O. venusta*, only 20–50% of the variance was explained by the given differences in size.

A more extended size range was covered by a data set for four subarctic species from the meso- and bathypelagic zone, namely *T. borealis* (F), *T. canadensis* (F, M), *O. grossa* (F, M) and *O. parila* (F) measured separately at a temperature of 3 °C (Nishibe 2005; Nishibe and Ikeda 2008; Fig. 2). The resulting regression for respiration (R ; $\mu\text{lO}_2 \text{ ind}^{-1} \text{ h}^{-1}$) on dry weight (DW ; $\mu\text{g ind}^{-1}$) is reported as:

$\text{Log}_{10} R = -3.392 + 0.815 * \text{log}_{10} DW$ (Nishibe 2005, p. 63) [which is equivalent to $R = 4.06 * 10^{-4} * DW^{0.815}$].

Individual values for respiration rates are given for *T. antarctica* (measured at 2 °C), *O. venusta* females and *Oncaea*

spp. (at 20 °C) from five different sources ranging from 0.018 to 0.080 $\mu\text{O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ (for references see legend of Fig. 14).

Figure 14 provides a compilation of results from respiration measurements related to dry weight. For comparison, all values are here adapted to 20 °C, applying a Q_{10} of 2.0 (Ikeda et al. 2001). The data from Klekowski et al. (1977) are represented by the median of 47 values; from Pasternak and Averianov (1980), regression lines are included for 3 groups of *O. venusta*, measured at 3 different temperatures. For a comparison of oncaeid vs calanoid copepods, the regression line of the global respiration model from Ikeda et al. (2001) for epipelagic calanoid copepods from a wide geographical and temperature range is also presented in the figure, applied to 20 °C.

The data from Nishibe and Ikeda (2008) may indicate that subarctic mesopelagic oncaeid copepods have generally lower respiration rates than the tropical oncaeid species from the epipelagic zone, though an exceptionally high value is reported for the Antarctic (upper mesopelagic) species *T. antarctica* by Mayzaud et al. (2002). Also, it may be indicated that oncaeids tend to have lower respiration values than calanoids, but the high variability in the data and especially the comparably high values provided by Pasternak and Averianov (1980) for *O. venusta* show that there is at least a large range of overlap and uncertainty. Differences in the results among studies will also be attributed to some extent to the differing methods and treatments of the experimental Oncaeidae.

Within one study, the remaining difference to be seen in Fig. 14 between the regressions from Pasternak and Averianov, obtained at different temperatures, also indicate that the Q_{10} value of 2.0, applied to standardize for 20 °C, is not sufficiently adequate in this case. These authors suggested a value of 2.3. It may well be that the Q_{10} value cannot be assumed to be constant over the very large range of temperatures from arctic to tropical regions, as done in Fig. 14 and as inherent in the model of Ikeda et al. (2001).

The Ikeda model is frequently used to calculate respiration rates of copepods from dry weight values. As can be seen from Fig. 14, this leads, however, to highly uncertain values when applied to oncaeids (see under “[Role of Oncaeidae in marine Ecosystems](#)”).

Metabolic rates

For a direct comparison of respiration rates among the various species showing large differences in body masses between species and/or sexes, Nishibe (2005) converted the respiration rate R to an “adjusted metabolic rate” ($\text{AMR} = R/(\text{bodyN})^{0.843}$). The exponent was derived from comprehensive regression statistics of $R(\mu\text{O}_2)$ and body $N(\mu\text{g})$ of marine epipelagic copepods by Ikeda et al. (2001). This

allowed a comparison with other mesopelagic copepod taxa, such as *Oithona atlantica* and several calanoid taxa examined using the same respiration method as in Nishibe (2005). A reduced AMR is indicated for oncaeids (Nishibe 2005, Table 4.5) which may be due to their pseudopelagic lifestyle and correspondingly low locomotive behaviour (Nishibe and Ikeda 2008).

Bioluminescence

Giesbrecht (1895) was the first who observed bioluminescence in an oncaeid species within the frame of his detailed study about bioluminescence “Leuchten” of pelagic copepods in the Mediterranean Sea. He reported it for *Triconia conifera* (as *Oncaea conifera*), but found other species of this family, namely *O. venusta*, *O. mediterranea*, and *O. media*, to be non-luminescent.

In addition, Giesbrecht investigated the morphological and the functional details of bioluminescence for *T. conifera*, e.g., the position and no. of glands “Hautdrüsen”, the colour of the flash (blue) and the kind of luminous matter (a cloudy, fine-grained mass), all of which he found to be quite different from other (calanoid) taxa (greenish colour, clear droplets in glands).

Close to a century later Herring et al. (1993) provided a comprehensive analysis of the bioluminescence of *T. conifera* (as *O. conifera*) from different oceanic regions, including four “forms” of this species as defined by Moulton (1973), which later were raised to specific level: the genuine *T. conifera* (Giesbrecht 1891), *T. furcula* (Farran 1936), *T. derivata* (Heron and Bradford-Grieve 1995) and *T. redacta* (Heron and Bradford-Grieve 1995), all of which were bioluminescent.

In their comprehensive study, Herring et al. reported on the flash kinetics, spectral distribution and detailed morphology of the gland structure, incl. SEM and TEM (histological sections), as well as observations of the swimming pattern of specimens. They discussed the unique anatomical and physiological characteristics of the luminescent system of *conifera*-group oncaeids, which differ from other luminous copepods (all calanoids) due to an internal, non-secreted bioluminescence, as well as by the number and position of glands. They assume that the significant difference is “... possibly related to the specialized ecological niche occupied by this species “; due to its low swimming speed and association with marine snow, bioluminescence might have a different function in this taxon.

Like Giesbrecht, Herring et al. (1993) also confirmed non-luminescence for other oncaeid species (*O. media*, *O. mediterranea*, *O. venusta*, *O. ornata*), and suspect a uniqueness in this respect of the entire *conifera*-group within the family. They point out that more investigation is required, including other species of this group, such as e.g., *T.*

borealis. So far it remains open whether especially small oncaeid species and other deep-living species like *Epicalymma* also show luminescence, and whether the assumed relation to the lifestyle can be verified.

Role of Oncaeidae in marine ecosystems

In the marine food web, oncaeid copepods are consumers of a wide variety of particles/organisms (see under “Feeding/food relationships”), however, quantification of feeding rates remains difficult, because the present knowledge is based on larger species within this family, and potential differences to the feeding behaviour of smaller oncaeid species of less than e.g., 0.8 mm female body length has not been investigated so far.

The variety of food items consumed by oncaeid copepods also makes any classification of their feeding type difficult. In an overview of plankton in the open Mediterranean Sea, Siokou-Frangou et al. (2010) regret that “data on the natural diet of the dominant *Clausocalanus*, *Oithona* and *Oncaea* species are almost lacking.” In attempts to identify functional groups of dominant copepods in the Mediterranean Sea, oncaeid copepods have been regarded as “omnivore” (Benedetti et al. 2016), but also as “detritivore” (Benedetti et al. 2018), which indicates the uncertainty of placement of this taxon in the food web.

Oncaeid copepods themselves are known as prey for various organisms, such as fish larvae (e.g. Arthur 1976; Govoni et al. 1986; Sampey et al. 2007) or small fishes (e.g. Kawamura and Hanaoka 1981; Hopkins and Baird 1985a; Hirsch and Christiansen 2010; Falkenhaus and Dalpadado 2014), in particular myctophids (e.g. Gorelova 1974; Hopkins and Baird 1985b; Takagi et al. 2009), various crustaceans, such as carnivorous copepods (Hopkins 1985b, 1987; Øresland 1991), mysids (Takahashi and Kawaguchi 1998), euphausiids, ostracods and amphipods (Hopkins 1987), for jelly fish (Cruz et al. 1869) as well as for chaetognaths (Newbury 1978; Sullivan 1980; Terazaki and Marumo 1982; Hopkins 1985b, 1987).

The active and passive role of oncaeids in the marine food web is obviously manifold but can yet hardly be assessed quantitatively and cannot be related to differences in the species composition.

In several more recent studies on the structure and function of marine ecosystems, attempts have been made to also consider the group of very small pelagic copepods, especially Oncaeidae, for a more complete picture than usually achieved (e.g., Hirai and Tsuda 2015; Bode et al. 2018; Tang et al. 2019; Koski et al. 2020; Koski and Lombard 2022). These attempts show that there is still a great deal of uncertainty included, due to problems in species identification and limited knowledge of the biology of Oncaeidae as pointed

out in some detail in the previous chapters. In the following some examples are presented, to address the main problems that still have to be solved in this context.

Carbon flux

- Bode et al. (2018) assessed the copepod’s impact on the vertical carbon flux down to 2000 m depth along a transect in the eastern Atlantic Ocean between 24°N and 21°S. By using a net with 150 µm mesh size they included small cyclopoid copepods, such as Oncaeidae and Oithonidae. In their study, calanoids consumed a major part of POC ingested in total by all copepods. On the vertical axis, however, the relative contribution of cyclopoids (mostly Oncaeidae) increased with depth, to over 27–47% in the deepest layers (their Table 2). The relative contribution consumed in total by non-calanoid copepods or specifically Oncaeidae remains uncertain, however, because the metabolic demands of the different copepod taxa were calculated by using respiration rates, which were measured directly on board for many calanoid taxa (their Table 1), while due to the lack of corresponding data for cyclopoid families the global respiration model from Ikeda et al. (2001) was applied. This model does not include small non-calanoid copepod taxa and may lead to quite different values as those measured directly for Oncaeidae, as shown in Fig. 14. It therefore remains uncertain, to which extent the Oncaeidae have in fact contributed to vertical C-flux, and it becomes obvious, that specific respiration measurements of oncaeid species are required for more reliable carbon flux estimates.
- Koski et al. (2020) addressed the gap in the knowledge about the degradation of sinking particles (marine snow) by aggregate-associated copepods (*Microsetella norvegica* and *Oncaea* spp.) using structural (abundance, biomass) as well as functional (feeding, respiration, reproduction) data for estimating the vertical carbon flux in a temperate region of the NE Atlantic (PAP site) down to 1000 m depth. The authors demonstrated that “zooplankton < 1 mm can have a significant influence on the vertical [carbon] flux” and addressed the need for a better consideration of these taxa in future zooplankton studies. In this study, oncaeid copepods were not identified to species, and several conversion factors were used for *Oncaea* spp. (= Oncaeidae), which are not specifically relevant for this taxon. For example, (1) the biomass calculation of oncaeids was estimated using a length/carbon relationship of Satapoomin (1999) conducted in a tropical area, not a temperate region; (2) for calculating oncaeid reproduction parameters, egg development times by Nielsen et al. (2002) were used, which are unsuitable for oncaeids, because they are based upon *Oithona* spe-

cies, (3) feeding rate of oncaeids was estimated on gut chl-*a* only, while no feeding experiment on aggregates was conducted, as done for *M. norvegica*. A subsequent study by Koski and Lombard (2022) generated results on carbon ingestion rates also for *Oncaea* spp. from feeding experiments. They indicate that a wide range of food sources can be utilized, but the ingestion rates show substantial differences among some food types supplied and the preferences differed obviously compared to *M. norvegica*. The authors conclude “that the aggregate degradation rates by copepods can vary manyfold depending on the quality of the aggregates and the copepod species.” The contribution of oncaeid copepods to the biological pump remains correspondingly uncertain.

- Differentiation between the live/dead status (=carcasses) of copepods in a sample is often not considered for zooplankton specimens, which “could lead to considerable errors in understanding their population dynamics and related ecological processes” (Tang et al. 2019 and literature cited therein). The authors investigated the importance of small copepods carcasses for the passive vertical C flux by using 50 µm mesh size nets for field sampling [in the Sargasso Sea] and for the first time explicitly conducted decomposition experiments with oncaeid copepods (as *Oncaea* spp.) for their calculations. Unfortunately, no information is given on the species composition of Oncaeidae and it has not been mentioned whether the size range of individuals in the experiments (“200–500 µm”, their p. 552) refers to total body length or to prosome length. Thus, the transferability of their results to other marine systems seems doubtful as the species composition might have a significant influence.

Growth and mortality rates (allometric scaling)

- Koski et al. (2021) investigated the population dynamics, vertical distribution and allometric scaling of growth and mortality rates of aggregate-colonizing copepods (*Microsetella norvegica* and *Oncaea* spp.) in a glacial fjord (Greenland). In contrast to data used for *Microsetella*, the database used for calculation of biomass, reproduction, and growth of the Oncaeidae was not determined for the species in the study area but was mainly derived from literature sources, based on calanoid, cyclopoid (*Oithona*), and harpacticoid species [see above “Uncertainties in calculated biomass values”]. So, the role of these cold-water Oncaeidae in the estimations of growth and mortality and the respective consequences for allometric scaling remains rather uncertain. This study is nonetheless an important contribution as it points to a main gap in the knowledge about non-calanoid copepods for understand-

ing the ocean ecosystem and discussing requirements for future studies.

Community structure using meta genetics

- In more recent times, metagenetic methods have been used to study regional and vertical differences in the community structure of zooplankton (in particular copepods) in various oceanic regions. In order to take into account also small-sized copepod species, studies conducted with fine mesh net size (or water bottles) were carried out in the Pacific (Hirai and Tsuda 2015; Hirai et al. 2020, 2021), the Red Sea (Pearman and Irigoien 2015) and the Mediterranean Sea (Di Capua et al. 2021) and the Arctic (Questel et al. 2021).
- The reference, however, made to specific groups of organisms depend on so far available sequencing data. For oncaeid copepods very little appropriate information is available in reference databases to date (e.g., Lindeque et al. 2013; Pearman and Irigoien 2015; Questel et al. 2021), and the comparability of this taxon with other taxonomic groups (families) is hardly given in metagenetic analyses. The interpretation of metabarcoding data requires a better fundamental genetic knowledge about species of this family as well as paired analyses of morphological and genetic data to validate the genetic results (Laakman et al. 2020; Matthews et al. 2021). The importance of traditional taxonomic expertise in the interpretation of metabarcoding data is an indispensable condition as emphasized by Pappalardo et al. (2021), who stated that “... a multi-marker approach combined with taxonomic expertise to develop a curated, vouchered, local database increases taxon detection with metabarcoding, and its potential as tool for zooplankton diversity surveys.”

Conclusion

The above examples address problems, that continue to be disregarded in marine ecological studies. The main difficulty appears to be a reliable taxonomic identification, in particular of the smallest species, causing a rather limited species-specific biological information so far. Thus, basic information for inclusion of oncaeids in ecosystem studies is missing and corresponding attempts could provide only speculative results. On the taxonomic side, the very limited knowledge about intraspecific variability of morphological characters should get more attention, and it appears essential to continue the time-consuming process of redescribing insufficiently described oncaeid species, and not yet described juveniles, including naupliar stages.

Present attempts to overcome taxonomic identification problems by using genetic markers, can be successful only if the genetic results have been obtained from specimens for which valid morphological identification is available. As world-wide only very few scientists are familiar with details of oncaeid morphology and species identification, a strong support for taxonomic research is required to solve the problems addressed above.

As partial solution, the absolute requirement of depositing voucher specimens of individual species used for genetics is emphasized. Providing photos of the species analysed, as used by some scientists (cf. BOLD database), can be a first step but does not absolve from the need to keep voucher specimens themselves for a later review of the morphological analyses. In this context the new method of using non-destructive DNA extraction for small pelagic copepods to perform integrative taxonomy (Cornils 2015) seems to be a promising step forward, especially for oncaeid copepods, which in many cases have a rather strong exoskeleton.

In general, continued support of morphological taxonomic research is required for Oncaeidae and other small copepod species in close cooperation with genetic methods as an essential basis for an adequate consideration of this numerically abundant group of organisms in future marine ecosystem studies.

Data/code availability

No associated data other than those given in the references are considered.

Appendix

References to numbered sampling locations in Fig. 6.

These references refer to quantitative plankton studies with mesh sizes of 0.1 mm or less, which consider oncaeids at least at family level.

