



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*

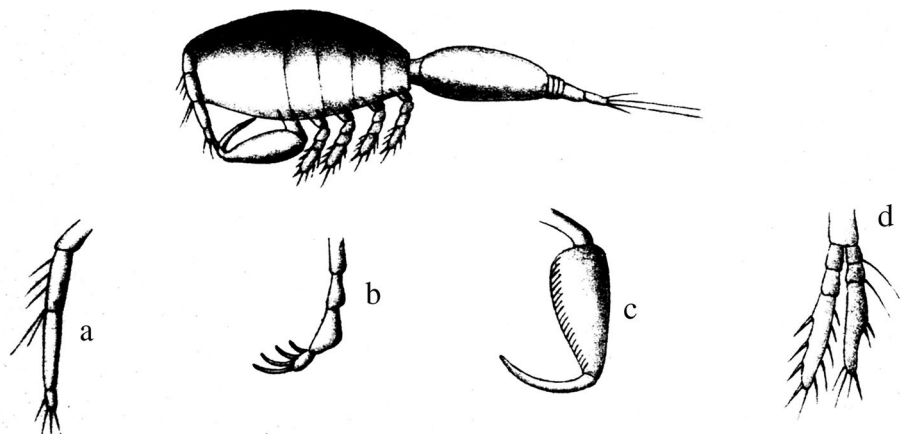
venusta (Fig. 1). The generic name *Oncaea* from Greek *onc-* meaning “hook”, was possibly directed to the distal endopod segment of the big maxilliped, which is drawn into a long-curved claw, which is typical for this family; Philippi 1843, p. 63: “...das Endglied ist eine sichelförmige Klaue.” Regrettably,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



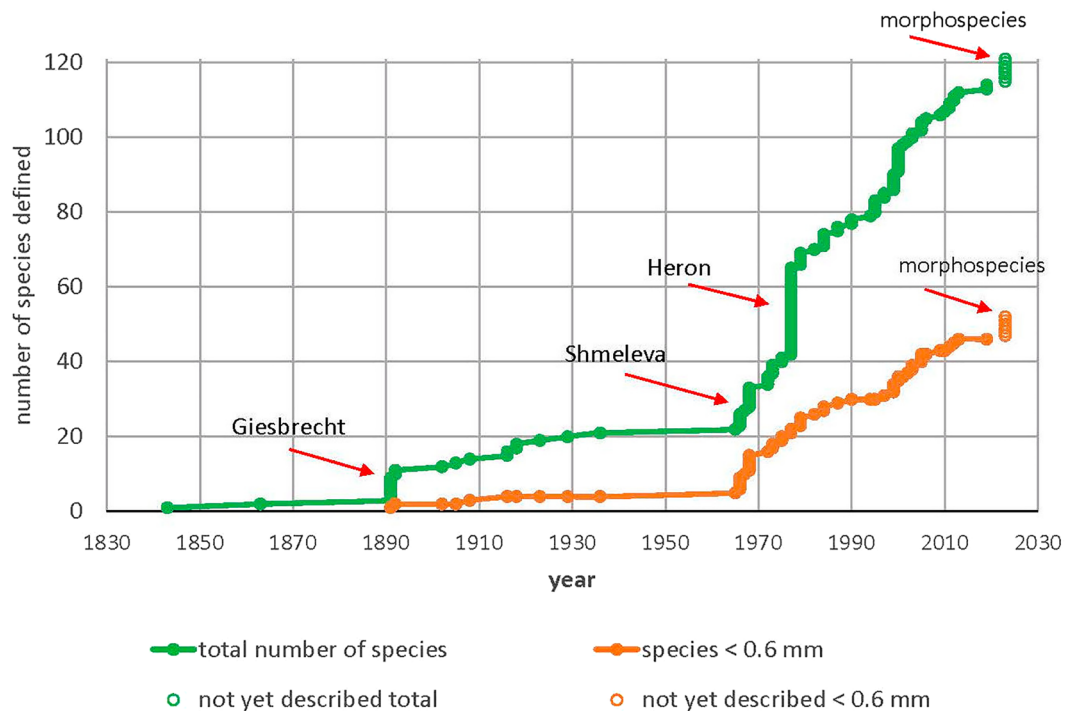


Fig. 2 Number of oncaeid species defined over time. Green line represents total number of species, orange line represents number of species <0.6 mm total female length. Authors are indicated, who made