- Shmeleva, A. A. (1964). Novye dlya Adriaticeskogo morya vidy kopepod i osobennosti ikh rasprostraneniya. New Copepoda species in the Adriatic and the characteristic features of their distribution in connection with hydrological conditions. *Okeanologiya*, 6, 1066–1072. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=111242>
- Delalo, E. P., 1966. The zooplankton of the eastern Mediterranean (Levantine Sea and Gulf of Sirte). *Issled. Plankt. Juzhn. Mor. Okeanogr. Kom. Akad. Nauk S.S.S.R.*, 62–81 (in Russian).
- LeBrasseur, R. J., & Kennedy, O. D. (1972). Microzooplankton in coastal and oceanic areas of the Pacific Subarctic Water Mass: a preliminary report. In *In: Takenouti, A.Y. (ed.). Biological Oceanography of the northern North Pacific Ocean. Dedicated to Shigeru Motoda. Tokyo* (pp. 355–365). <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=99199>
- Gordeeva, K. T., & Shmeleva, A. A. (1973). Pelagic copepods of the tropical Atlantic and the peculiarities of distribution of their mass species. Pelagicheskie kopepody tropicheskoi Atlantiki i osobennosti raspredeleniya ikh massovykh vidov. In *In: Vidovoi sostav i raspredelenie okeanicheskogo planktona. (Species composition and distribution of the oceanic plankton.) Trudy vses. gidrobiol. Obshch. (Vol. 20, pp. 109–143).* <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=89259>
- Judkins, D. G. (1980). Vertical distribution of zooplankton in relation to the oxygen minimum off Peru. *Deep-Sea Research, Part A, Oceanographic Research Papers*, 27A, 475–487. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=95288>
- Dagg T. Cowles T. Whitley S. Smith S. Howe & D. Judkins, M. J. (1980). Grazing and excretion by zooplankton in the Peru upwelling system during April 1977. *Deep-Sea Research, Part A, Oceanographic Research Papers*, 27(A), 43–59. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=83220>
- Paffenhöfer, G. A. (1980). Zooplankton distribution as related to summer hydrographic conditions in Onslow Bay, North Carolina. *Bulletin of Marine Science*, 30(4), 819–832. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=106708>
- See no. 5.
- See no. 6.
- Star, J. L., & Mullin, M. M. (1981). Zooplankton assemblages in three areas of the North Pacific as revealed by continuous horizontal transects. *Deep-Sea Research*, 28A(11), 1303–1322. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=193540>
- Davis, C. C. (1982). A preliminary quantitative study of the zooplankton from Conception Bay, insular Newfoundland, Canada. *Internationale Revue Der Gesamten Hydrobiologie*, 67(5), 713–747. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=83829>
- Böttger-Schnack, R. (1992). Community structure and vertical distribution of cyclopoid and poecilostomatoid copepods in the Red Sea. III. Re-evaluation for separating a new species of *Oncaea*. *Marine Ecology Progress*

- Series*, 80, 301–304. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78333>
13. Roman, M. R., Reeve, M. R., & Froggatt, J. L. (1983). Carbon production and export from Biscayne Bay, Florida. I. Temporal patterns in primary production, seston and zooplankton. *Estuarine, Coastal and Shelf Science*, 17(1), 45–59. [https://doi.org/10.1016/0272-7714\(83\)90044-6](https://doi.org/10.1016/0272-7714(83)90044-6)
 14. Paffenhöfer, G. A. (1983). Vertical zooplankton distribution on the northeastern Florida shelf and its relation to temperature and food abundance. *Journal of Plankton Research*, 5(1), 15–33. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=106710>
 15. See no. 13.
 16. Lie, U., Magnesen, T., Tunberg, B., & Aksnes, D. (1983). Preliminary studies on the vertical distribution of size-fractions in the zooplankton community in Lindåspollene, western Norway. *Sarsia*, 68(1), 65–79. <https://doi.org/10.1080/00364827.1983.10420558>; Magnesen, T. (1989). Vertical distribution of size-fractions in the zooplankton community in Lindaspollene, western Norway, 2. Diel variation. *Sarsia*, 74(1), 69–77. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=100875>; Magnesen, T. (1989). Vertical distribution of size-fractions in the zooplankton community in Lindaspollene, western Norway, 1. Seasonal variation. *Sarsia*, 74(1), 59–68. <https://doi.org/10.1080/00364827.1989.10413422>
 17. Michel, H. B., & Herring, D. C. (1984). Diversity and abundance of Copepoda in the northwestern Arabian Gulf. In *In: Vervoort, W. & J.C. Vaupel Klein von (eds.). Studies on Copepoda II. Proceedings of the First International Conference on Copepoda, Amsterdam, The Netherlands, 24–28 August 1981. Crustaceana, Supplement (Vol. 7, pp. 326–335).* <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=103409>
 18. Chojnacki, J., & Węgleńska, T. (1984). Periodicity of composition, abundance, and vertical distribution of summer zooplankton (1977/1978) in Ezcurra Inlet, Admiralty Bay (King George Island, South Shetland). *Journal of Plankton Research*, 6(6), 997–1017. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=72794>
 19. Heron, G. A., English, T. S., & Damkaer, D. M. (1984). Arctic Ocean Copepoda of the genera *Lubbockia*, *Oncaea*, and *Epicalymma* (Poecilostomatoida: Oncaeidae), with remarks on distributions. *Journal of Crustacean Biology*, 4(3), 448–490. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=89475>
 20. Paffenhöfer, G.-A., Wester, B. T., & Nicholas, W. D. (1984). Zooplankton abundance in relation to state and type of intrusion onto the southeastern United States shelf during summer. *Journal of Marine Research*, 42, 995–1017. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=106721>
 21. Böttger, R. (1985). Untersuchungen zur Verteilung der kleinen Metazoa im Plankton des Roten Meeres, unter besonderer Berücksichtigung cyclopoider und harpacticoider Copepoden. *Ph.D. Thesis, Universität Hamburg, Hamburg, Germany*, 1–248. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78324>
 22. See no. 21
 23. Roman, M., Gauzens, A., & Cowles, T. (1985). Temporal and spatial changes in epipelagic microzooplankton and mesozooplankton biomass in warm-core Gulf Stream ring 82-B. *Deep Sea Research Part A. Oceanographic Research Papers*, 32, 1007–1022. [https://doi.org/10.1016/0198-0149\(85\)90059-7](https://doi.org/10.1016/0198-0149(85)90059-7)
 24. Mullin, M. M., Brooks, E. R., Reid, F. M. H., Napp, J., & Stewart, E. F. (1985). Vertical structure of nearshore plankton off Southern California: a storm and a larval fish food web. *Fishery Bulletin*, 83(2), 151–170.
 25. Michel, H. B., Behbehani, M., & Herring, D. (1986a). Zooplankton of the western Arabian Gulf South of Kuwait waters. *Kuwait Bulletin of Marine Science*, 8, 1–36. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=103411>
 26. Michel M. Behbehani D. Herring M. Arar M. Shoushani & T. Brakonieccki, H. B. (1986b). Zooplankton diversity, distribution and abundance in Kuwait waters. *Kuwait Bulletin of Marine Science*, 8:37–105. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=217872>
 27. Groendahl, F., & Hernroth, L. (1986). Vertical distribution of copepods in the Eurasian part of the Nansen Basin, Arctic Ocean. In *In: Schriever, G., H.K. Schminke & C.-t. Shih (eds.). Proceedings of the Second International Conference on Copepoda, Ottawa, Canada, 13–17 August, 1984. Syllogeus (pp. 311–320).* <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=89998>
 28. Villate, L. F., & Alcaraz, M. (1986). Spatial segregation of copepods in the Abra port of Bilbao. In *In: Schriever, G., H.K. Schminke & C.-t. Shih (eds.). Proceedings of the Second International Conference on Copepoda, Ottawa, Canada, 13–17 August, 1984. Syllogeus (Vol. 58, pp. 610–618).* <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=119210>
 29. Valentin, J. L., Monteiro-Ribas, W. M., Mureb, M. A., & Pessotti, E. (1987). Sur quelques zooplanctontes abondants dans l'upwelling de Cabo Frio (Brésil). *Journal of Plankton Research*, 9(6), 1195–1216. <https://doi.org/10.1093/plankt/9.6.1195>
 30. Cowles, T. J., Roman, M. R., Gauzens, A. L., & Copley, N. J. (1987). Short-term changes in the biology of

- a warm-core ring: zooplankton biomass and grazing. *Limnology and Oceanography*, 32(3), 653–664. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=82833>
31. Paffenhöfer G A, Sherman, B. K., & Lee, T. N. (1987). Abundance, distribution and patch formation of zooplankton. *Progress in Oceanography*, 19(3/4), 403–436. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=106720>
 32. Böttger, R. (1987). The vertical distribution of micro- and small mesozooplankton in the central Red Sea. *Biological Oceanography*, 4, 383–402. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78325>
 33. Böttger-Schnack, R. (1988). Observations on the taxonomic composition and vertical distribution of cyclopoid copepods in the central Red Sea. *Hydrobiologia*, 167–168(1), 311–318. <https://doi.org/10.1007/BF00026319> —Böttger-Schnack, R. (1990). Community structure and vertical distribution of cyclopoid copepods in the Red Sea I. Central Red Sea, autumn 1980. *Marine Biology*, 106, 473–485. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78331>
 34. Franz, H. G. (1988). Vernal abundance, structure and development of epipelagic copepod populations of the eastern Weddell Sea (Antarctica). *Polar Biology*, 9, 107–114. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=87303>
 35. Hopkins, T. L., & Torres, J. J. (1988). The Zooplankton Community in the Vicinity of the Ice Edge, Western Weddell Sea, March 1986. *Polar Biology*, 9(2), 79–87. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=13329>
 36. Böttger-Schnack, R. (1990). Community structure and vertical distribution of cyclopoid copepods in the Red Sea II. Aspects of seasonal and regional differences. *Marine Biology*, 106, 487–501. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78330>
 37. Checkley, D. M., Uye, S., Dagg, M. J., Mullin, M. M., Omori, M., Onbe, T., & Zhu, M.-Y. (1992). Diel variation of the zooplankton and its environment at neritic stations in the Inland Sea of Japan and the north-west Gulf of Mexico. *Journal of Plankton Research*, 14, 1–40. <http://plankt.oxfordjournals.org/>
 38. See no. 37.
 39. Metz, C. (1993). *Verbreitung von Cyclopoida (Copepoda, Crustacea) im Weddellmeer*. University Kiel.—Metz, C. (1995). Seasonal variation in the distribution and abundance of *Oithona* and *Oncaea* species (Copepoda, Crustacea) in the southeastern Weddell Sea, Antarctica. *Polar Biology*, 15:187–194. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=103259>
 40. Hopkins, T. L., Ainley, D. G., Torres, J. J., & Lancraft, T. M. (1993). Trophic structure in open waters of the marginal ice zone of the Scotia-Weddell confluence region during spring (1983). *Polar Biology*, 13, 389–397. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=93091>
 41. Roman, M. R., Dam, H. G., Gauzens, A. L., Urban-Rich, J., Foley, D. G., & Dickey, T. D. (1995). Zooplankton variability on the equator at 140°W during the JGOFS EqPac study. *Deep-Sea Research, Part II, Topical Studies in Oceanography*, 42, 673–693. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=111445>
 42. Böttger-Schnack, R. (1995). Summer distribution of micro- and small mesozooplankton in the Red Sea and Gulf of Aden, with special reference to non-calanoïd copepods. *Marine Ecology Progress Series*, 118, 81–103. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78335>
 43. Kršinić, F. (1995). Changes in the microzooplankton assemblages in the northern Adriatic Sea during 1989 to 1992. *Journal of Plankton Research*, 17(5), 935–953. <https://doi.org/10.1093/plankt/17.5.935>
 44. Webber, M. K., & Roff, J. C. (1995). Annual structure of the copepod community and its associated pelagic environment off Discovery Bay, Jamaica. *Marine Biology*, 123, 467–479.
 45. Böttger-Schnack, R. (1996). Vertical structure of small metazoan plankton, especially non-calanoïd copepods. I. Deep Arabian Sea. *Journal of Plankton Research*, 18(7), 1073–1101. <https://doi.org/10.1093/plankt/18.7.1073>
 46. Metz, C. (1996). Lebensstrategien dominanter antarktischer Oithonidae (Cyclopoida, Copepoda) und Oncaeidae (Poecilosomatoida, Copepoda) im Bellingshausenmeer. *Ber. Polarforsch.*, 207, 1–136.
 47. Böttger-Schnack, R. (1997). Vertical structure of small metazoan plankton, especially non-calanoïd copepods. II. Deep Eastern Mediterranean (Levantine Sea). *Oceanologica Acta*, 20, 399–419. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78337>
 48. Kršinić, F. (1998). Vertical distribution of protozoan and microcopepod communities in the South Adriatic Pit. *Journal of Plankton Research*, 20(6), 1033–1060. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=98004>
 49. Kršinić, F., & Viličić, D. (1989). Microzooplankton in the Kotor Bay, (The southern Adriatic). Mikrozooplankton u kotorskom zaljevu (Juzni Jadran). *Studia Marina, Kotor, Yugoslavia*, 20:3–20. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=98004>

- [marinespecies.org/aphia.php?p=sourcedetails&id=407881](https://www.marinespecies.org/aphia.php?p=sourcedetails&id=407881)
50. Schnack-Schiel, S. B., Hagen, W., & Mizdalski, E. (1998). Seasonal carbon distribution of copepods in the eastern Weddell Sea, Antarctica. *Journal of Marine Systems, Special Volume*, 17, 305–311. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=112695>
 51. Uye, S. I., Nagano, N., & Shimazu, T. (2000). Abundance, biomass, production and trophic roles of micro- and net- zooplankton in Ise Bay, central Japan, in Winter. *Journal of Oceanography*, 56, 389–398. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=118301>
 52. Lugomela, C., Wallberg, P., & Nielsen, T. G. (2001). Plankton composition and cycling of carbon during the rainy season in a tropical coastal ecosystem, Zanzibar, Tanzania. *Journal of Plankton Research*, 23(10), 1121–1136. <https://doi.org/10.1093/plankt/23.10.1121>
 53. Youssara, F., & Gaudy, R. (2001). Variations of zooplankton in the frontal area of the Alboran sea (Mediterranean sea) in winter 1997. *Oceanologica Acta*, 24(4), 361–376. [https://doi.org/10.1016/S0399-1784\(01\)01154-9](https://doi.org/10.1016/S0399-1784(01)01154-9)
 54. Fortier, M., Fortier, L., Hattori, H., Saito, H., & Legendre, L. (2001). Visual predators and the diel vertical migration of copepods under Arctic sea ice during the midnight sun. *Journal of Plankton Research*, 23(11), 1263–1278.
 55. Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S., Ishizaka, J., Ikeda, T., & Takahashi, M. Mac. (2002). Community and trophic structures of pelagic copepods down to greater depths in the western subarctic Pacific (WEST-COSMIC). *Deep Sea Research Part I: Oceanographic Research Papers*, 49(6), 1007–1025. [https://doi.org/10.1016/S0967-0637\(02\)00008-0](https://doi.org/10.1016/S0967-0637(02)00008-0)
 56. Dubischar, C. D., Lopes, R. M., & Bathmann, U. V. (2002). High summer abundances of small pelagic copepods at the Antarctic Polar Front—implications for ecosystem dynamics. *Deep Sea Research Part II: Topical Studies in Oceanography*, 49(18), 3871–3887. [https://doi.org/10.1016/S0967-0645\(02\)00115-7](https://doi.org/10.1016/S0967-0645(02)00115-7)
 57. Kršinić, F., & Grbec, B. (2002). Some distributional characteristics of small zooplankton at two stations in the Otranto Strait (Eastern Mediterranean). *Hydrobiologia*, 482(1980), 119–136. <https://doi.org/10.1023/A:1021212431253>
 58. Paffenhöfer, G. A., & Mazzocchi, M. G. (2003). Vertical distribution of subtropical epiplanktonic copepods. *Journal of Plankton Research*, 25(9), 1139–1156. <https://doi.org/10.1093/plankt/25.9.1139>
 59. Munk, P., Hansen, B. W., Nielsen, T. G., & Thomsen, H. A. (2003). Changes in plankton and fish larvae communities across hydrographic fronts off West Greenland. *Journal of Plankton Research*, 25(7), 815–830.
 60. Nishibe, Y., & Ikeda, T. (2004). Vertical distribution, abundance and community structure of oncaeid copepods in the Oyashio region, western subarctic Pacific. *Marine Biology*, 145(5), 931–941. <https://doi.org/10.1007/s00227-004-1392-9>
 61. Thor, P., Nielsen, T. G., Tiselius, P., Juul-Pedersen, J.-P., Michel, C., Moller, E. F., Dahl, K., Selander, E., & Gooding, S. (2005). Post spring bloom community structure of pelagic copepods in the Disko Bay, Western Greenland. *Journal of Plankton Research*, 27(4), 341–356. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=117244>
 62. Hopcroft, R. R., Clarke, C., Nelson, R. J., & Raskoff, K. A. (2005). Zooplankton communities of the Arctic's Canada Basin: the contribution by smaller taxa. *Polar Biology*, 28(3), 198–206. <https://doi.org/10.1007/s00300-004-0680-7>
 63. Papastephanou, K. M., Bollens, S. M., & Slaughter, A. M. (2006). Cross-shelf distribution of copepods and the role of event-scale winds in a northern California upwelling zone. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 53(25–26), 3078–3098. <https://doi.org/10.1016/j.dsr2.2006.07.014>
Bollens, S. M., Breckenridge, J. K., van den Hooff, R. C., & Cordell, J. R. (2011). Mesozooplankton of the lower San Francisco Estuary: spatio-temporal patterns, ENSO effects and the prevalence of non-indigenous species. *Journal of Plankton Research*, 33(9), 1358–1377. <https://doi.org/10.1093/plankt/fbr034>
 64. Møller, E. F., Nielsen, T. G., & Richardson, K. (2006). The zooplankton community in the Greenland Sea: Composition and role in carbon turnover. *Deep Sea Research Part I: Oceanographic Research Papers*, 53, 76–93. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=103853>
 65. Kršinić, F., Bojanić, D., Precali, R., & Kraus, R. (2007). Quantitative variability of the copepod assemblages in the northern Adriatic Sea from 1993 to 1997. *Estuarine, Coastal and Shelf Science*, 74(3), 528–538. <https://doi.org/10.1016/j.ecss.2007.05.036>
 66. Nishibe, Y., Koizumi, Y., & Ueda, H. (2007). Spatio-temporal variation of copepod community structure in the Bungo Channel, Japan. *Frontiers Science Series*, 48, 401–404. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=105381>
 67. Koski, M., Møller, E. F., Maar, M., & Visser, A. W. (2007). The fate of discarded appendicularian houses: degradation by the copepod, *Microsetella norvegica*,