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

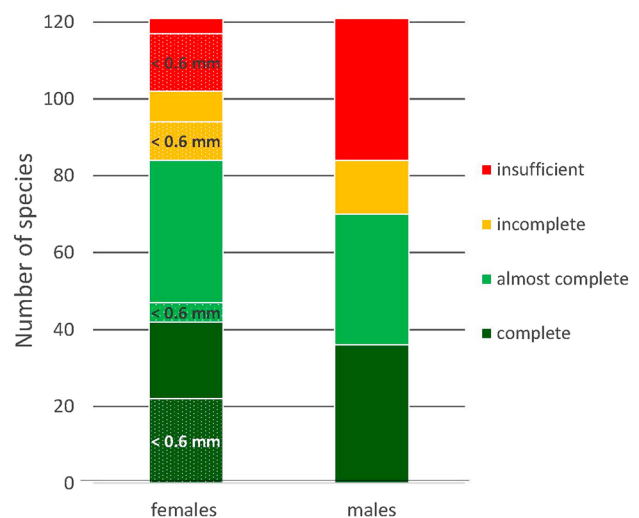


Fig. 3 Quality of taxonomic description of oncaeid species grouped into four categories: insufficient, sufficient but incomplete, almost complete, complete description. For females the portion of small species (<0.6 mm total length) is indicated for each category. (See text for details)

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, nucleotide codes are available for 32 valid species out of the total of 114 oncaeid species, representing 4 genera (Fig. 5). 17 nucleotide 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 nucleotide 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 nucleotide 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., nucleotide sequences are not yet available. Regional examples are given in Table 3.

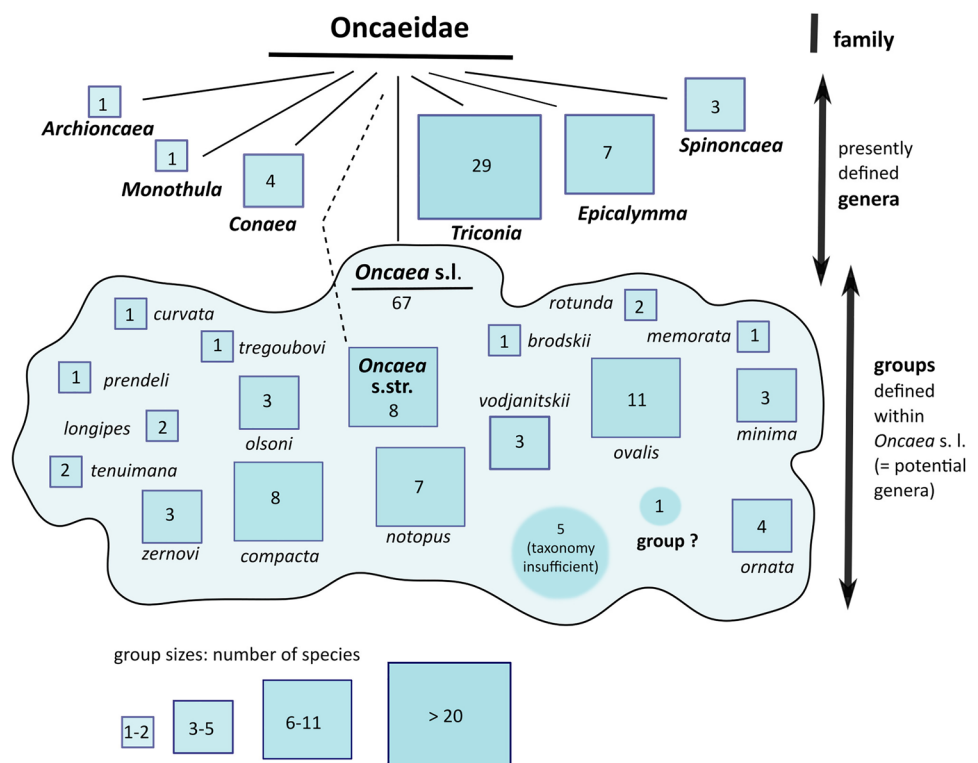
Usability of different genetic markers

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 nucleotides 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



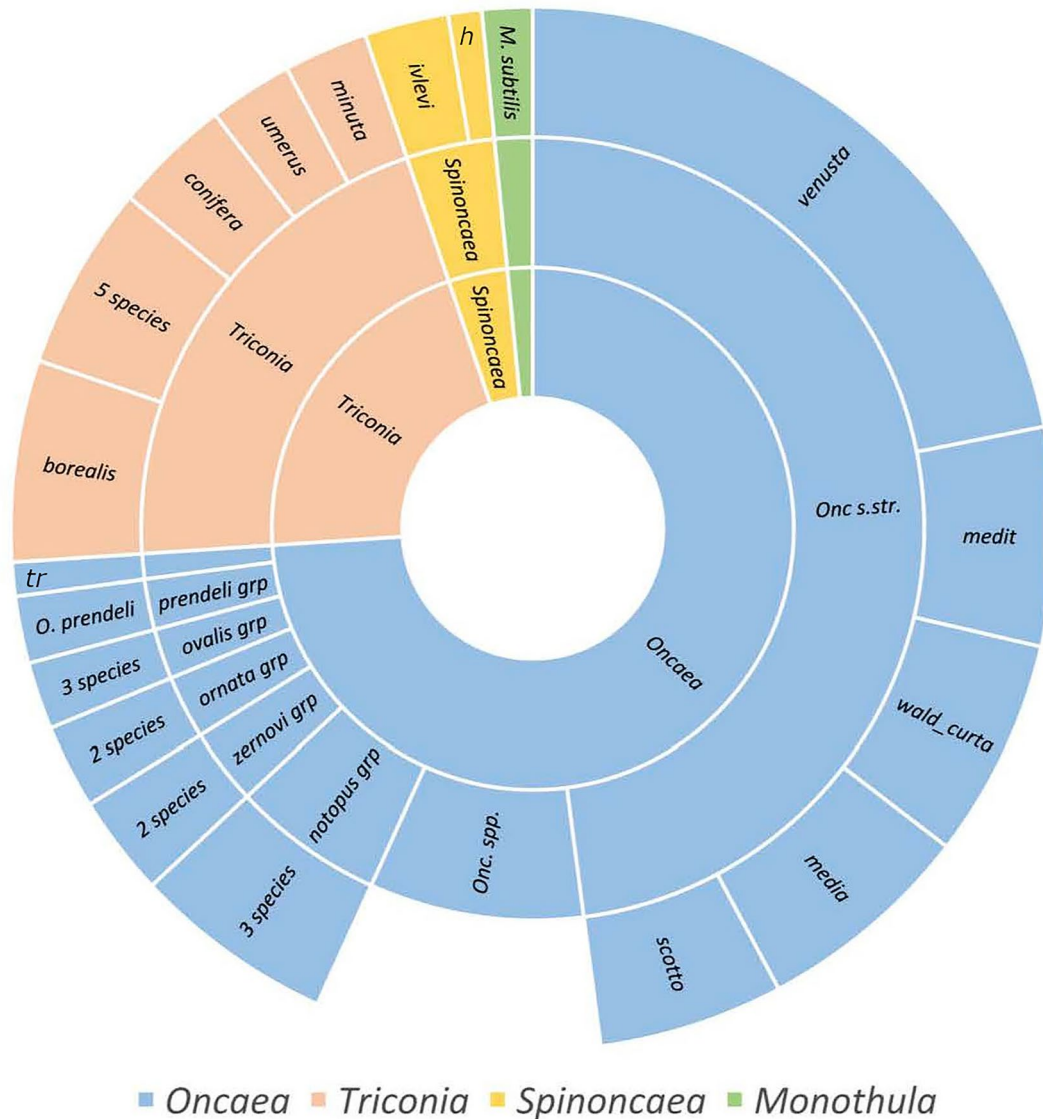


Fig. 5 Percentage distribution of individual genetic codes among species, groups, and genera of Oncaeidae as reported in GenBank (total number of codes=193). Abbreviated taxon names: *Onc.*

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).