- and other agents. *Journal of Plankton Research*, 29(7), 641–654. <https://doi.org/10.1093/plankt/fbm046>
68. Khelifi-Touhami, M., Semroud, R., Hamdi, E. H., Ounissi, M., Haridi, A., Nejib Daly, M., & Aissa, P. (2007). The planctonic copepod communities from the southern Mediterranean Sea (Algeria, Tunisia) with a redescription of *Paracalanus indicus* Wolfenden 1905 (Copepoda: Calanoida). *Cahiers de Biologie Marine*, 48(4), 327–338. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=122163>
 69. Nishibe, Y., & Ikeda, T. (2007). Vertical distribution, population structure and life cycles of four oncaeid copepods in the Oyashio region, western subarctic Pacific. *Marine Biology*, 150, 609–625. <https://doi.org/10.1007/s00227-006-0382-5>
 70. McKinnon, A. D., Duggan, S., Carleton, J. H., & Böttger-Schnack, R. (2008). Summer planktonic copepod communities of Australia's North West Cape (Indian Ocean) during the 1997–99 El Niño/La Niña. *Journal of Plankton Research*, 30(7), 839–855. <https://doi.org/10.1093/plankt/fbn043>
 71. Böttger-Schnack, R., Hagen, W., & Schnack-Schiel, S. B. (2001). The microcopepod fauna in the Gulf of Aqaba, northern Red Sea: species diversity and distribution of Oncaeidae (Poecilostomatoida). *Journal of Plankton Research*, 23(9), 1029–1035. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=72154>
Böttger-Schnack, R., Schnack, D., & Hagen, W. (2008). Microcopepod community structure in the Gulf of Aqaba and northern Red Sea, with special reference to Oncaeidae. *Journal of Plankton Research*, 30(5), 529–550. <https://doi.org/10.1093/plankt/fbn018>
 72. Tanimura, A., Hattori, H., Miyamoto, Y., Hoshiai, T., & Fukuchi, M. (2008). Diel changes in vertical distribution of *Oithona similis* (Cyclopoida) and *Oncaea curvata* (Poecilostomatoida) under sea ice in mid-summer near Syowa Station, Antarctica. *Polar Biology*, 31(5), 561–567. <https://doi.org/10.1007/s00300-007-0388-6>
Tanimura, A., Hoshino, K., Nonaka, Y., Miyamoto, Y., & Hattori, H. (1997). Vertical distribution of *Oithona similis* and *Oncaea curvata* (Cyclopoida, Copepoda) under sea ice near Syowa station in the Antarctic winter. *Proceedings of the NIPR (National Institute of Polar Research) Symposium on Polar Biology, Tokyo, 10*, 134–144.
 73. Takahashi, T., & Uchiyama, I. (2008). Seasonal changes in the density and vertical distribution of nauplii, copepodites and adults of the genera *Oithona* and *Oncaea* (Copepoda) in the surface water of Toyama Bay, southern Sea of Japan. *Plankton & Benthos Research*, 3(3143–151.), (3):143–151. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=126875>
 74. Schnack-Schiel, S. B., Michels, J., Mizdalski, E., Schodlok, M. P., & Schröder, M. (2008). Composition and community structure of zooplankton in the sea ice-covered western Weddell Sea in spring 2004—with emphasis on calanoid copepods. *Deep Sea Research Part II: Topical Studies in Oceanography*, 55(8–9), 1040–1055. <https://doi.org/10.1016/j.dsr2.2007.12.013>
 75. Nishibe, Y., Hirota, Y., & Ueda, H. (2009). Community structure and vertical distribution of oncaeid copepods in Tosa Bay, southern Japan. *Journal of the Marine Biological Association of the United Kingdom*, 89(3), 491–498. <https://doi.org/10.1017/S0025315409003087>
 76. Miyashita, L. K., de Melo Junior, M., & Lopes, R. M. (2009). Estuarine and oceanic influences on copepod abundance and production of a subtropical coastal area. *Journal of Plankton Research*, 31(8), 815–826. <https://doi.org/10.1093/plankt/fbp039>
 77. Böttger-Schnack, R., & Schnack, D. (2009). Taxonomic diversity and identification problems of oncaeid microcopepods in the Mediterranean Sea. *Marine Biodiversity*, 39(2), 131–145. <https://doi.org/10.1007/s12526-009-0013-8>
 78. See no. 77
 79. Arendt, K. E., Nielsen, T. G., Rysgaard, S., & Tønneson, K. E. (2010). Differences in plankton community structure along the Godthåbsfjord; from the Greenland Ice Sheet to offshore waters. *Marine Ecology Progress Series*, 401:49–62. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=143846>
 80. Drira, Z., Belhassen, M., Ayadi, H., Hamza, A., Zarrad, R., Bouaïn, A., & Aleya, L. (2010). Copepod community structure related to environmental factors from a summer cruise in the Gulf of Gabès (Tunisia, eastern Mediterranean Sea). *Journal of the Marine Biological Association of the United Kingdom*, 90, 145. <https://doi.org/10.1017/S0025315409990403>
 81. Beltrão, R., Monde, M., & Ueda, H. (2011). Characteristics and regional classification of the copepod community in Ariake Bay with note on comparison with 3 decades ago. *Journal of Oceanography*, 67(1), 47–58. <https://doi.org/10.1007/s10872-011-0005-8>
 82. Minowa, M., Kobari, T., Akamatsu, H., Ichikawa, T., Fukuda, R., & Higashi, M. (2011). Seasonal changes in abundance, biomass and depth distribution of mesozooplankton community in Kagoshima Bay. *Bulletin of Japanese Society of Fisheries Oceanography*, 75(2), 71–81.
 83. Andersen, N. G., Nielsen, T. G., Jakobsen, H. H., Munk, P., & Riemann, L. (2011). Distribution and production of plankton communities in the subtropical convergence zone of the Sargasso Sea. II. Proto-

- zooplankton and copepods. *Marine Ecology Progress Series*, 426, 71–86. <https://doi.org/10.3354/meps09047>
84. Svensen, C., Seuthe, L., Vasilyeva, Y., Pasternak, A., & Hansen, E. (2011). Zooplankton distribution across Fram Strait in autumn: Are small copepods and protozooplankton important? *Progress in Oceanography*, 91(4), 534–544. <https://doi.org/10.1016/j.pocean.2011.08.001>
 85. Ward, P., Atkinson, A., & Tarling, G. (2012). Meso-zooplankton community structure and variability in the Scotia Sea: A seasonal comparison. *Deep Sea Research Part II: Topical Studies in Oceanography*, 59–60, 78–92. <https://doi.org/10.1016/j.dsr2.2011.07.004>
 86. Kršinić, F., & Grbec, B. (2012). Spatial distribution of copepod abundance in the epipelagic layer of the south Adriatic Sea. *Acta Adriatica*, 53, 57–70.
 87. Uysal, Z., & Shmeleva, A. A. (2012). Species composition, abundance and biomass of copepoda in plankton of the northern levantine basin (Eastern Mediterranean). *Crustaceana*, 85(8), 909–935. <https://doi.org/10.1163/156854012X650179>
 88. McKinnon, A. D., Duggan, S., Böttger-Schnack, R., Gusmão, L. F. M., & O’Leary, R. A. (2013). Depth structuring of pelagic copepod biodiversity in waters adjacent to an Eastern Indian Ocean coral reef. *Journal of Natural History*, 47(5–12), 639–665. <https://doi.org/10.1080/00222933.2012.673645>
 89. Ojima, M., Takahashi, K. T., Iida, T., Odate, T., & Fukuchi, M. (2013). Distribution patterns of micro- and meso-zooplankton communities in sea ice regions of Lützow-Holm Bay, East Antarctica. *Polar Biology*, 36(9), 1293–1304. <https://doi.org/10.1007/s00300-013-1348-y>
 90. Arendt, K. E., Juul-Pedersen, T., Mortensen, J., Blicher, M. E., & Rysgaard, S. (2013). A 5-year study of seasonal patterns in mesozooplankton community structure in a sub-Arctic fjord reveals dominance of *Microsetella norvegica* (Crustacea, Copepoda). *Journal of Plankton Research*, 35(1), 105–120. <https://doi.org/10.1093/plankt/fbs087>
 91. Itoh, H., Nakata, K., Sasaki, K., Ichikawa, T., & Hidaka, K. (2014). Seasonal and diel changes in the vertical distribution of oncaeid copepods in the epipelagic zone of the Kuroshio Extension region. *Plankton Benthos Research*, 9(1), 1–14.
 92. Itoh, H., Nishioka, J., & Tsuda, A. (2014). Community structure of mesozooplankton in the western part of the Sea of Okhotsk in summer. *Progress in Oceanography*, 126, 224–232. <https://doi.org/10.1016/j.pocean.2014.05.008>
 93. Riisgaard, K., Swalethorp, R., Kjellerup, S., Juul-Pedersen, T., & Nielsen, T. G. (2014). Trophic role and top-down control of a subarctic protozooplankton community. *Marine Ecology Progress Series*, 500, 67–82. <https://doi.org/10.3354/meps10706>
 94. Ojima, M., Takahashi, K. T., Tanimura, A., Odate, T., & Fukuchi, M. (2015). Spatial distribution of micro- and meso-zooplankton in the seasonal ice zone of east Antarctica during 1983–1995. *Polar Science*, 9(3), 319–326. <https://doi.org/10.1016/j.polar.2015.05.002>
 95. Kersten, O. (2015). *Abyssal Near-bottom zooplankton in the Eastern Tropical North Pacific*. Hawaii Pacific University.
 96. Lischka, S., & Hagen, W. (2016). Seasonal dynamics of mesozooplankton in the Arctic Kongsfjord (Svalbard) during year-round observations from August 1998 to July 1999. *Polar Biology*, 39(10), 1859–1878. <https://doi.org/10.1007/s00300-016-2005-z>
 97. Ojima, M., Takahashi, K. T., Iida, T., Moteki, M., Miyazaki, N., Tanimura, A., & Odate, T. (2017). Variability of the fauna within drifting sea ice floes in the seasonal ice zone of the Southern Ocean during the austral summer. *Polar Science*, 12, 19–24. <https://doi.org/10.1016/j.polar.2017.02.005>
 98. Makabe, R., Tanimura, A., Tamura, T., Hirano, D., Shimada, K., Hashihama, F., & Fukuchi, M. (2017). Meso-zooplankton abundance and spatial distribution off Lützow-Holm Bay during austral summer 2007–2008. *Polar Science*, 12, 25–33. <https://doi.org/10.1016/j.polar.2016.09.002>
 99. Takahashi, K. T., Ojima, M., Tanimura, A., Odate, T., & Fukuchi, M. (2017). The vertical distribution and abundance of copepod nauplii and other micro- and meso-zooplankton in the seasonal ice zone of Lützow-Holm Bay during austral summer 2009. *Polar Biology*, 40(1), 79–93. <https://doi.org/10.1007/s00300-016-1925-y>
 100. Carlotti, F., Pagano, M., Guilloux, L., Donoso, K., Valdés, V., Grosso, O., & Hunt, B. P. V. (2018). Meso-zooplankton structure and functioning in the western tropical South Pacific along the 20th parallel south during the OUTPACE survey (February–April 2015). *Biogeosciences*, 15(23), 7273–7297. <https://doi.org/10.5194/bg-15-7273-2018>
 101. Munk, P., Nielsen, T. G., Jaspers, C., Ayala, D. J., Tang, K. W., Lombard, F., & Riemann, L. (2018). Vertical structure of plankton communities in areas of European eel larvae distribution in the Sargasso Sea. *Journal of Plankton Research*, 40(4), 362–375. <https://doi.org/10.1093/plankt/fby025>
 102. Lučić, D., Hure, M., Bobanović-Čolić, S., Njire, J., Vidjak, O., Onofri, I., Gangai Zovko, B., & Batistić, M. (2019). The effect of temperature change and oxygen reduction on zooplankton composition and vertical distribution in a semi-enclosed marine system. *Marine*

- Biology Research*, 15(4–6), 325–342. <https://doi.org/10.1080/17451000.2019.1655161>
103. Eriksen, R. S., Davies, C. H., Bonham, P., Coman, F. E., Edgar, S., McEnulty, F. R., McLeod, D., Miller, M. J., Rochester, W., Slotwinski, A., Tonks, M. L., Uribe-Palomino, J., & Richardson, A. J. (2019). Australia's Long-Term Plankton Observations: The Integrated Marine Observing System National Reference Station Network. *Frontiers in Marine Science*, 6: 161. <https://doi.org/10.3389/fmars.2019.00161>
 104. Middelbo, A. B., Møller, E. F., Arendt, K. E., Thyrring, J., & Sejr, M. K. (2019). Spatial, seasonal and inter-annual variation in abundance and carbon turnover of small copepods in Young Sound, Northeast Greenland. *Polar Biology*, 42(1), 179–193. <https://doi.org/10.1007/s00300-018-2416-0>
 105. Kršinić, F., Böttger-Schnack, R., & Vidjak, O. (2020). Small copepods of the deep South Adriatic Pit: diversity, seasonal and multi-annual dynamics, and implications from the regional hydrography. *Environmental Monitoring and Assessment*, 192(8), 545. <https://doi.org/10.1007/s10661-020-08462-4>
 106. Koski, M., Valencia, B., Newstead, R., & Thiele, C. (2020). The missing piece of the upper mesopelagic carbon budget? Biomass, vertical distribution and feeding of aggregate-associated copepods at the PAP site. *Progress in Oceanography*, 181(July 2019), 102,243. <https://doi.org/10.1016/j.pocean.2019.102243>
 107. Abe, Y., Hildebrandt, N., Matsuno, K., Niehoff, B., & Yamaguchi, A. (2020). Comparison of the vertical distribution of pelagic copepod abundance, biomass and community structure between the Atlantic and Pacific sectors of the Arctic Ocean. *Bulletin of Fisheries Sciences Hokkaido University*. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=406841>
 108. Jaspe, B. T., Campos, W. L., & Metillo, E. (2020). Abundance, distribution and species composition of cyclopoid copepods along a transect traversing the upwelling zone off northern zamboanga peninsula, philippines. *Asian Fisheries Science*, 33(4), 307–314. <https://doi.org/10.33997/j.afs.2020.33.4.001>
 109. Koski, M., Swalethorp, R., Kjellerup, S., & Nielsen, T. G. (2021). Aggregate-colonizing copepods in a glacial fjord: Population dynamics, vertical distribution and allometric scaling of growth and mortality rates of *Microsetella norvegica* and *Oncaea* spp. *Progress in Oceanography*, 197, 102,670. <https://doi.org/10.1016/j.pocean.2021.102670>
 110. Coguiec, E., Ershova, E. A., Daase, M., Vonnahme, T. R., Wangensteen, O. S., Gradinger, R., Praebel, K., & Berge, J. (2021). Seasonal variability in the zooplankton community structure in a sub-Arctic fjord as revealed by morphological and molecular approaches. *Frontiers in Marine Science*, 8, 705,042. <https://doi.org/10.3389/fmars.2021.705042>
 111. Vargas, C., Tönnesson, K., Sell, A., Maar, M., Møller, E., Zervoudaki, T., Giannakourou, A., Christou, E., Satapoomin, S., Petersen, J., Nielsen, T., & Tiselius, P. (2002). Importance of copepods versus appendicularians in vertical carbon fluxes in a Swedish fjord. *Marine Ecology Progress Series*, 241, 125–138. <https://doi.org/10.3354/meps241125>
 - Titelman, J., & Fiksen, Ø. (2004). Ontogenetic vertical distribution patterns in small copepods: field observations and model predictions. *Marine Ecology Progress Series*, 284(1), 49–63. <https://doi.org/10.3354/meps284049>
 112. Davies, C. H., Beckley, L. E., & Richardson, A. J. (2022). Copepods and mixotrophic Rhizaria dominate zooplankton abundances in the oligotrophic Indian Ocean. *Deep-Sea Research Part II-Topical Studies In Oceanography*, 202, 105,136. <https://doi.org/10.1016/j.dsr2.2022.105136>
 113. Abdel-Rahman, N., & Aboul-Ezz, S. (1999). Seasonal distribution of Copepoda in the Gulf of Suez. *Journal of the Egyptian German Society of Zoology*, 28(D), 111–123. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=72928>
 114. Daly Yahia, M., Souissi, S., & Daly Yahia-Kéfi, O. (2004). Spatial and temporal structure of planktonic copepods in the Bay of Tunis (southwestern Mediterranean Sea). In In: Hwang, J.S., J.S. Ho & C.T. Shih, (eds). *Proceedings of the 8th International Conference on Copepoda, Special Issue: Contemporary Studies on Copepoda, Zoological Studies: Vol. 43 (2)*, 366–375. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=83404>
 115. Zervoudaki, S., Nielsen, T., Christou, E., & Siokou-Frangou I. (2006). Zooplankton distribution and diversity in a frontal area of the Aegean Sea. *Marine Biology Research*, 2(3), 149–168. <https://doi.org/10.1080/17451000600702037>
 116. Favareto, L., Perbiche-Neves, G., Serafim-Júnior, M., & Sartori, L. (2009). Selectivity of plankton nets over planktonic Copepoda in two sub-tropical estuaries. Seletividade de redes de plâncton sobre Copepoda planctônicos em dois estuários sub-tropicais. *Acta Limnologica Brasiliensia*, 21(1), 67–77. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=410833>
 117. Itoh, H., & Aoki, N. (2010). Temporal and spatial distribution of planktonic copepods in Tokyo Bay: Seasonal occurrence in the innermost part of the bay, in the early 1990s. *Bulletin of Plankton Society of Japan*, 57(2), 94–104. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=149920>

118. Calbet, A., Garrido, S., Saiz, E., Alcaraz, M., & Duarte, C. M. (2001). Annual Zooplankton Succession in Coastal NW Mediterranean Waters: The Importance of the Smaller Size Fractions. *Journal of Plankton Research*, 23(3), 319–331. <https://doi.org/10.1093/plankt/23.3.319>
119. Aguirre, G., Capitanio, F., Lovrich, G., & Esnal, G. (2012). Seasonal variability of metazooplankton in coastal sub-Antarctic waters (Beagle Channel). *Marine Biology Research*, 8(4), 341–353. <https://doi.org/10.1080/17451000.2011.627922>
120. Tseng, L. -C., Dahms, H. -U., Kumar, R., Chen, Q. -C., & Hwang, J. -S. (2013). Autumn community structure in the shallow mixed layer of the subtropical South China Sea reveals a peculiar copepod and zooplankton assemblage. *Journal of Natural History*, 47(5–12), 667–683. <https://doi.org/10.1080/00222933.2012.716866>

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References

- Abe Y, Hildebrandt N, Matsuno K, Niehoff B, Yamaguchi A (2020) Comparison of the vertical distribution of pelagic copepod abundance, biomass and community structure between the Atlantic and Pacific sectors of the Arctic Ocean. *Bull Fish Sci Hokkaido Univ* 70(1):91–102. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=406841>
- Aberle N, Hansen T, Boettger-Schnack R, Burmeister A, Post AF, Sommer U (2010) Differential routing of ‘new’ nitrogen toward higher trophic levels within the marine food web of the Gulf of Aqaba, Northern Red Sea. *Mar Biol* 157(1):157–169. <https://doi.org/10.1007/s00227-009-1306-y>
- Albuquerque R, Bode A, González-Gordillo JI, Duarte CM, Queiroga H (2021) Trophic structure of neuston across tropical and subtropical oceanic provinces assessed with stable isotopes. *Front Mar Sci* 7:606088. <https://doi.org/10.3389/fmars.2020.606088>
- Allredge AL (1972) Abandoned larvacean houses: a unique food source in the pelagic environment. *Science, New York* 177:885–887. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=72241>
- Arthur DK (1976) Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax* and *Trachurus symmetricus*. *Fish Bull* 74(3):517–530
- Benedetti F, Gasparini S, Ayata S-D (2016) Identifying copepod functional groups from species functional traits. *J Plankton Res* 38(1):159–166. <https://doi.org/10.1093/plankt/fbv096>
- Benedetti F, Vogt M, Righetti D, Guilhaumon F, Ayata S-D (2018) Do functional groups of planktonic copepods differ in their ecological niches? *J Biogeogr* 45(3):604–616. <https://doi.org/10.1111/jbi.13166>
- Beroujon T, Christiansen JS, Norrbin F (2022) Spatial occurrence and abundance of marine zooplankton in Northeast Greenland. *Mar Biodiv* 52:1–19. <https://doi.org/10.1007/s12526-022-01280-6>
- Bersano, JGF, Boxshall GA (1996) Planktonic copepods of the genus *Oncaea* Philippi (Poecilostomatoida: Oncaeidae) from the waters off southern Brazil. *Nauplius, Rio Grande* (dated 1994) 2:29–41. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=77058>
- Bielecka L, Żmijewska MI (1997) The antarctic cyclopoid *Oncaea antarctica*—some aspects of its biology and ecology. *Oceanol Stud* 26(1):149–163. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=77567>
- Björnberg T, Lopes R, Björnberg M (1994) Chave para a identificação de náuplios de copépodos planctônicos marinhos do Atlântico Sul-Occidental. *Nauplius, Rio Grande* 2:1–16. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=77779>
- Björnberg TKS (1972) Developmental stages of some tropical and subtropical planktonic marine copepods. In: *Studies on the Fauna of Curaçao and Other Caribbean Islands* 136:1–185. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=77754>
- Bode M, Koppelman R, Teuber L, Hagen W, Auel H (2018) Carbon budgets of mesozooplankton copepod communities in the eastern atlantic ocean—regional and vertical patterns between 24°N and 21°S. *Global Biogeochem Cycles* 32(5):840–857. <https://doi.org/10.1029/2017GB005807>
- Bode-Dalby M, Würth R, de Oliveira LDF, Lamont T, Verheye HM, Schukat A, Hagen W, Auel H (2023) Small is beautiful: the important role of small copepods in carbon budgets of the

- southern Benguela upwelling system. *J Plankton Res* 45:110–128. <https://doi.org/10.1093/plankt/fbac061>
- Bollens SM, Breckenridge JK, Vanden Hooff RC, Cordell JR (2011) Mesozooplankton of the lower San Francisco Estuary: spatio-temporal patterns, ENSO effects and the prevalence of non-indigenous species. *J Plankton Res* 33(9):1358–1377. <https://doi.org/10.1093/plankt/fbr034>
- Boltovskoy D (ed) (1999) south atlantic zooplankton vol. 2 (Copepoda, Poecilostomatoida). In: South Atlantic Zooplankton Vol. 2:969–1097. Backhuys Publishers, Leiden 1999
- Bortolus A (2008) Error cascades in the biological Sciences: the unwanted consequences of using bad taxonomy in ecology. *Ambio*, 37(2):114–118. <http://www.ambio.kva.se>
- Böttger R (1982) Studies on the small invertebrate plankton of the Sargasso Sea. *Helgoländer Meeresuntersuchungen*, 35:369–383. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78323>
- Böttger R (1985) Untersuchungen zur Verteilung der kleinen Metazoa im Plankton des Roten Meeres, unter besonderer Berücksichtigung cyclopoider und harpacticoider Copepoden. Ph.D. Thesis, Universität Hamburg, Hamburg, Germany:1–248. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78324>
- Böttger-Schnack R (1990a) Community structure and vertical distribution of cyclopoid copepods in the Red Sea I. Central Red Sea, autumn 1980. *Mar Biol* 106:473–485. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78331>
- Böttger-Schnack R (1990b) Community structure and vertical distribution of cyclopoid copepods in the Red Sea II. Aspects of seasonal and regional differences. *Mar Biol* 106:487–501. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78330>
- Böttger-Schnack R (1994) The microcopepod fauna in the Eastern Mediterranean and Arabian Seas: a comparison with the Red Sea fauna. *Hydrobiologia* 292–293(1):271–282. <https://doi.org/10.1007/BF00229951>
- Böttger-Schnack R (1995) Summer distribution of micro- and small mesozooplankton in the Red Sea and Gulf of Aden, with special reference to non-calanoid copepods. *Marine Ecol Prog Ser* 118:81–103. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78335>
- Böttger-Schnack R (1996) Vertical structure of small metazoan plankton, especially non-calanoid copepods. I. Deep Arabian Sea. *J Plankton Res* 18(7):1073–1101. <https://doi.org/10.1093/plankt/18.7.1073>
- Böttger-Schnack R (1997) Vertical structure of small metazoan plankton, especially non-calanoid copepods. II. Deep Eastern Mediterranean (Levantine Sea). *Oceanol Acta* 20:399–419. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78337>
- Böttger-Schnack R (1999) 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* 96:37–128
- Böttger-Schnack R (2001) Taxonomy of Oncaeidae (Copepoda, Poecilostomatoida) from the Red Sea. II. Seven species of *Oncaea* s.str. *Bull Br Mus Nat Hist London (Zool)* 67(1):25–84
- Böttger-Schnack R (2002) Taxonomy of Oncaeidae (Copepoda, Poecilostomatoida) from the Red Sea. VI. Morphology and zoogeography of *Oncaea bispinosa* sp. nov., a sistertaxon of *O. zernovi* Shmeleva. *J Plankton Res* 24(11):1107–1129. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78341>
- Böttger-Schnack R (2003) Taxonomy of Oncaeidae (Copepoda, Poecilostomatoida) from the Red Sea. V. Three species of *Spinoncaea* gen. nov. (*ivlevi*-group), with notes on zoogeographical distribution. *Zool J Linnean Soc* 137(2):187–226. <https://doi.org/10.1046/j.1096-3642.2003.00056.x>
- Böttger-Schnack R (2005) Taxonomy of Oncaeidae (Copepoda: Cyclopoida) from the Red Sea. VII. *Oncaea cristata*, a new species related to the *ovalis*-complex, and a revision of *O. ovalis* Shmeleva and *O. bathyalis* Shmeleva from the Mediterranean. *Cah Biol Mar* 46:161–209
- Böttger-Schnack R (2009) Taxonomy of Oncaeidae (Copepoda, Cyclopoida s.l.) from the Red Sea. IX. *Epicalymma bulbosa* sp. nov., first record of the genus in the Red Sea. *J Plankton Res* 31(9):1027–1043. <https://doi.org/10.1093/plankt/fbp051>
- Böttger-Schnack R (2011) Taxonomic re-examination and distribution of copepods reported as *Oncaea notopus* Giesbrecht, 1891 (Copepoda, Oncaeidae) in the Mediterranean Sea. *Mar Biodiv* 41:325–341. <https://doi.org/10.1007/s12526-010-0072-x>
- Böttger-Schnack R, Boxshall GA (1990) Two new *Oncaea* species (Copepoda: Poecilostomatoida) from the Red Sea. *J Plankton Res* 12 (4):861–871. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=72143>
- Böttger-Schnack R, Huys R (1997a) *Archioncaea arabica* gen. et sp. nov., a remarkable oncaeid (Copepoda: Poecilostomatoida) from the northern Arabian Sea. *Cahiers de Biologie Marine* 38:79–89. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=72144>
- Böttger-Schnack R, Huys R (1997b) Morphological observations on *Oncaea mediterranea* (Claus, 1863) (Copepoda, Poecilostomatoida) with a comparison of Red Sea and eastern Mediterranean populations. *Bull Br Mus Nat Hist London (Zool)* 63(2):137–147. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=72149>
- Böttger-Schnack R, Huys R (1998) Species groups within the genus *Oncaea* Philippi, 1843 (Copepoda, Poecilostomatoida). *J Mar Syst* 15:369–371
- Böttger-Schnack R, Huys R (2001) Taxonomy of Oncaeidae (Copepoda, Poecilostomatoida) from the Red Sea. III. Morphology and phylogenetic position of *Oncaea subtilis* Giesbrecht, 1892. *Hydrobiologia* 453/454:467–481.
- Böttger-Schnack R, Huys R (2004) Size polymorphism in *Oncaea venusta* Philippi, 1843 and the validity of *O. frosti* Heron, 2002: a commentary. *Hydrobiologia* 513(1):1–5. <https://doi.org/10.1023/B:hydr.0000018301.50664.3d>
- Böttger-Schnack R, Machida RJ (2011) Comparison of morphological and molecular traits for species identification and taxonomic grouping of oncaeid copepods. *Hydrobiologia* 666:111–125. <https://doi.org/10.1007/s10750-010-0094-1>
- Böttger-Schnack R, Schnack D (2005) Population structure and fecundity of the microcopepod *Oncaea bispinosa* in the Red Sea—a challenge to general concepts for the scaling of fecundity. *Mar Ecol Prog Ser* 302:159–175. <https://doi.org/10.3354/meps302159>
- Böttger-Schnack R, Schnack D (2009) Taxonomic diversity and identification problems of oncaeid microcopepods in the Mediterranean Sea. *Mar Biodiv* 39(2):131–145. <https://doi.org/10.1007/s12526-009-0013-8>
- Böttger-Schnack R, Schnack D (2013) Definition of species groups of Oncaeidae (Copepoda: Cyclopoida) as basis for a worldwide identification key. *J Nat Hist* 47(5–12):265–288. <https://doi.org/10.1080/00222933.2012.708453>
- Böttger-Schnack R, Schnack D (2016–2022) Oncaeidae of the World Ocean—Interactive identification key for female Oncaeidae (Copepoda)—OncIdent. Available at: <https://rb-schnack.de/login-for-identification-key.html> accessed at.
- Böttger-Schnack R, Schnack D (2019) OncIdent—an interactive identification key for Oncaeidae Giesbrecht, 1893 [“1892”] (Copepoda: Cyclopoida). *Mar Biodiv* 49(2):1043–1046. <https://doi.org/10.1007/s12526-018-0863-z>
- Böttger-Schnack R, Schnack D, Weikert H (1989) Biological observations on small cyclopoid copepods in the Red Sea. *J Plankton Res*