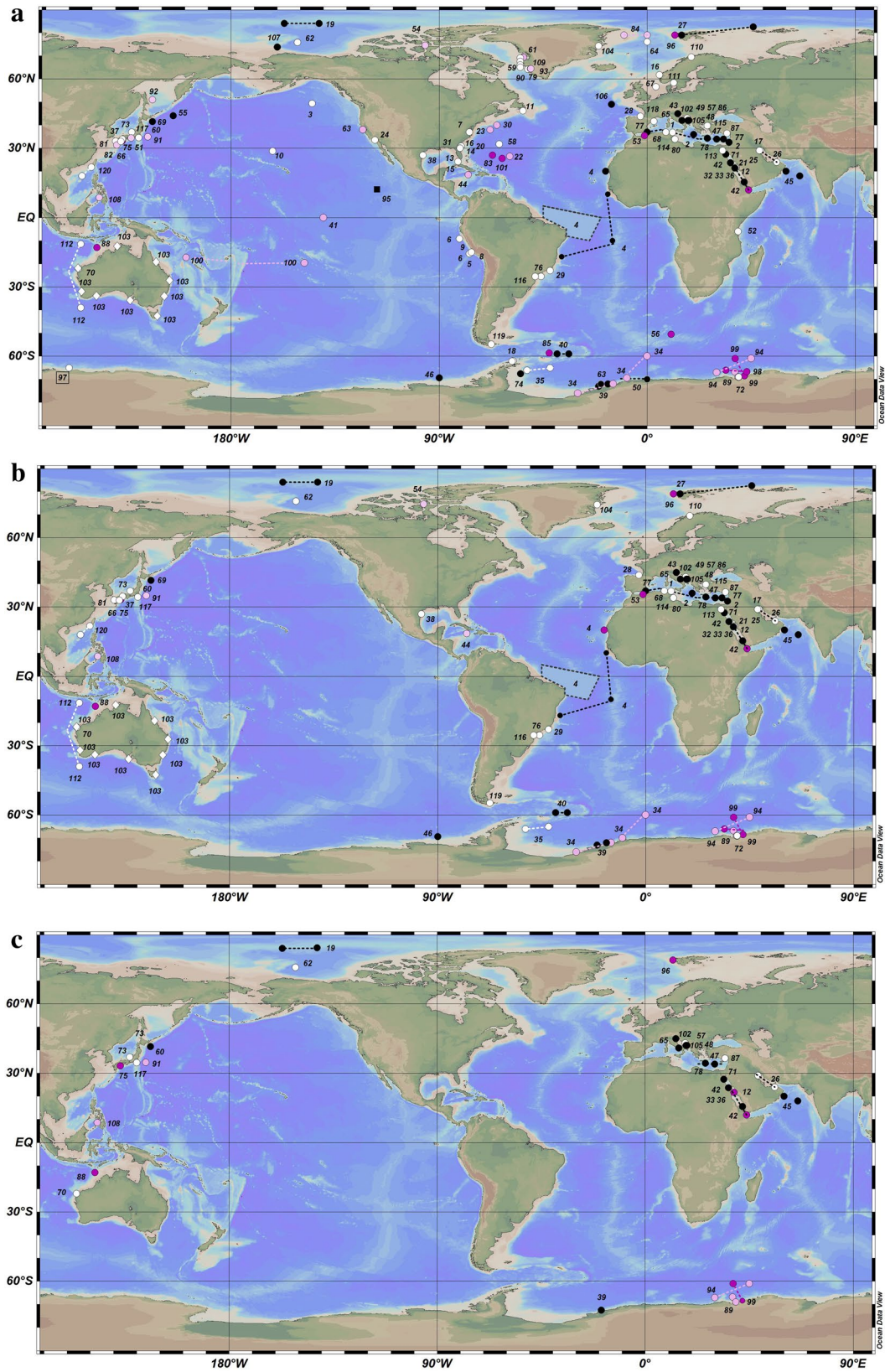


Fig. 6 **a** Geographical distribution of quantitative zooplankton studies considering Oncaeidae at least on family level, based on small mesh net samples (100 µm or less). Numbers refer to references given in the appendix, listed (with few exceptions) in a time sequence from 1964 – 2022. White dots=samples 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.

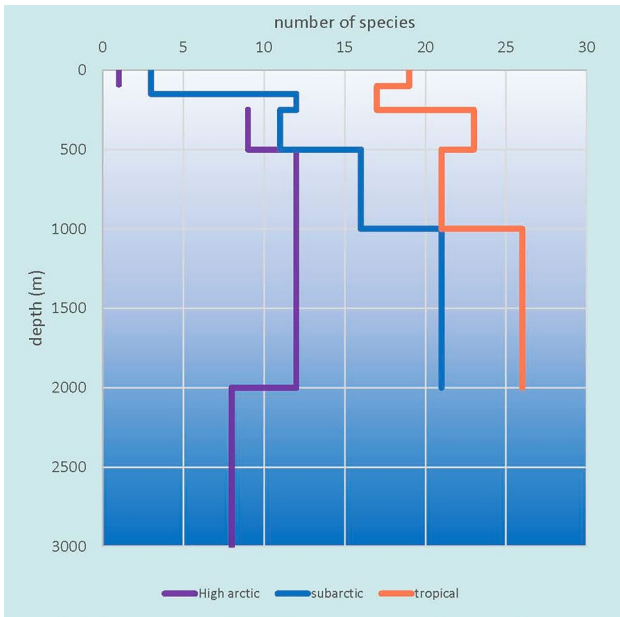


Fig. 7 Number of oncaeid species encountered per depth zone in three different climatic regions; data taken from Heron et al. (1984) for High arctic, Nishibe and Ikeda (2004) for subarctic, and Böttger-Schnack (1996) for tropical (Arabian Sea) region