- 11(5):1089–1101. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=72127>
- Böttger-Schnack R, Schnack D, Hagen W (2008) Microcopepod community structure in the Gulf of Aqaba and northern Red Sea, with special reference to Oncaeidae. *J Plankton Res* 30(5):529–550. <https://doi.org/10.1093/plankt/fbn018>
- Boxshall GA (1977a) The planktonic copepods of the northeastern Atlantic Ocean: some taxonomic observations on the Oncaeidae (Cyclopoida). *Bull Br Museum (Natl Hist) Zool* 31(3):103–155. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78534>
- Boxshall GA (1977b) The depth distribution and community organisation of the planktonic cyclopoids (Crustacea: Copepoda) of the Cape Verde Islands region. *J Mar Biol Assoc UK* 57:543–568. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78537>
- Boxshall GA, Böttger R (1987) Two new species of *Oncaea* (Copepoda: Poecilostomatoidea) from the Red Sea and a redescription of *O. atlantica* Shmeleva. *J Plankton Res* 9(3):553–564. <https://doi.org/10.1093/plankt/9.3.553>
- Boxshall GA, Halsey S (2004) An introduction to copepod diversity. *Ray Soc Lond* 166:1–966. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=78616>
- Brugnano C, Granata A, Guglielmo L, Zagami G (2012) Spring diel vertical distribution of copepod abundances and diversity in the open Central Tyrrhenian Sea (Western Mediterranean). *J Mar Syst* 105–108:207–220. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=406088>
- Bucklin A, Peijnenburg KTCA, Kosobokova KN, O'Brien TD, Blanco-Bercial L, Cornils A, Falkenhaus T, Hopcroft RR, Hosia A, Laakmann S, Li C, Martell L, Questel JM, Wall-Palmer D, Wang M, Wiebe PH, Weydmann-Zwolicka A (2021) Toward a global reference database of COI barcodes for marine zooplankton. *Mar Biol* 168:78. <https://doi.org/10.1007/s00227-021-03887-y>
- Bunker AJ, Hirst AG (2004) Fecundity of marine planktonic copepods: global rates and patterns in relation to chlorophyll a, temperature and body weight. *Mar Ecol Prog Ser* 279:161–181. <https://doi.org/10.3354/meps279161>
- Calbet A, Garrido S, Saiz E, Alcaraz M, Duarte CM (2001) Annual zooplankton succession in coastal NW mediterranean waters: the importance of the smaller size fractions. *J Plankton Res* 23(3):319–331. <https://doi.org/10.1093/plankt/23.3.319>
- Checkley DM, Uye S, Dagg MJ, Mullin MM, Omori M, Onbe T, Zhu M-Y (1992) Diel variation of the zooplankton and its environment at neritic stations in the Inland Sea of Japan and the north-west Gulf of Mexico. *J Plankton Res* 14:1–40. <http://plankt.oxfordjournals.org/>
- Cho K, Kim W-S, Böttger-Schnack R, Lee W (2013) A new species of the *dentipes*-subgroup of *Triconia* and a redescription of *T. giesbrechti* and *T. elongata* (Copepoda: Cyclopoida: Oncaeidae) from the tropical Pacific and the Korea Strait. *J Natl Hist* 47(25–28):1707–1743. <https://doi.org/10.1080/00222933.2013.771757>
- Cho K, Kim W, Lee W (2017) Redescription of two species of *Triconia* (Copepoda, Cyclopoida, Oncaeidae) based on their first records in the tropical Pacific. *Kor J Environ Biol* 35(1):64–82. <https://doi.org/10.11626/KJEB.2017.35.1.064>
- Cho K, Böttger-Schnack R, Kim W-S, Lee W (2019) Two new species of the *similis*-subgroup of *Triconia* Böttger-Schnack, 1999 (Copepoda, Oncaeidae) and a redescription of *T. denticula* Wi, Shin & Soh, 2011 from the northeastern equatorial Pacific. *Zoosystema* 41(1):567–593. <https://doi.org/10.5252/zoosystema.2019v41a28>
- Cho K, Kim JG, Lee J (2020) New record of *Oncaea prendeli* (Copepoda, Cyclopoida, Oncaeidae) in Korean waters. *Ocean Polar Res* 42:283–292
- Cho K, Park C, Böttger-Schnack R (2021) Taxonomy of three species of the genus *Spinoncaea* (Copepoda, Oncaeidae) in the North Pacific Ocean with focus on morphological variability. *ZooKeys* 1043:147–191. <https://doi.org/10.3897/zookeys.1043.64438>
- Chojnacki J, Węgleńska T (1984) Periodicity of composition, abundance, and vertical distribution of summer zooplankton (1977/1978) in Ezcurra Inlet, Admiralty Bay (King George Island, South Shetland). *J Plankton Res* 6(6):997–1017. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=72794>
- Claus C (1863) Die frei lebenden Copepoden mit besonderer Berücksichtigung der Fauna Deutschlands, der Nordsee und des Mittelmeeres. Verlag von Wilhelm Engelmann, Leipzig:1–230, pls.1–37. <https://doi.org/10.5962/bhl.title.11418>
- Cornils A (2015) Non-destructive DNA extraction for small pelagic copepods to perform integrative taxonomy. *J Plankton Res* 37(1):6–10. <https://doi.org/10.1093/plankt/fbu105>
- Cruz J, Cerveira I, Andrade I, Baptista V, Teodósio MA (2021) Prey selectivity and feeding rates of the scyphozoan *Catostylus tagi* (Haeckel 1869). *J Plankton Res* 43(6):986–990. <https://doi.org/10.1093/plankt/fbab065>
- Dagg MJ, Govoni JJ (1996) Is ichthyoplankton predation an important source of copepod mortality in subtropical coastal waters? *Mar Freshw Res* 47(2):137–144. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=83199>
- Darnis G, Fortier L (2014) Temperature, food and the seasonal vertical migration of key arctic copepods in the thermally stratified Amundsen Gulf (Beaufort Sea, Arctic Ocean). *J Plankton Res* 36(4):1092–1108. <https://doi.org/10.1093/plankt/fbu035>
- Delalo EP (1966) The zooplankton of the eastern Mediterranean (Levantine Sea and Gulf of Sirte). *Issled. Plankt. Juzhn. Mor. Okeanogr. Kom. Akad. Nauk S.S.S.R.* 7:62–81 (in Russian)
- Di Capua I, Maffucci F, Pannone R, Mazzocchi MG, Biffali E, Amato A (2017) Molecular phylogeny of Oncaeidae (Copepoda) using nuclear ribosomal internal transcribed spacer (ITS rDNA). *PLoS One* 12(4):e0175662. <https://doi.org/10.1371/journal.pone.0175662>
- Di Capua I, Piredda R, Mazzocchi MG, Zingone A (2021) Metazoan diversity and seasonality through eDNA metabarcoding at a Mediterranean long-term ecological research site. *ICES J Mar Sci* 78(9):3303–3316. <https://doi.org/10.1093/icesjms/fsab059>
- Elvers D, Böttger-Schnack R, Blohm D, Hagen W (2006) Sympatric size variants of the microcopepod *Oncaea venusta* exhibit distinct lineages in DNA sequences. *Mar Biol* 149:503–513. <https://doi.org/10.1007/s00227-005-0234-8>
- Ershova EA, Hopcroft RR, Kosobokova KN (2015) Inter-annual variability of summer mesozooplankton communities of the western Chukchi Sea: 2004–2012. *Polar Biol* 38(9):1461–1481. <https://doi.org/10.1007/s00300-015-1709-9>
- Ershova EA, Wangenstein OS, Descoteaux R, Barth-Jensen C, Præbel K (2021) Metabarcoding as a quantitative tool for estimating biodiversity and relative biomass of marine zooplankton. *ICES J Mar Sci* 78(9):3342–3355. <https://doi.org/10.1093/icesjms/fsab171>
- Eslake D, Kirkwood R, Burton H, Zipan W (1991) Temporal changes in zooplankton composition in a hypersaline, Antarctic lake subject to periodic seawater incursions. *Hydrobiologia* 210(1–2):93–99. <https://doi.org/10.1007/BF00014325>
- Falkenhaus T, Dalpadado P (2014) Diet composition and food selectivity of sprat (*Sprattus sprattus*) in Hardangerfjord, Norway. *Mar Biol Res* 10(3):203–215. (online 2013). <https://doi.org/10.1080/17451000.2013.810752>
- Farran GP (1908) Second report on the Copepoda of the Irish Atlantic slope. Report on the Sea and Inland Fisheries of Ireland for 1906.2. Scientific Investigations, Ireland, 2:19–120. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=86311>

- Farran GP (1929) Crustacea. Part X.-Copepoda. Natural History Report of the British Museum, British Antarctic ('Terra Nova') Expedition 1910, Zoology 8:203–306. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=86324>
- Farran GP (1936) Copepoda. Great barrier reef expedition 1928–29, Scientific Reports, British Museum (Natural History), London: 73–142. <https://www.biodiversitylibrary.org/page/49513487#page/115/mode/1up>
- Favareto L, Perbiche-Neves G, Serafim-Júnior M, Sartori L (2009) Selectivity of plankton nets over planktonic Copepoda in two sub-tropical estuaries. Seletividade de redes de plâncton sobre Copepoda planctônicos em dois estuários sub-tropicais. Acta Limnol Brasil 21(1):67–77. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=410833>
- Fortier M, Fortier L, Hattori H, Saito H, Legendre L (2001) Visual predators and the diel vertical migration of copepods under Arctic sea ice during the midnight sun. J Plankton Res 23(11):1263–1278
- Franz HG (1988) Vernal abundance, structure and development of epipelagic copepod populations of the eastern Weddell Sea (Antarctica). Polar Biol 9:107–114. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=87303>
- Früchtl F (1923) Cladocera und Copepoda der Aru-Inseln. (Vorläufige Mitteilung: artenliste und kurze Diagnosen der neuen Formen). Abhandlungen Senckenbergische Naturforschende Gesellschaft 35:449–457. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=87519>
- Fyttis G, Demetriou M, Di Capua I, Samuel-Rhoads Y (2015) Observations on the reproductive biology of two cyclopoid copepods: *Oncaea media* and *O. scottodicarloi*. Geophys Res Abstr 17:EGU2015–10559.
- Gallienne CP, Robins DB (2001) Is *Oithona* the most important copepod in the world's oceans? J Plankton Res 23(12):1421–1432
- Gaudy R, Boucher J (1983) Relation between respiration, excretion (ammonia and inorganic phosphorus) and activity of amylase and trypsin in different species of pelagic copepods from an Indian Ocean equatorial area. Mar Biol Berlin 75:37–45. <https://doi.org/10.1007/BF00392628>
- Giesbrecht W (1891) Elenco dei Copepodi pelagici raccolti dal Tenente di vascello Gaetano Chierchia durante il viaggio della R. Corvetta "Vettor Pisani" negli anni 1882–1885 e dal Tenente di vascello Francesco Orsini nel Mar Rosso, nel 1884. Atti Della Reale Accademia Nazionale Dei Lincei, Classe Di Scienze Fisiche Matematiche e Naturali Rendiconti 7(10):474–481. <https://www.biodiversitylibrary.org/page/44535672>
- Giesbrecht W (1892–1893) Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Fauna und Flora des Golfes von Neapel und der Angrenzenden Meeres-Abschnitte, Herausgegeben von der Zoologischen Station zu Neapel 19:1–831, pls. 1–54
- Giesbrecht W (1895) Mittheilungen über Copepoden 7–9. Mittheilungen aus der Zoologischen Station zu Neapel 11:631–694. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=88648>
- Giesbrecht W (1896) Über pelagische Copepoden des Rothen Meeres, gesammelt vom Marinestabsarzt Dr. Augustin Krämer. Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere 9:315–328, pls. 1–2. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=88653>
- Giesbrecht W (1902) Zoologie Copepoden. In: Résultats du voyage du S.Y. Belgica en 1897–1898–1899. Rapports scientifiques publiés aux frais du Gouvernement Belge 1–49, pls. 1–13
- Gilmer RW, Harbison GR (1986) Morphology and field behavior of pteropod molluscs: feeding methods in the families Cavoliniidae, Limacinidae and Peraclididae (Gastropoda: Thecosomata). Mar Biol 91(1):47–57. <https://doi.org/10.1007/bf00397570>
- Go YB, Oh BC, Terazaki M (1998) Feeding behaviour of the poecilosomatoid copepods *Oncaea* spp. on chaetognaths. In: Dahms HU, Glatzel T, Hirche HJ, Schiel S, Schminke HK (eds) Proceedings of the 6th International Conference on Copepoda, Journal of Marine Systems Spec. 15:475–482. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=77284>
- Gonzalez HE, Kurbjewit F, Bathmann UV (1994) Occurrence of cyclopoid copepods and faecal material in the Halley Bay region, Antarctica, during January–February 1991. Polar Biol 14(5):331–342. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=89151>
- Gordeeva KT (1972) Novye vidy roda *Oncaea* (Copepoda, Cyclopoida) iz tropicheskoi zony Atlanticheskogo okeana. New species of the genus *Oncaea* (Copepoda, Cyclopoida) from the tropical zone of the Atlantic Ocean. Zoologicheskii Zhurnal 51(7):963–968. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=89249>
- Gordeeva KT (1973) Novye vidy veslonogikh rachkov roda *Oncaea* (Cyclopoida) iz tropicheskoi Atlantiki. New species of the genus *Oncaea* (Cyclopoida) from the tropic Atlantic. Zoologicheskii Zhurnal 52(10):1572–1576. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=89250>
- Gordeeva KT (1975a) Pelagicheskie Cyclopoida (Copepoda) iz tropicheskoi Atlantiki i Yuzhnykh morei. Pelagic cyclopoids from the tropical Atlantic and the southern seas. Zoologicheskii Zhurnal 54(5):776–779. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=89256>
- Gordeeva KT (1975b) Novyi vid roda *Oncaea* (Copepoda) iz batipelagiali tropicheskoi zony Atlantiki i Meksikanskogo zaliva. A new species of the genus *Oncaea* (Copepoda) from the bathypelagial in the tropic zone of the Atlantic and Gulf of Mexico. Zoologicheskii Zhurnal 54(9): 1397–1399. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=89257>
- Gordeeva KT, Shmeleva AA (1973) Pelagic copepods of the tropical Atlantic and the peculiarities of distribution of their mass species. Pelagicheskie kopepody tropicheskoi Atlantiki i osobennosti raspredeleniya ikh massovykh vidov. In: Vidovoi sostav i raspredelenie okeanicheskogo planktona (Species composition and distribution of the oceanic plankton) Trudy vses gidrobiol Obshch 20:109–143. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=89259>
- Gorelova TA (1974) Zooplankton from the stomachs of juvenile lantern fish of the family Myctophidae. Oceanology 14:575–580. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=158498>
- Govoni JJ, Ortner PB, Al-Yamani F, Hill LC (1986) Selective feeding of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae in the northern Gulf of Mexico. Mar Ecol Prog Ser 28:175–183
- Green EP, Dagg MJ (1997) Mesozooplankton associations with medium to large marine snow aggregates in the northern Gulf of Mexico. J Plankton Res 19(4):435–447. <https://doi.org/10.1093/plankt/19.4.435>
- Groendahl F, Hernroth L (1986) Vertical distribution of copepods in the Eurasian part of the Nansen Basin, Arctic Ocean. In: Schriever G, Schminke HK, Shih C-T (eds) Proceedings of the Second International Conference on Copepoda, Ottawa, Canada, 13–17 August, 1984. Syllogeus 58:311–320. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=89998>
- Guidi-Guilvard LD, Thistle D, Khripounoff A, Gasparini S (2009) Dynamics of benthic copepods and other meiofauna in the benthic boundary layer of the deep NW Mediterranean Sea. Mar Ecol Prog Ser 396:181–195. <https://doi.org/10.3354/meps08408>
- Hanaoka T (1952) On nauplius of *Oncaea mediterranea* and *Corycaeus* sp. Bull Naikai Reg Fish Res Lab 1:37–41. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=90783>

- Harris RP, Wiebe PH, Lenz J, Skjoldal HR, Huntley H (eds) (2000) ICES zooplankton methodology manual. In: International Council for the Exploration of the Seas, Academic Press, London & San Diego:1–648. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=91050>
- Hernández-León S, Ikeda T (2005) A global assessment of mesozooplankton respiration in the ocean. *J Plankton Res* 27(2):153–158. <https://doi.org/10.1093/plankt/fbh166>
- Heron GA (1977) Twenty-six species of Oncaeidae (Copepoda: Cyclopoida) from the southwest Pacific-Antarctic area. In: Pawson DL (ed) *Biology of the Antarctic Seas*, 6. Antarctic Research Series, Washington, 26(2):37–96. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=92081>
- Heron GA (2002) *Oncaea frosti*, a new species (Copepoda: Poecilostomatoida) from the Liberian coast and the Gulf of Mexico. In: Lee CE, Strom S, Yen J (eds) *Progress in Zooplankton Biology: Ecology, and Behavior*, Hydrobiologia, Kluwer Academic Publishers, The Netherlands 480:145–154. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=92082>
- Heron GA, Bradford-Grieve JM (1995) The marine fauna of New Zealand: Pelagic Copepoda: Poecilostomatoida: Oncaeidae. New Zealand Oceanographic Institute Memoir, Wellington 104:1–57. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=89473>
- Heron GA, Frost BW (2000) Copepods of the family Oncaeidae (Crustacea: Poecilostomatoida) in the northeast Pacific Ocean and inland coastal waters of Washington State. *Proc Biol Soc Wash* 113(4):1015–1063. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=92083>
- Heron GA, English TS, Damkaer DM (1984) Arctic Ocean Copepoda of the genera *Lubbockia*, *Oncaea*, and *Epicalymma* (Poecilostomatoida: Oncaeidae), with remarks on distributions. *J Crust Biol* 4(3):448–490. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=89475>
- Herring PJ, Latz MI, Bannister NJ, Widder EA (1993) Bioluminescence of the poecilostomatoid copepod *Oncaea conifera*. *Mar Ecol Prog Ser* 94(3):297–309. <https://doi.org/10.3354/meps094297>
- Hirai J, Tsuda A (2015) Metagenetic community analysis of epipelagic planktonic copepods in the tropical and subtropical Pacific. *Mar Ecol Prog Ser* 534:65–78. <https://doi.org/10.3354/meps11404>
- Hirai J, Tachibana A, Tsuda A (2020) Large-scale metabarcoding analysis of epipelagic and mesopelagic copepods in the Pacific. *PLoS One* 15(5):0233189. <https://doi.org/10.1371/journal.pone.0233189>
- Hirai J, Hidaka K, Nagai S, Shimizu Y (2021) DNA/RNA metabarcoding and morphological analysis of epipelagic copepod communities in the Izu Ridge off the southern coast of Japan. *ICES J Mar Sci* 78(9):3444–3456. <https://doi.org/10.1093/icesjms/fsab064>
- Hirakawa K (1995) Effects of temperature on egg production of a warm-water copepod *Oncaea venusta* Philippi (Poecilostomatoida). *Bull Jpn Sea Natl Fish Res Inst* 45:39–45. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=92589>
- Hirsch S, Christiansen B (2010) The trophic blockage hypothesis is not supported by the diets of fishes on Seine Seamount. *Mar Ecol* 31(SUPPL. 1):107–120. <https://doi.org/10.1111/j.1439-0485.2010.00366.x>
- Hirst AG, Bunker AJ (2003) Growth of marine planktonic copepods: global rates and patterns in relation to chlorophyll a, temperature, and body weight. *Limnol Oceanogr* 48(5):1988–2010. <https://doi.org/10.4319/lo.2003.48.5.1988>
- Hirst AG, Kiørboe T (2002) Mortality of marine planktonic copepods: global rates and patterns. *Mar Ecol Prog Ser* 230:195–209. <https://doi.org/10.3354/meps230195>
- Ho JS (1984) Copepoda associated with sponges, cnidarians, and tunicates of the Sea of Japan. In: Report of the Sado Marine Biological Station, Niigata University 14:21–63. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=24546>
- Hopcroft RR, Roff JC (1998) Zooplankton growth rates: the influence of female size and resources on egg production of tropical marine copepods. *Mar Biol* 132:79–86. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=91398>
- Hopcroft RR, Roff JC, Lombard D (1998) Production of tropical copepods in Kingston Harbour, Jamaica: the importance of small species. *Mar Biol* 130(4):593–604. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=93056>
- Hopcroft RR, Roff JC, Chavez FP (2001) Size paradigms in copepod communities: a re-examination. *Hydrobiologia* 453(1):133–141. <https://doi.org/10.1023/A:1013167917679>
- Hopcroft RR, Clarke C, Nelson RJ, Raskoff KA (2005) Zooplankton communities of the Arctic's Canada Basin: the contribution by smaller taxa. *Polar Biol* 28(3):198–206. <https://doi.org/10.1007/s00300-004-0680-7>
- Hopcroft RR, Kosobokova KN, Pinchuk AI (2010) Zooplankton community patterns in the Chukchi Sea during summer 2004. *Deep Sea Res Part II: Top Stud Oceanogr* 57(1–2):27–39. <https://doi.org/10.1016/j.dsr2.2009.08.003>
- Hopkins TL (1985) Food web of an Antarctic midwater ecosystem. *Mar Biol* 89(2):197–212. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=5447>
- Hopkins TL (1987) Midwater food web in McMurdo Sound, Ross Sea, Antarctica. *Mar Biol* 96:93–106. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=14568>
- Hopkins TL, Baird RC (1985a) Feeding ecology of four hatchetfishes (Sternoptychidae) in the eastern Gulf of Mexico. *Bull Mar Sci* 36(2):260–277. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=193474>
- Hopkins TL, Baird RC (1985b) Aspects of the trophic ecology of the mesopelagic fish *Lamppanyctus alatus* (Family Myctophidae) in the eastern Gulf of Mexico. *Biol Oceanogr* 3:285–313. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=93090>
- Hopkins TL, Torres JJ (1988) The Zooplankton Community in the Vicinity of the Ice Edge, Western Weddell Sea, March 1986. *Polar Biol* 9:79–87. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=5448>
- Horne CR, Hirst AG, Atkinson D, Neves A, Kiørboe T (2016) A global synthesis of seasonal temperature–size responses in copepods. *Glob Ecol Biogeogr* 25(8):988–999. <https://doi.org/10.1111/geb.12460>
- Hoshiai T, Tanimura A (1986) Sea ice meiofauna at Syowa Station, Antarctica. In: *Memoirs of the National Institute of Polar Research Special Issue, Proceedings of the Eighth Symposium on Polar Biology*, Tokyo 44:118–124. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=193476>
- Huys R, Böttger-Schnack R (1996–1997) On the Diphyletic origin of the Oncaeidae Giesbrecht, 1892 (Copepoda: Poecilostomatoida) with a phylogenetic analysis of the Lubbockidae fam. nov. *Zoologischer Anzeiger* 235(3–4):243–261
- Huys R, Boxshall G (1991) Copepod evolution, vol 159. Ray Society, London. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=93637>
- Hwang JS, Turner JT (1995) Behaviour of cyclopoid, harpacticoid, and calanoid copepods from coastal waters of Taiwan. *Mar Ecol* 16(3):207–216. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=93690>
- Ikeda T, Kanno Y, Ozaki K, Shinada A (2001) Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. *Mar Biol* 139(3):587–596. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=92192>
- Itoh H, Nakata K, Sasaki K, Ichikawa T, Hidaka K (2014) Seasonal and diel changes in the vertical distribution of oncaeid

- copepods in the epipelagic zone of the Kuroshio Extension region. *Plankton Benthos Res* 9(1):1–14
- Judkins DG (1980) Vertical distribution of zooplankton in relation to the oxygen minimum off Peru. *Deep Sea Res Part A Oceanogr Res Pap* 27A:475–487. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=95288>
- Kattner G, Albers C, Graeve M, Schnack-Schiel SB (2003) Fatty acid and alcohol composition of the small polar copepods, *Oithona* and *Oncaea*: indication on feeding modes. *Polar Biol* 26(10):666–671. <https://doi.org/10.1007/s00300-003-0540-x>
- Kawamura A, Hamaoka S (1981) Feeding habits of the gonostomatid fish, *Vinciguerria nimbaria* collected from the stomach of Bryde's whales in the southwestern north Pacific. *Bulletin of Plankton Society of Japan* 28(2):141–151. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=206581>
- Kazachenko VN, Avdeev GV (1977) Paraziticheskie kopepody (Copepoda, Crustacea) v sborakh 57-go reisa NIS "Vityaz" v zapadnoi tropicheskoi chasti Tikhogo okeana i moryakh Indomalaiskogo arhipelaga. Parasitic copepods (Crustacea) collected during the 57th cruise of the RV "Vityaz" in the western tropical Pacific and seas of the Indo-malayan Archipelago. *Glubokovodnye Biologicheskie Issledovaniya v Zapadnoi Tropicheskoi Chasti Tikhogo Okeana. Trudy Instituta Okeanologii Jmeni PP Sirsova* 107:30–48. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=96117>
- Kersten O (2015) Abyssal near-bottom zooplankton in the Eastern Tropical North Pacific. MSc Thesis, Hawaii Pacific University pp1–192.
- Khodami S, McArthur JV, Blanco-Bercial L, Martinez Arbizu P (2017) Molecular phylogeny and revision of copepod orders (Crustacea: Copepoda). *Sci Rep* 7(1):1–11. <https://doi.org/10.1038/s41598-017-06656-4>
- Khodami S, Mercado-Salas NF, Tang D, Martinez Arbizu P (2018) Molecular evidence for the retention of the Thaumtopsyllidae in the order Cyclopoida (Copepoda) and establishment of four suborders and two families within the Cyclopoida. *Mol Phylogenet Evol* 138(September 2018):43–52. <https://doi.org/10.1016/j.ympev.2019.05.019>
- Kiko R, Michels J, Mizdalski E, Schnack-Schiel SB, Werner I (2008) Living conditions, abundance and composition of the metazoan fauna in surface and sub-ice layers in pack ice of the western Weddell Sea during late spring. *Deep Sea Res Part II Top Stud Oceanogr* 55(8–9):1000–1014. <https://doi.org/10.1016/j.dsr2.2007.12.012>
- Kjørboe T (2000) Colonization of marine snow aggregates by invertebrate zooplankton: abundance, scaling, and possible role. *Limnol Oceanogr* 45(2):479–484. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=96971>
- Klekowski RZ, Kukina IV, Tumantseva NI (1977) Respiration in the microzooplankton of the equatorial upwellings in the eastern Pacific Ocean. In: *Pelagic ecosystems of the eastern Pacific Ocean upwellings. 17th cruise of the R/V "Akademic Kurchatov"*. *Polskie Archiwum Hydrobiologii* 24 (Suppl.): 467–489. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=97149>
- Kobari T, Tokumo Y, Sato I, Kume G, Hirai J (2021) Metabarcoding analysis of trophic sources and linkages in the plankton community of the Kuroshio and neighboring waters. *Sci Rep* 11(1):23265. <https://doi.org/10.1038/s41598-021-02083-8>
- Koga F (1984) Morphology, ecology, classification and specialization of copepods nauplius. *Bull Nansei Reg Fish Res Lab* 16:95–229. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=92315>
- Kosikhina OV (1980) Pitanie morskikh veslonogikh rachkov roda *Oncaea* (Cyclopoida). Nutrition of marine Copepoda of the *Oncaea* genus (Cyclopoida). *Ekologiya Morya* 4:46–49. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=92336>
- Koski M, Lombard F (2022) Functional responses of aggregate-colonizing copepods. *Limnol Oceanogr* 67(9):2059–2072. <https://doi.org/10.1002/lno.12187>
- Koski M, Møller EF, Maar M, Visser AW (2007) The fate of discarded appendicularian houses: degradation by the copepod, *Microsetella norvegica*, and other agents. *J Plankton Res* 29(7):641–654. <https://doi.org/10.1093/plankt/fbm046>
- Koski M, Boutorh J, De La Rocha C (2017) Feeding on dispersed vs. aggregated particles: the effect of zooplankton feeding behavior on vertical flux. *PLoS One* 12(5):e0177958. <https://doi.org/10.1371/journal.pone.0177958>
- Koski M, Valencia B, Newstead R, Thiele C (2020) The missing piece of the upper mesopelagic carbon budget? Biomass, vertical distribution and feeding of aggregate-associated copepods at the PAP site. *Prog Oceanogr* 181:102243. <https://doi.org/10.1016/j.pocean.2019.102243>
- Koski M, Swaethorp R, Kjellerup S, Nielsen TG (2021) Aggregate-colonizing copepods in a glacial fjord: Population dynamics, vertical distribution and allometric scaling of growth and mortality rates of *Microsetella norvegica* and *Oncaea* spp. *Prog Oceanogr* 197:102670. <https://doi.org/10.1016/j.pocean.2021.102670>
- Kršinić F (1980) Comparison of methods used in micro-zooplankton research in neritic waters of the eastern Adriatic. *Nova Thalassia* 4:91–106. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=407761>
- Kršinić F, Viličić D (1989) Microzooplankton in the Kotor Bay, (The southern Adriatic). *Mikrozooplankton u kotorskom zaljevu (Juzni Jadran)*. *Studia Marina, Kotor, Yugoslavia* 20:3–20. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=407881>
- Kršinić F, Bojanić D, Precali R, Kraus R (2007) Quantitative variability of the copepod assemblages in the northern Adriatic Sea from 1993 to 1997. *Estuar Coast Shelf Sci* 74(3):528–538. <https://doi.org/10.1016/j.ecss.2007.05.036>
- Kršinić F, Čalić M, Carić M (2016) The population structure of planktonic protists and small metazoans in Mali Ston Bay (Adriatic Sea)—implications for determination of trophic state and shellfish culturing potential. *Acta Adriat* 57(1):17–38
- Kršinić F, Böttger-Schnack R, Vidjak O (2020) Small copepods of the deep South Adriatic Pit: diversity, seasonal and multi-annual dynamics, and implications from the regional hydrography. *Environ Monit Assess* 192(8):545. <https://doi.org/10.1007/s10661-020-08462-4>
- Kuei HYN, Björnberg TKS (2003) Developmental stages of *Oncaea curta* Sars, 1916 (Copepoda, Poecilostomatoida). *Nauplius* 10(1):1–14. [for 2002] <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=98158>
- Laakmann S, Blanco-Bercial L, Cornils A (2020) The crossover from microscopy to genes in marine diversity: from species to assemblages in marine pelagic copepods. *Philos Trans R Soc B Biol Sci* 375:1814. <https://doi.org/10.1098/rstb.2019.0446rstb20190446>
- Lampitt RS, Wishner KF, Turley CM, Angel MV (1993) Marine snow studies in the Northeast Atlantic Ocean: distribution, composition and role as a food source for migrating plankton. *Mar Biol* 116:689–702. <https://doi.org/10.1007/BF00355486>
- LeBrasseur RJ, Kennedy OD (1972) Microzooplankton in coastal and oceanic areas of the Pacific Subarctic Water Mass: a preliminary report. In: Takenouti AY (ed) *Biological Oceanography of the northern North Pacific Ocean*. Dedicated to Sigeru Motoda. Idenmitsu Shoten, Tokyo, 355–365. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=99199>
- Lindeque PK, Parry HE, Harmer RA, Somerfield PJ, Atkinson A (2013) Next generation sequencing reveals the hidden diversity