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,

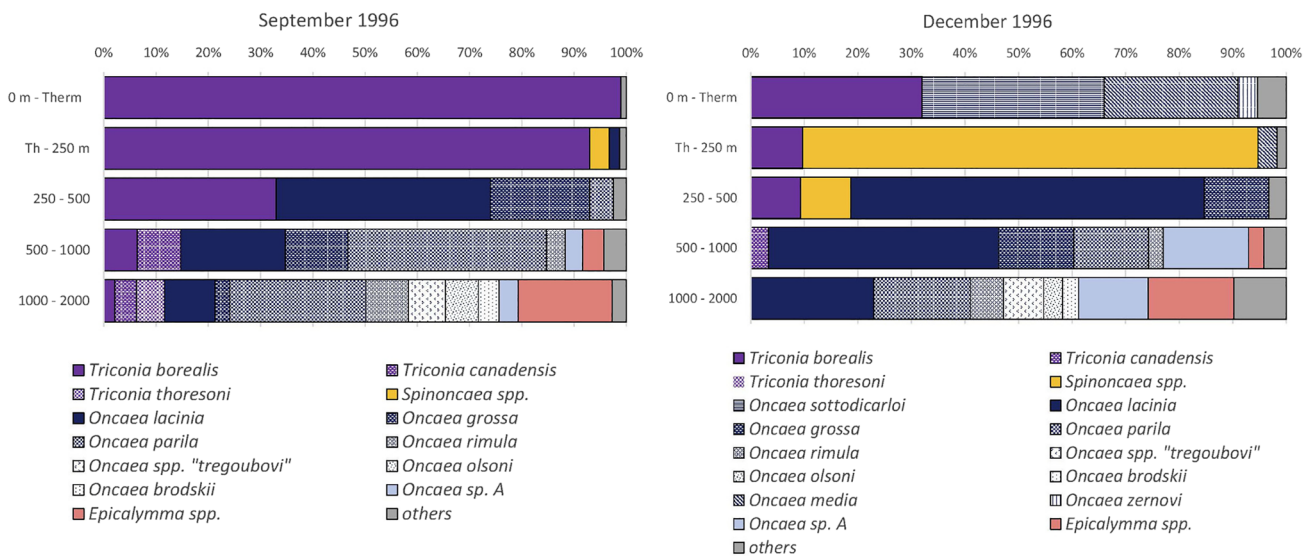


Fig. 8 Example for differences in the vertical structure of oncaeid communities at the same station, depending on the hydrographic condition. Data from Nishibe and Ikeda (2004, Table 4). *Th* = Therm = Thermocline

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.

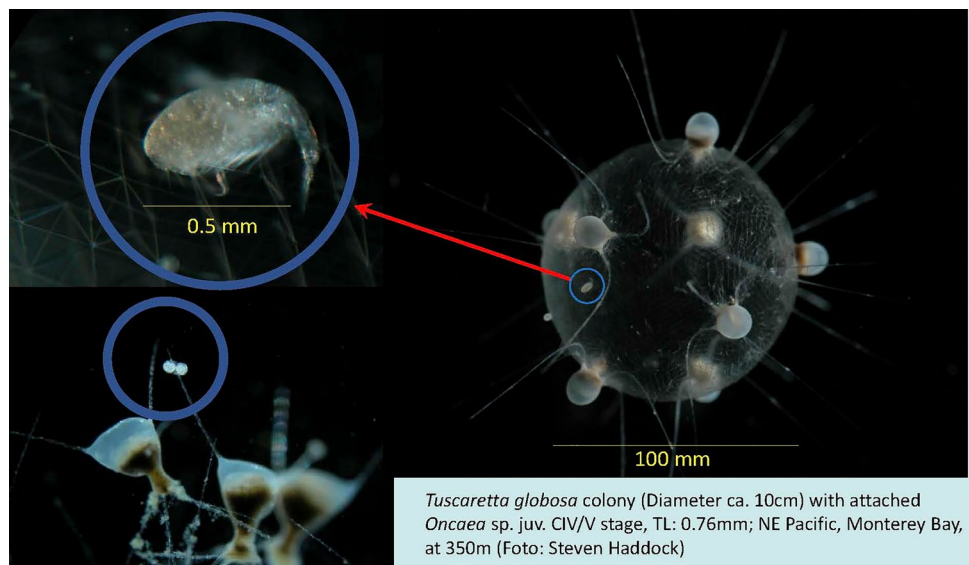
Association with substrates

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:

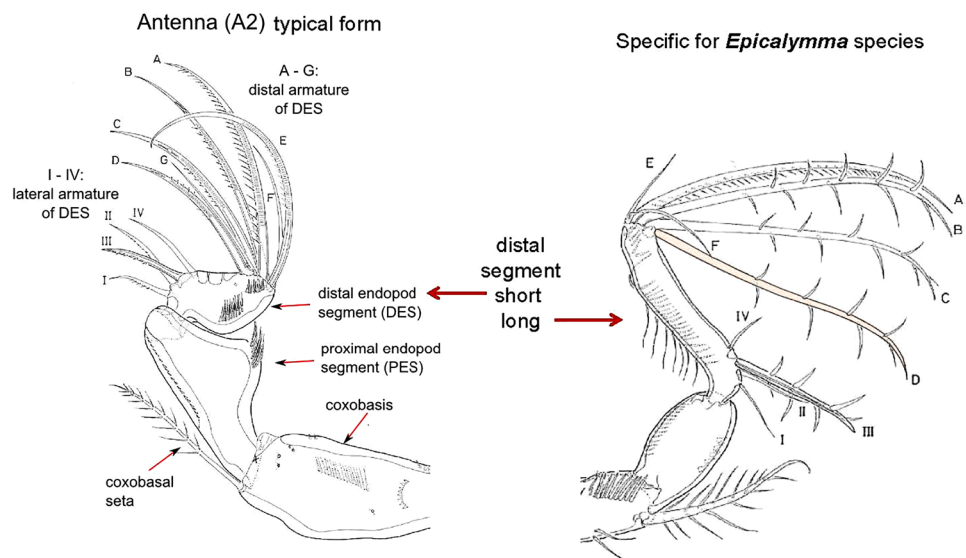
- 1- The antennules (A1) are comparably short and suitable for folding backwards to creep into appendicularian houses for feeding on the inner food-concentrating filter, which the copepods tend to prefer to the outer incurrent filters (cf. Ohtsuka and Kubo 1991)
- 2- The strong terminal setae of the 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)



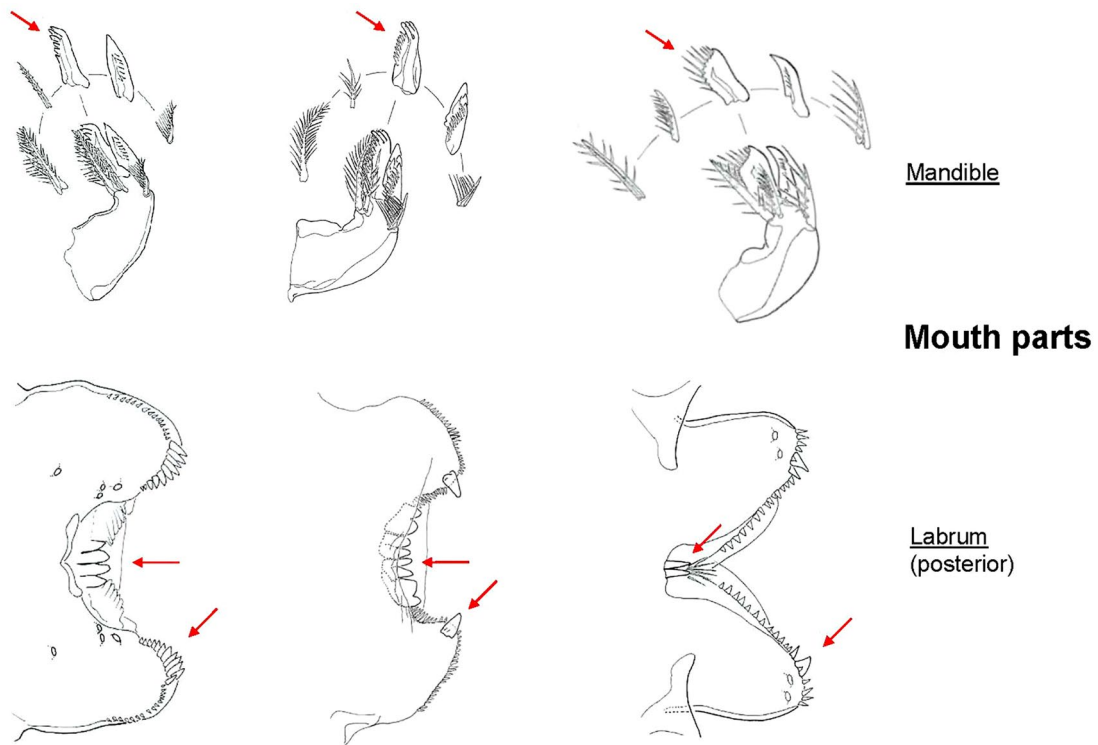
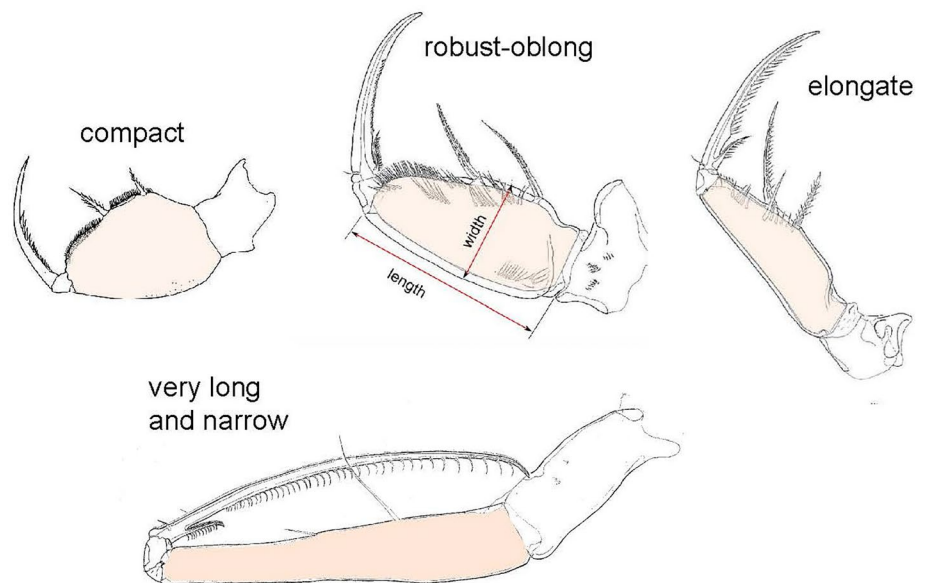