- of zooplankton assemblages. *PLoS One* 8(11):e81327. <https://doi.org/10.1371/journal.pone.0081327>
- Lischka S, Hagen W (2016) Seasonal dynamics of mesozooplankton in the Arctic Kongsfjord (Svalbard) during year-round observations from August 1998 to July 1999. *Polar Biol* 39(10):1859–1878. <https://doi.org/10.1007/s00300-016-2005-z>
- Lučić D, Hure M, Bobanović-Čolić S, Njire J, Vidjak O, Onofri I, Gangai Zovko B, Batistić M (2019) The effect of temperature change and oxygen reduction on zooplankton composition and vertical distribution in a semi-enclosed marine system. *Mar Biol Res* 15(4–6):325–342. <https://doi.org/10.1080/17451000.2019.1655161>
- Lundgreen RBC, Jaspers C, Traving SJ, Ayala DJ, Lombard F, Grosart HP, Nielsen TG, Munk P, Riemann L (2019) Eukaryotic and cyanobacterial communities associated with marine snow particles in the oligotrophic Sargasso Sea. *Sci Rep* 9(1):1–12. <https://doi.org/10.1038/s41598-019-45146-7>
- Makabe R, Tanimura A, Fukuchi M (2012) Comparison of mesh size effects on mesozooplankton collection efficiency in the Southern Ocean. *J Plankton Res* 34(5):432–436. <https://doi.org/10.1093/plankt/fbs014>
- Makabe R, Tanimura A, Tamura T, Hirano D, Shimada K, Hashihama F, Fukuchi M (2017) Meso-zooplankton abundance and spatial distribution off Lütjow-Holm Bay during austral summer 2007–2008. *Polar Sci* 12:25–33. <https://doi.org/10.1016/j.polar.2016.09.002>
- Malt SJ (1982a) New and little known species of Oncaeidae (Cyclopoida) from the northeastern Atlantic. *Bull Br Museum (Nat Hist)*, Zool 42(3):185–205. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=101017>
- Malt SJ (1982b) Developmental stages of *Oncaea media* Giesbrecht, 1891 and *Oncaea subtilis* Giesbrecht, 1892. *Bull Br Museum (Nat Hist)*, Zool 43(3):129–151. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=101018>
- Malt SJ (1983a) Polymorphism and pore signature pattern in the copepod genus *Oncaea* (Cyclopoida). *J Mar Biol Assoc UK* 63:449–466. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=101021>
- Malt SJ (1983b) Crustacea, order: Copepoda, suborder: Cyclopoida, family: Oncaeidae, genus: *Oncaea*. Fiches d'Identification Du Zooplancton, Conseil International Pour l'Exploration de La Mer 169–170. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=101019>
- Matthews SA, Goetze E, Ohman MD (2021) Recommendations for interpreting zooplankton metabarcoding and integrating molecular methods with morphological analyses. *ICES J Mar Sci* 78(9):3387–3396. <https://doi.org/10.1093/icesjms/fsab107>
- Mayzaud P, Razouls S, Errhif A, Tirelli V, Labat JP (2002) Feeding, respiration and egg production rates of copepods during austral spring in the Indian sector of the Antarctic Ocean: Role of the zooplankton community in carbon transformation. *Deep Sea Res Part 1 Oceanogr Res Pap* 49(6):1027–1048. [https://doi.org/10.1016/S0967-0637\(02\)00012-2](https://doi.org/10.1016/S0967-0637(02)00012-2)
- McKinnon AD, Duggan S, Böttger-Schnack R, Gusmão LFM, O'Leary RA (2013) Depth structuring of pelagic copepod biodiversity in waters adjacent to an Eastern Indian Ocean coral reef. *J Nat Hist* 47(5–12):639–665. <https://doi.org/10.1080/00222933.2012.673645>
- Melo Júnior M, Miyashita LK, Lopes RM (2021) A 3-year study of the seasonal variability of abundance, biomass and reproductive traits of *Oncaea venusta* (Copepoda, Oncaeidae) in a subtropical coastal area. *J Plankton Res* 43(5):751–761. <https://doi.org/10.1093/plankt/fbab055>
- Metz C (1993) Verbreitung von Cyclopoida (Copepoda, Crustacea) im Weddellmeer. Diploma Thesis, University of Kiel, 1–80 + suppl.
- Metz C (1995) Seasonal variation in the distribution and abundance of *Oithona* and *Oncaea* species (Copepoda, Crustacea) in the south-eastern Weddell Sea, Antarctica. *Polar Biol* 15:187–194. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=103259>
- Metz C (1996) Life strategies of dominant Antarctic Oithonidae (Cyclopoida, Copepoda) and Oncaeidae (Poecilostomatoida, Copepoda) in the Bellingshausen Sea. Lebensstrategien dominanter antarktischer Oithonidae (Cyclopoida, Copepoda) und Oncaeidae (Poecilostomatoida, Copepoda) im Bellingshausenmeer. Ph.D. Dissertation, Universität Kiel; and Berichte zur Polarforschung/Reports on Polar Research 207:1–123. (in German, English Abstract) <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=103260>
- Metz C (1998) Feeding of *Oncaea curvata* (Poecilostomatoida, Copepoda). *Mar Ecol Prog Ser* 169:229–235. <https://doi.org/10.3354/meps169229>
- Miyamoto H, Itoh H, Okazaki Y (2017) Temporal and spatial changes in the copepod community during the 1974–1998 spring seasons in the Kuroshio region; a time period of profound changes in pelagic fish populations. *Deep Sea Res Part I Oceanogr Res Pap* 128:131–140. <https://doi.org/10.1016/j.dsr.2017.07.007>
- Miyashita LK, de Melo JM, Lopes RM (2009) Estuarine and oceanic influences on copepod abundance and production of a subtropical coastal area. *J Plankton Res* 31(8):815–826. <https://doi.org/10.1093/plankt/fbp039>
- Mizdalski E (1988) Weight and length data of zooplankton in the Weddell Sea in austral spring 1986 (ANT V/3). *Berichte zur Polarforschung, Bremerhaven* 55:1–72. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=103751>
- Moulton TP (1973) Principal component analysis of variation in form within *Oncaea conifera* Giesbrecht, 1891, a species of copepod (Crustacea). *Syst Zool* 22(2):141–156. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=101787>
- Munk P, Hansen BW, Nielsen TG, Thomsen HA (2003) Changes in plankton and fish larvae communities across hydrographic fronts off West Greenland. *J Plankton Res* 25(7):815–830
- Munk P, Nielsen TG, Jaspers C, Ayala DJ, Tang KW, Lombard F, Riemann L (2018) Vertical structure of plankton communities in areas of European eel larvae distribution in the Sargasso Sea. *J Plankton Res* 40(4):362–375. <https://doi.org/10.1093/plankt/fby025>
- Nakata K, Koyama S, Matsukawa Y (2001a) Interannual variation in spring biomass and gut content composition of copepods in the Kuroshio current, 1971–89. *Fish Oceanogr* 10(4):329–341. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=104939>
- Nakata K, Matsukawa Y, Shimoda T, Ichikawa T (2001b) Biomass, productivity, and size composition of copepods in the epipelagic zone in the subtropical waters off the Okinawa Main Island, during spring 1996. *Bull Natl Res Inst Far Seas Fish* 16:75–92. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=102850>
- Nakata K, Itoh H, Ichikawa T, Sasaki K (2004) Seasonal changes in the reproduction of three oncaeid copepods in the surface layer of the Kuroshio Extension. *Fish Oceanogr* 13(Suppl. 1):21–33. <https://doi.org/10.1111/j.1365-2419.2004.00316.x>
- Nassogne A (1972) Études Préliminaires Sur Le Rôle du Zooplancton Dans la Constitution et Le Transport de la Matière Organique Au Sein de la Chaîne Alimentaire Marine En Mer Ligure. Ph.D. Thesis, University of Amsterdam, 1–237. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=104985>
- Newbury TK (1978) Consumption and growth rates of chaetognaths and copepods in subtropical oceanic water. *Pacific Sci* 32:61–78. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=105194>

- Nielsen TG, Møller EF, Satapoomin S, Ringuette M, Hopcroft RR (2002) Egg hatching rate of the cyclopoid copepod *Oithona similis* in arctic and temperate waters. *Mar Ecol Prog Ser* 236:301–306. <https://doi.org/10.3354/meps236301>
- Nishibe Y (2005) The biology of oncaeid copepods (Poecilostomatoida) in the Oyashio region, western subarctic Pacific: its community structure, vertical distribution, life cycle and metabolism. Ph.D Thesis, Hokkaido University, 92pp + appendix.
- Nishibe Y, Ikeda T (2004) Vertical distribution, abundance and community structure of oncaeid copepods in the Oyashio region, western subarctic Pacific. *Mar Biol* 145(5):931–941. <https://doi.org/10.1007/s00227-004-1392-9>
- Nishibe Y, Ikeda T (2007a) Vertical distribution, population structure and life cycles of four oncaeid copepods in the Oyashio region, western subarctic Pacific. *Mar Biol* 150:609–625. <https://doi.org/10.1007/s00227-006-0382-5>
- Nishibe Y, Ikeda T (2007b) Laboratory observations on early development of the oncaeid copepod *Triconia canadensis* from the mesopelagic zone of the western subarctic Pacific. *J Mar Biol Assoc UK* 87(2):479–482. <https://doi.org/10.1017/S0025315407055336>
- Nishibe Y, Ikeda T (2008) Metabolism and elemental composition of four oncaeid copepods in the western subarctic Pacific. *Mar Biol* 153:397–404. <https://doi.org/10.1007/s00227-007-0816-8>
- Nishibe Y, Hirota Y, Ueda H (2009) Community structure and vertical distribution of oncaeid copepods in Tosa Bay, southern Japan. *J Mar Biol Assoc UK* 89(3):491–498. <https://doi.org/10.1017/S0025315409003087>
- Nishibe Y, Takahashi K, Ichikawa T, Hidaka K, Kurogi H, Segawa K, Saito H (2015) Degradation of discarded appendicularian houses by oncaeid copepods. *Limnol Oceanogr* 60(3):967–976. <https://doi.org/10.1002/lno.10061>
- Ohtsuka S, Kubo N (1991) Larvaceans and their houses as important food for some pelagic copepods. In: Uye, S.I., S. Nishida, J.S. Ho (eds.). Proceedings of the Fourth International Conference on Copepoda. *Bull Plankton Soc Jpn* 535–551. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=105853>
- Ohtsuka S, Kubo N, Okada M, Gushima K (1993) Attachment and feeding of pelagic copepods on larvacean houses. *J Oceanogr* 49:115–120. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=105886>
- Ohtsuka S, Böttger-Schnack R, Okada M, Onbé T (1996) In situ feeding habits of *Oncaea* (Copepoda: Poecilostomatoida) from the upper 250 m of the central Red Sea, with special reference to consumption of appendicularian houses. *Bull Plankton Soc Jpn* 43(2):89–105. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=105887>
- Ojima M, Takahashi KT, Iida T, Odate T, Fukuchi M (2013) Distribution patterns of micro- and meso-zooplankton communities in sea ice regions of Lützow-Holm Bay East Antarctica. *Polar Biol* 36(9):1293–1304. <https://doi.org/10.1007/s00300-013-1348-y>
- Ojima M, Takahashi KT, Tanimura A, Odate T, Fukuchi M (2015) Spatial distribution of micro- and meso-zooplankton in the seasonal ice zone of east Antarctica during 1983–1995. *Polar Sci* 9(3):319–326. <https://doi.org/10.1016/j.polar.2015.05.002>
- Øresland V (1991) Feeding of the carnivorous copepod *Euchaeta antarctica* in Antarctic waters. *Mar Ecol Prog Ser* 78:41–47. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=365441>
- Paffenhöfer GA (1980) Zooplankton distribution as related to summer hydrographic conditions in Onslow Bay, North Carolina. *Bull Mar Sci* 30(4):819–832. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=106708>
- Paffenhöfer GA (1983) Vertical zooplankton distribution on the northeastern Florida shelf and its relation to temperature and food abundance. *J Plankton Res* 5(1):15–33. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=106710>
- Paffenhöfer GA (1993) On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). *J Plankton Res* 15(1):37–55. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=102104>
- Paffenhöfer GA (2006) Oxygen consumption in relation to motion of marine planktonic copepods. *Mar Ecol Prog Ser* 317:187–192
- Paffenhöfer GA, Mazzocchi MG (2003) Vertical distribution of subtropical epiplanktonic copepods. *J Plankton Res* 25(9):1139–1156. <https://doi.org/10.1093/plankt/25.9.1139>
- Paffenhöfer GA, Wester BT, Nicholas WD (1984) Zooplankton abundance in relation to state and type of intrusion onto the southeastern United States shelf during summer. *J Mar Res* 42:995–1017. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=106721>
- Paffenhöfer GA, Sherman BK, Lee TN (1987) Abundance, distribution and patch formation of zooplankton. *Prog Oceanogr* 19(3/4):403–436. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=106720>
- Paffenhöfer GA, Strickler JR, Lewis KD, Richman S (1996) Motion behavior of nauplii and early copepodid stages of marine planktonic copepods. *J Plankton Res* 18(9):1699–1715. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=106723>
- Pappalardo P, Collins AG, Pagenkopp Lohan KM, Hanson KM, Truskey SB, Jaeckle W, Ames CL, Goodheart JA, Bush SL, Biancani LM, Strong EE, Vecchione M, Harasewych MG, Reed K, Lin C, Hartil EC, Whelpley J, Blumberg J, Matterson K, Redmond NE, Becker A, Boyle MJ, Osborn KJ (2021) The role of taxonomic expertise in interpretation of metabarcoding studies. *ICES J Mar Sci*. <https://doi.org/10.1093/icesjms/fsab082>
- Pasternak AF, Averianov AA (1980) Respiration of minute forms of zooplankton and net growth efficiency of some copepods in the Peruvian Upwelling region. *Polskie Arch Hydrobiol* 27:485–496. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=107099>
- Pasternak AF (1984) Feeding of copepods of genus *Oncaea* (Cyclopoida) in the southeastern Pacific Ocean. *Oceanology* 24:609–612. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=107096>
- Pearman JK, Irigoien X (2015) Assessment of zooplankton community composition along a depth profile in the Central Red Sea. *PLoS One*. <https://doi.org/10.1371/journal.pone.0133487>
- Petipa TS, Borichenko VL (1985) Carbon content in copepods' body from various dynamic zones of the Indian Ocean. *Polskie Arch Hydrobiol* 32:473–479. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=106182>
- Philippi A (1843) Fernere Beobachtungen über die Copepoden des Mittelmeeres. *Archiv für Naturgeschichte* 9:54–71. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=527>
- Plounevez S, Champalbert G (1999) Feeding Behaviour and Trophic Environment of *Engraulis encrasicolus* (L.) in the Bay of Biscay. *Estuarine Coast Shelf Sci* 49(2):177–191. <https://doi.org/10.1006/ecss.1999.0497>
- Questel JM, Clarke C, Hopcroft RR (2013) Seasonal and interannual variation in the planktonic communities of the northeastern Chukchi Sea during the summer and early fall. *Cont Shelf Res* 67:23–41. <https://doi.org/10.1016/j.csr.2012.11.003>
- Questel JM, Hopcroft RR, DeHart HM, Smoot CA, Kosobokova KN, Bucklin A (2021) Metabarcoding of zooplankton diversity within the Chukchi Borderland, Arctic Ocean: improved resolution from multi-gene markers and region-specific DNA databases. *Mar Biodiv*. <https://doi.org/10.1007/s12526-020-01136-x>
- Razouls C, Desreumaux N, Kouwenberg J, de Bovée F (2005–2022) Biodiversity of Marine Planktonic Copepods (morphology, geographical distribution, and biological data). Sorbonne University, CNRS. <http://copepodes.obs-banyuls.fr/en>