Fig. 11 Mouth parts of Oncaeidae. Left: *Triconia similis* (Böttger-Schnack 1999, Fig. 3C, D; middle: *Oncaea serrulata* (Böttger-Schnack 2011, Fig. 2C, D); right: *Oncaea bispinosa* (Böttger-Schnack 2002, Fig. 3C, D)

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 Fransz (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 Fransz (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.

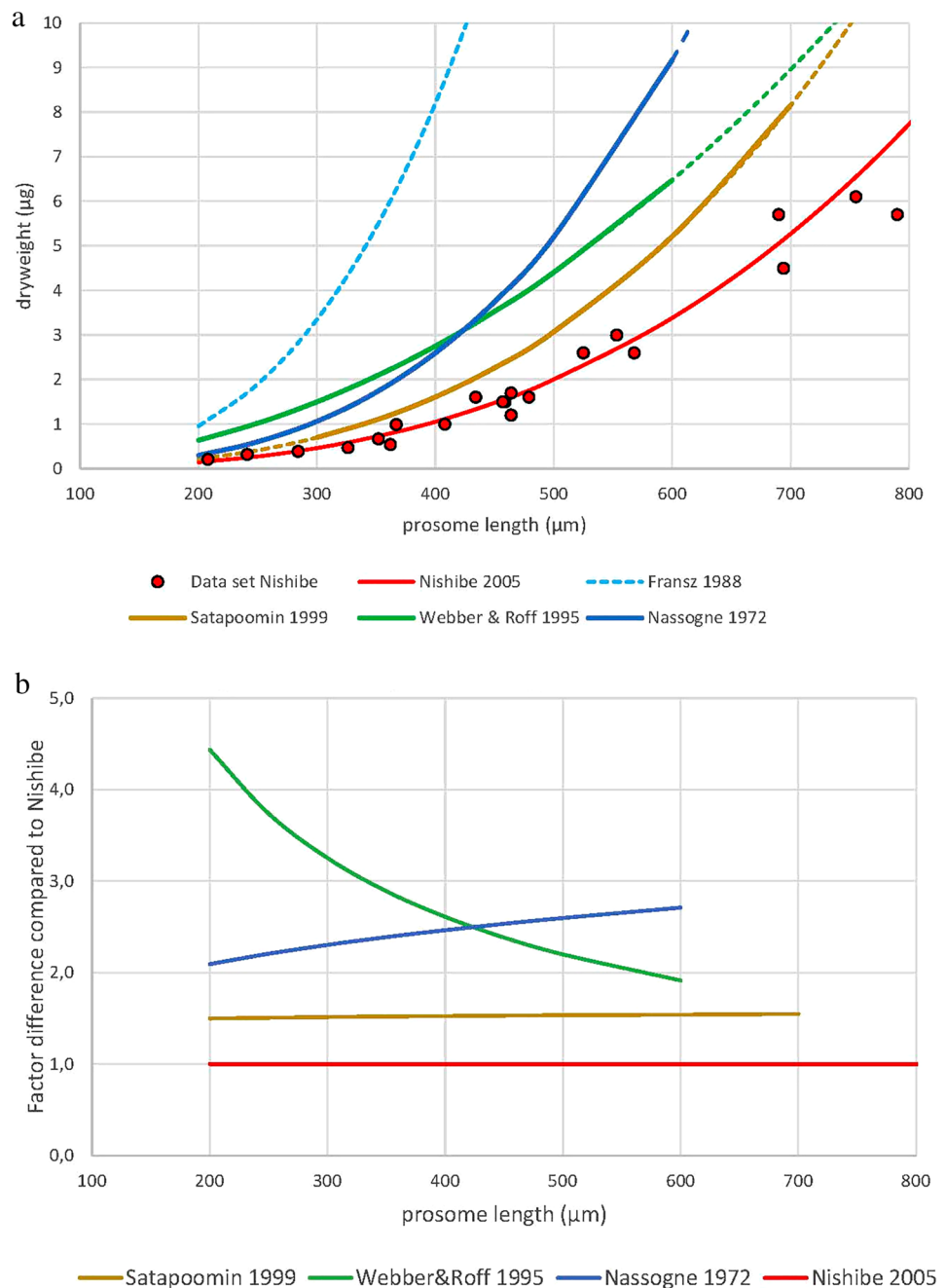
Part A of the figure shows the different length–weight regressions so far established for oncaeid copepods by Nassogne (1972), Webber and Roff (1995), and Satapoomin (1999) from warm-temperate/tropical areas and those established for subarctic waters by Nishibe (2005). Dashed lines denote extrapolated 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 Fransz (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 Fransz (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:

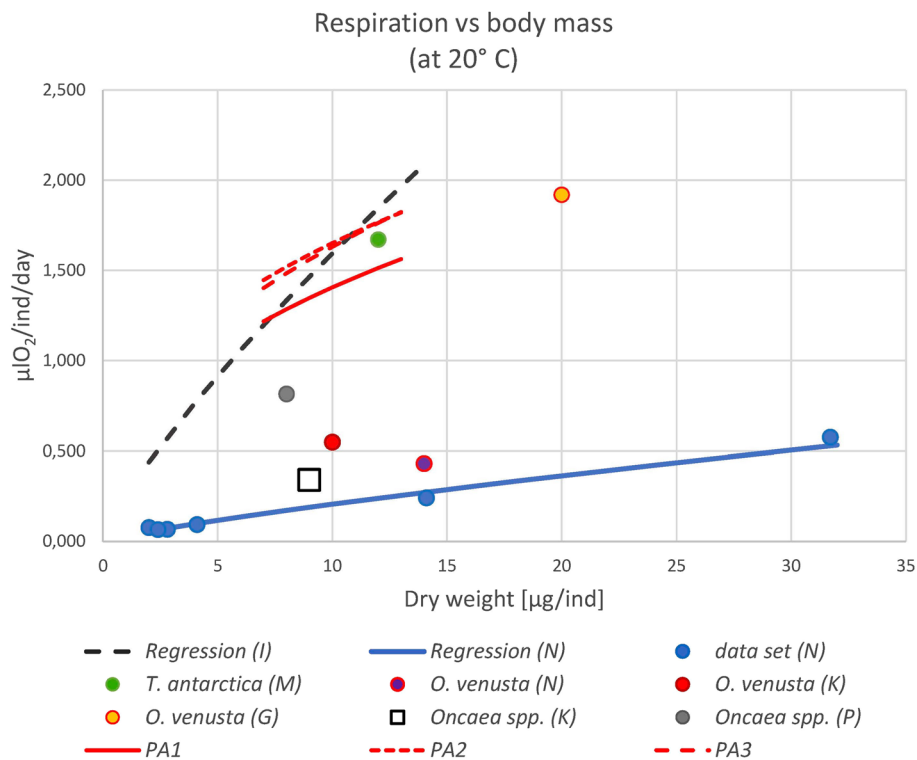


Fig. 14 Compilation of information about respiration rates of Oncaeidae in relation to body mass. For comparability, all values measured at different temperatures are adapted to 20 °C using $Q_{10}=2.0$ (Ikeda et al. 2001). **Individual data points:** (1) *T. antarctica* (M)=Mayzaud et al. 2002, measured 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:

$$\text{Log}_{10} R = -3.392 + 0.815 * \text{log}_{10} DW \text{ (Nishibe 2005, p. 63)}$$

[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.

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