- Rezai H, Yusoff FM, Arshad A, Kawamura A, Nishida S, Ross OBH (2004) Spatial and temporal distribution of copepods in the Straits of Malacca. *Zool Stud* 43(2):486–497
- Richter C (1994) Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. In PhD Thesis; *Berichte zur Polarforschung* 154(1):1–79+appendix. <http://epic.awi.de/26332/1/BerPolarforsch1994Oncaea154.pdf>
- Roff JC, Turner JT, Webber MK, Hopcroft RR (1995) Bacterivory by tropical copepod nauplii: extent and possible significance. *Aquat Microb Ecol* 9:165–175
- Roman MR, Dam HG, Gauzens AL, Urban-Rich J, Foley DG, Dickey TD (1995) Zooplankton variability on the equator at 140°W during the JGOFS EqPac study. *Deep-Sea Research, Part II. Top Stud Oceanogr* 42:673–693. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=111445>
- Rose M (1933) Faune de France 26—Copépodes pélagiques 1–374.
- Roura Á, Strugnell JM, Guerra Á, González ÁF, Richardson AJ (2018) Small copepods could channel missing carbon through meta-zoan predation. *Ecol Evol* 8(22):10868–10878. <https://doi.org/10.1002/ece3.4546>
- Sampey A, McKinnon AD, Meekan MG, McCormick MI (2007) Glimpse into guts: overview of the feeding of larvae of tropical shorefishes. *Mar Ecol Prog Ser* 339:243–257. <https://doi.org/10.3354/meps339243>
- Sars GO (1916) Liste systématique des Cyclopoïdés, Harpacticoidés et Monstrilloïdés recueillis pendant les campagnes de S.A.S. le Prince Albert de Monaco, avec descriptions et figures des espèces nouvelles. *Bulletin de l'Institut Océanographie (Fondation Albert Ier, Prince de Monaco)* 323:1–23. <https://www.marin.especies.org/aphia.php?p=sourcedetails&id=379621>
- Satapoomin S (1999) Carbon content of some common tropical Andaman Sea copepods. *J Plankton Res* 21(11):2117–2123. <https://doi.org/10.1093/plankt/21.11.2117>
- Satapoomin S, Nielsen T, Hansen P (2004) Andaman Sea copepods: spatio-temporal variations in biomass and production, and role in the pelagic food web. *Mar Ecol Prog Ser* 274:99–122. <https://doi.org/10.3354/meps274099>
- Sazhina LI (1982) Nauplii massovykh vidov Copepoda Atlanticheskogo okeana. Nauplii of mass species of Atlantic Copepoda. *Zoologicheskii Zhurnal* 61(8):1154–1164. <https://www.marin.especies.org/aphia.php?p=sourcedetails&id=112439>
- Sazhina LI (1985) Fecundity and growth rate of copepods in different dynamic zones of Equatorial Countercurrent of the Indian Ocean. *Polskie Archiwum Hydrobiologii* 32:491–505. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=112444>
- Schnack-Schiel SB, Haas C, Michels J, Mizdalski E, Schünemann H, Steffens M, Thomas DN (2008) Copepods in sea ice of the western Weddell Sea during austral spring 2004. *Deep Sea Res Part II* 55(8–9):1056–1067. <https://doi.org/10.1016/j.dsr2.2007.12.014>
- Seuront L, Hwang J-S, Tseng L-C, Schmitt FG, Souissi S, Wong C-K (2004) Individual variability in the swimming behavior of the sub-tropical copepod *Oncaea venusta* (Copepoda: Poecilostomatoida). *Mar Ecol Prog Ser* 283:199–217. <https://doi.org/10.3354/meps283199>
- Shmeleva AA (1966) New species of the genus *Oncaea* (Copepoda, Cyclopoida) from the Adriatic Sea. *Novye vidy roda Oncaea* (Copepoda, Cyclopoida) iz Adriaticeskogo morya. *Zoologicheskii Zhurnal* 45(6):932–935. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=111248>
- Shmeleva AA (1967) New *Oncaea* species (Copepoda, Cyclopoida) from south-western part of the Atlantic Ocean. *Novyi vid Oncaea* (Copepoda, Cyclopoida) iz yugozapadnoi chasti Atlanticheskogo okeana. *Zoologicheskii Zhurnal* 46(4):621–622. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=111249>
- Shmeleva AA (1968) New species of planktonic Copepoda, Cyclopoida from the Adriatic Sea. *Novy vidy planktonnykh Copepoda, Cyclopoida iz Adriaticeskogo morya. Zoologicheskii Zhurnal* 47(12):1784–1793. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=111252>
- Shmeleva AA (1969) Espèces nouvelles du genre *Oncaea* (Copepoda, Cyclopoida) de la Mer Adriatique. *Bulletin de l'Institut Océanographique, Monaco* 68(1393):1–28. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=111253>
- Shmeleva AA (1979) *Novye vidy i ryad ne izvestnykh ranee samstov roda Oncaea* (Copepoda, Cyclopoida) iz Sredizemnogo morya. New species and some previously unknown males of the genus *Oncaea* (Copepoda, Cyclopoida) from the Mediterranean. *Zoologicheskii Zhurnal* 58(4):491–498. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=102996>
- Shmeleva AA, Delalo EP (1965) *Novii vid roda Oncaea* (Copepoda, Cyclopoida) iz Sredizemnogo morya. A new species of the genus *Oncaea* (Copepoda, Cyclopoida) from the Mediterranean Sea. *Zoologicheskii Zhurnal* 44:1562–1565. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=103004>
- Siokou-Frangou I, Christaki U, Mazzocchi MG, Montresor M, Ribera d'Alcalá M, Vaque D, Zingone A (2010) Plankton in the open Mediterranean Sea: a review. *Biogeosciences* 7(5):1543–1586. <https://doi.org/10.5194/bg-7-1543-2010>
- Soviadan YD, Benedetti F, Brandão MC, Ayata SD, Irissou JO, Jamet JL, Kiko R, Lombard F, Gnanndi K, Stemmann L (2022) Patterns of mesozooplankton community composition and vertical fluxes in the global ocean. *Prog Oceanogr* 200:102717. <https://doi.org/10.1016/j.pocean.2021.102717>
- Star JL, Mullin MM (1981) Zooplankton assemblages in three areas of the North Pacific as revealed by continuous horizontal transects. *Deep Sea Res* 28A(11):1303–1322. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=193540>
- Steinberg DK, Silver MW, Pilskaln CH, Coale SL, Paduan JB (1994) Midwater zooplankton communities on pelagic detritus (giant larvacean houses) in Monterey Bay, California. *Limnol Oceanogr* 39(7):1601–1620
- Sullivan BK (1980) In situ feeding behavior of *Sagitta elegans* and *Eukrohnia hamata* (Chaetognatha) in relation to the vertical distribution and abundance of prey at Ocean Station “P”. *Limnol Oceanogr* 25(2):317–326. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=115608>
- Sun RX, Wang YG, Wang G, Xiang P, Chen XY, Xing BP (2022) Research advance in the taxonomy and ecology of Oncaeidae Giesbrecht, 1893. *Front Mar Sci*. <https://doi.org/10.3389/fmars.2022.919877>
- Suzuki H, Sasaki H, Fukuchi M (2003) Loss processes of sinking fecal pellets of zooplankton in the mesopelagic layers of the Antarctic marginal ice zone. *J Oceanogr* 59(6):809–818. <https://doi.org/10.1023/B:JOCE.0000009572.08048.0d>
- Swadling KM, Gibson JAE, Ritz DA, Nichols PD (1997a) Horizontal patchiness in sympagic organisms of the Antarctic fast ice. *Antarct Sci* 9:399–406. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=115969>
- Swadling KM, Gibson JAE, Ritz DA, Nichols PD, Hughes DE (1997b) Grazing of phytoplankton by copepods in eastern Antarctic coastal waters. *Mar Biol* 128:39–48. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=115971>
- Takagi K, Yatsu A, Itoh H, Moku M, Nishida H (2009) Comparison of feeding habits of myctophid fishes and juvenile small epipelagic fishes in the western North Pacific. *Mar Biol* 156(4):641–659. <https://doi.org/10.1007/s00227-008-1115-8>
- Takahashi K, Kawaguchi K (1998) Diet and feeding rhythm of the sand-burrowing mysids *Archaeomysis kokuboi* and *A. japonica* in Otsuchi Bay, northeastern Japan. *Mar Ecol Prog Ser* 162:191–199. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=17314>

- Takahashi T, Uchiyama I (2008) Seasonal changes in the density and vertical distribution of nauplii, copepodites and adults of the genera *Oithona* and *Oncaea* (Copepoda) in the surface water of Toyama Bay, southern Sea of Japan. *Plankton Benthos Res* 3:143–151. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=126875>
- Takahashi KT, Ojima M, Tanimura A, Odate T, Fukuchi M (2017) The vertical distribution and abundance of copepod nauplii and other micro- and mesozooplankton in the seasonal ice zone of Lützow-Holm Bay during austral summer 2009. *Polar Biol* 40(1):79–93. <https://doi.org/10.1007/s00300-016-1925-y>
- Tande KS, Drobysheva S, Nesterova V, Nilssen EM, Edvardsen A, Tereschenko V (2000) Patterns in the variations of copepod spring and summer abundance in the northeastern Norwegian Sea and the Barents Sea in cold and warm years during the 1980s and 1990s. *ICES J Mar Sci* 57(6):1581–1591. <https://doi.org/10.1006/jmsc.2000.0982>
- Tang KW, Backhaus L, Riemann L, Koski M, Grossart H-P, Munk P (2019) Copepod carcasses in the subtropical convergence zone of the Sargasso Sea: implications for microbial community composition, system respiration and carbon flux. *J Plankton Res* 41(4):549–560. <https://doi.org/10.1093/plankt/fbz038>
- Tanimura A, Hoshino K, Nonaka Y, Miyamoto Y, Hattori H (1997) Vertical distribution of *Oithona similis* and *Oncaea curvata* (Cyclopoida, Copepoda) under sea ice near Syowa station in the Antarctic winter. In: Proceedings of the NIPR (National Institute of Polar Research) Symposium on Polar Biology, Tokyo 10:134–144
- Tanimura A, Hattori H, Miyamoto Y, Hoshiai T, Fukuchi M (2008) Diel changes in vertical distribution of *Oithona similis* (Cyclopoida) and *Oncaea curvata* (Poecilostomatoida) under sea ice in mid-summer near Syowa Station. *Antarctica Polar Biol* 31(5):561–567. <https://doi.org/10.1007/s00300-007-0388-6>
- Terazaki M, Marumo R (1982) Feeding habits of meso- and bathypelagic Chaetognatha, *Sagitta zetesios*, Fowler. *Oceanologica Acta* 5(4):461–464. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=206580>
- Thor P, Nielsen TG, Tiselius P, Juul-Pedersen J-P, Michel C, Møller EF, Dahl K, Selander E, Gooding S (2005) Post spring bloom community structure of pelagic copepods in the Disko Bay, Western Greenland. *J Plankton Res* 27(4):341–356. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=117244>
- Titelman J, Fiksen Ø (2004) Ontogenetic vertical distribution patterns in small copepods: field observations and model predictions. *Mar Ecol Prog Ser* 284(1):49–63. <https://doi.org/10.3354/meps284049>
- Titelman J, Varpe O, Eliassen S, Fiksen Ø (2007) Copepod mating: chance or choice? *J Plankton Res* 29(12):1023–1030. <https://doi.org/10.1093/plankt/fbm076>
- Tsalkina AV (Zsalkina) (1970) Vertical distribution and diurnal migration of some Cyclopoida (Copepoda) in the tropical region of the Pacific Ocean. *Mar Biol* 5(4):275–282. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=193561>
- Tsalkina AV (1972) Vertikal'noe raspredelenie i sutochnye migratsii Cyclopoida (Copepoda) v severo-vostochnoi chasti Indiiskogo okeana. Vertical distribution and diurnal migration of Cyclopoida (Copepoda) in the northeastern Indian Ocean. *Okeanologiya, Oceanology*. 12(4):677–688 (figs 1–5, tabs. 1–6. (14-viii-1972, Russian, 12(4): 566–576, figs 1–5, tabs. 1–6.) English)
- Tsalkina AV (1977) Vertical distribution and diurnal migration of Cyclopoida (Copepoda) in the waters of the North Trade Wind Current and the Sulu Sea. Pelagic Ecosystems of the Eastern Pacific Ocean Upwellings. 17th Cruise of the R/V “Akademik Kurchatov”. *Polskie Archiwum Hydrobiologii* 24(Suppl.):337–362. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=117842>
- Turner JT (1986a) Zooplankton feeding ecology: contents of fecal pellets of the cyclopoid copepods *Oncaea venusta*, *Corycaeus amazonicus*, *Oithona plumifera*, and *O. simplex* from the northern Gulf of Mexico. *Publicazioni Della Stazione Zoologica Di Napoli, I. Mar Ecol* 7(4):289–302. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=117989>
- Turner JT (1986b) Zooplankton feeding ecology: contents of fecal pellets of the copepod *Undinula vulgaris* from continental shelf waters of the Gulf of Mexico. *Publicazioni Della Stazione Zoologica Di Napoli, I. Mar Ecol* 7(1):1–14. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=117990>
- Turner JT, Tester PA (1992) Zooplankton feeding ecology: bacterivory by metazoan microzooplankton. *J Exp Marine Biol Ecol* 160(2):149–167. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=118003>
- Valentin JL, Monteiro-Ribas WM, Mureb MA, Pessotti E (1987) Sur quelques zooplanctons abondants dans l'upwelling de Cabo Frio (Bresil). *J Plankton Res* 9(6):1195–1216. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=215437>
- Vargas C, Tönnesson K, Sell A, Maar M, Møller E, Zervoudaki T, Giannakourou A, Christou E, Satapoomin S, Petersen J, Nielsen T, Tiselius P (2002) Importance of copepods versus appendicularians in vertical carbon fluxes in a Swedish fjord. *Mar Ecol Prog Ser* 241:125–138. <https://doi.org/10.3354/meps241125>
- Vinogradov MY, Flint MV, Shushkina EA, Tutubalin VN, Uger YG (1987) On the comparative catchability of big volume bottles and plankton nets for vertical hauls. *Oceanology* 27:242–247
- Walter TC, Boxshall G (2023) World of Copepods Database. Oncaeiidae Giesbrecht, 1893. World Register of Marine Species. <https://www.marinespecies.org/aphia.php?p=taxdetails&id=128586>
- Ward P, Atkinson A, Tarling G (2012) Mesozooplankton community structure and variability in the Scotia Sea: a seasonal comparison. *Deep Sea Res Part II* 59–60:78–92. <https://doi.org/10.1016/j.dsr2.2011.07.004>
- Webber MK, Roff JC (1995) Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. *Mar Biol* 123:481–495
- Weikert H (1982) The vertical distribution of zooplankton in relation to habitat zones in the area of the Atlantis II Deep, central Red Sea. *Mar Ecol Prog Ser* 8:120–143. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=119905>
- Weydmann A, Søreide JE, Kwaśniewski S, Leu E, Falk-Petersen S, Berge J (2013) Ice-related seasonality in zooplankton community composition in a high Arctic fjord. *J Plankton Res* 35(4):831–842. <https://doi.org/10.1093/plankt/ftb031>
- Wi JH, Böttger-Schnack R, Soh HY (2010) Species of *Triconia* of the *conifera*-subgroup (Copepoda, Oncaeidae) from Korean waters, including a new species. *J Crustac Biol* 30(4):673–691. <https://doi.org/10.1651/10-3301.1>
- Wi J, Shin K, Soh H (2011) The *similis*-subgroup within *Triconia* (Copepoda: Cyclopoida: Oncaeidae) from Korean waters (East China Sea), including a new species. *Zool Stud* 50(5):588–604
- Wi JH, Böttger-Schnack R, Soh HY (2012) Two new species belonging to the *dentipes*- and *conifera*-subgroups of *Triconia* (Copepoda: Cyclopoida: Oncaeidae) from the East China Sea. *J Crustac Biol* 32(5):843–859. <https://doi.org/10.1163/193724012X650659>
- Wickstead JH (1962) Food and feeding in pelagic copepods. *Proc Zool Soc Lond* 139(4):545–555. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=120178>
- Wishner KF (1979) The biomass and ecology of the deep sea benthopelagic (near-bottom) plankton. In: Dissertation Abstracts International, B, Sciences and Engineering, 40, (41476.). University of California. [PhD dissertation, University of California, San Diego, 144pp.]
- Wu CH, Hwang JS, Yang JS (2004) Diets of three copepods (Poecilostomatoida) in southern Taiwan Strait. In: Hwang JS, Ho JS, Shih

- CT (eds) Proceedings of the 8th International Conference on Copepoda, Special Issue: Contemporary Studies on Copepoda. *Zool Stud* 43(2):388–392. <https://www.marinespecies.org/aphia.php?p=sourcedetails&id=120934>
- Yamaguchi A, Watanabe Y, Ishida H, Harimoto T, Furusawa K, Suzuki S, Ishizaka J, Ikeda T, Takahashi MM (2002a) Community and trophic structures of pelagic copepods down to greater depths in the western subarctic Pacific (WEST-COSMIC). *Deep Sea Res Part I* 49(6):1007–1025. [https://doi.org/10.1016/S0967-0637\(02\)00008-0](https://doi.org/10.1016/S0967-0637(02)00008-0)
- Yamaguchi A, Watanabe Y, Ishida H, Harimoto T, Furusawa K, Suzuki S, Ishizaka J, Ikeda T, Takahashi MM (2002b) Structure and size distribution of plankton communities down to the greater depths in the western North Pacific Ocean. *Deep Sea Res Part II* 49(24–25):5513–5529. [https://doi.org/10.1016/S0967-0645\(02\)00205-9](https://doi.org/10.1016/S0967-0645(02)00205-9)
- Zervoudaki S, Nielsen TG, Christou ED, Siokou-Frangou I (2006) Zooplankton distribution and diversity in a frontal area of the Aegean Sea. *Mar Biol Res* 2(3):149–168. <https://doi.org/10.1080/17451000600702037>
- Zervoudaki S, Christou ED, Nielsen TG, Siokou-Frangou I, Assimakopoulou G, Giannakourou A, Maar M, Pagou K, Krasakopoulou E, Christaki U, Moraitou-Apostolopoulou M (2007) The importance of small-sized copepods in a frontal area of the Aegean Sea. *J Plankton Res* 29(4):317–338. <https://doi.org/10.1093/plankt/fbm018>

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