

RESEARCH ARTICLE

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Are taxonomic details of relevance to ecologists? An example from oncaeid microcopepods of the Red Sea

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Abstract The marine microcopepod family Oncaeidae in the Red Sea has been the subject of comprehensive ecological studies over the past 15 years, providing for the first time insights into their community structure, vertical distribution and feeding ecology. Owing to taxonomic problems in species identification, however, many of the earlier ecological results were based on provisionally named species or morphotypes. A recent, ongoing taxonomic study of Red Sea Oncaeidae resulted in a considerable increase in the estimated numbers of species, since many of the species had not been described before. The present paper focuses on the potential significance of an improved taxonomic resolution of oncaeids with respect to various ecological aspects in this area, such as indicator species, community analysis and vertical distribution. The progress in our knowledge of the diversity of Red Sea Oncaeidae is summarized, including latest findings on the taxonomy and zoogeography of very small species (<0.5 mm), and the importance of sibling species in the family is pointed out. The south–north gradient in species diversity of Oncaeidae within the Red Sea appears to be greater than previously assumed, since several of the newly described species were restricted to the southern part. The number of endemic species among Red Sea oncaeids is very low, however, most of the new species being also recorded outside the Red Sea. New quantitative data on the

abundance and vertical distribution of selected oncaeid siblings obtained during a recent cruise in the northern Red Sea are provided to exemplify the changes in the knowledge of oncaeid community structure attributable to the improved taxonomic resolution. The potential ecological importance of a more differentiated consideration of oncaeid species in marine microcopepod communities is discussed.

Introduction

The classification of individuals into groups (species, form variants) with ecologically uniform reactions is a fundamental requirement for the analysis of structures and functions of marine plankton communities and their variation in space and time. Among marine planktonic copepods, the taxonomy of larger species in the size range 1–3 mm (mostly calanoids) is much better known than that of microcopepod species <1 mm in body length, most of which belong to non-calanoid taxa. Even though an increasing consideration of small-sized metazoans in marine zooplankton studies has led to the recognition of microcopepods as an important fraction of the plankton community (e.g. LeBrasseur and Kennedy 1972; Judkins 1980; Cowles et al. 1987; Hopcroft et al. 2001), information on their community structure and vertical distribution is still limited (e.g. Böttger-Schnack 1990a, 1990b, 1995; Hopcroft et al. 1998; Kršinić 1998) and the few available biological data (e.g. on grazing) are often based on higher taxonomic categories, such as genera or even families (e.g. Arinardi et al. 1990; Sutton et al. 2001).

The ecosystem of the Red Sea has been studied intensively over the past 25 years (Head 1987; Beckmann 1996, and literature cited therein), providing fundamental insights into the vertical structure (e.g. Weikert 1982, 1987; Beckmann 1984, 1996; Böttger 1987; Böttger-Schnack 1994) and function (e.g. Lenz et al. 1988; Schneider et al. 1991) of the pelagic

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communities. This unique environment is characterized by constant and exceptionally high deep-sea temperatures of 21.7°C and salinities of ~40.5 PSU between ~200 m and the near-bottom layer at 2000 m depth (Morcos 1970; Edwards 1987). Within the oceanic zooplankton community, small-sized organisms (size-fraction 100–300 µm) are of particular importance, exhibiting greater relative abundances and a higher respiration rate in the central Red Sea than in the adjacent Gulf of Aden (Schneider and Lenz 1991; Schneider et al. 1994). Among the small metazoan plankton of the open Red Sea, microcopepods of the poecilostomatoid family Oncaeidae, measuring between 0.2 and 1.2 mm long as adults, represent one of the most abundant and diversified taxa in the lower epipelagic and the meso- and bathypelagic zones (Böttger-Schnack 1990a, 1990b, 1994, 1995).

The ecological data on the diversity and vertical distribution of oncaeid species in the past from the Red Sea included several uncertainties attributable to difficulties in species identification. Some oncaeid species, for instance, exhibited a conspicuous bimodal vertical distribution, with peak abundances in the epi- and upper mesopelagic zone, not found in other Red Sea zooplankton species (Böttger-Schnack 1990a, 1990b). It remained uncertain, however, whether this pattern could be related to vertical differences in hydrographic conditions, e.g. oxygen gradients, or reflect the different depth distributions of two closely related species (Böttger-Schnack 1990a). Another example was the latitudinal decrease in species numbers in the Red Sea, which was found to be much smaller for non-calanoids, especially Oncaeidae (Böttger-Schnack 1995), than had been reported for other zooplankton taxa (Halim 1969; Weikert 1987; Beckmann 1996). It was hypothesized that oncaeid copepods may be less sensitive to the strong horizontal gradients in environmental conditions (especially the increasing salinity) in the Red Sea and do not follow the latitudinal trend of a reduced species richness from south to north in this area. However, within the *Oncaea* species a number of form or size variants were found in the southern parts, which seemed to be rare or absent in the central area (Böttger-Schnack 1995). Since most of these variants have not yet been described in the literature, their taxonomic status had to be ascertained.

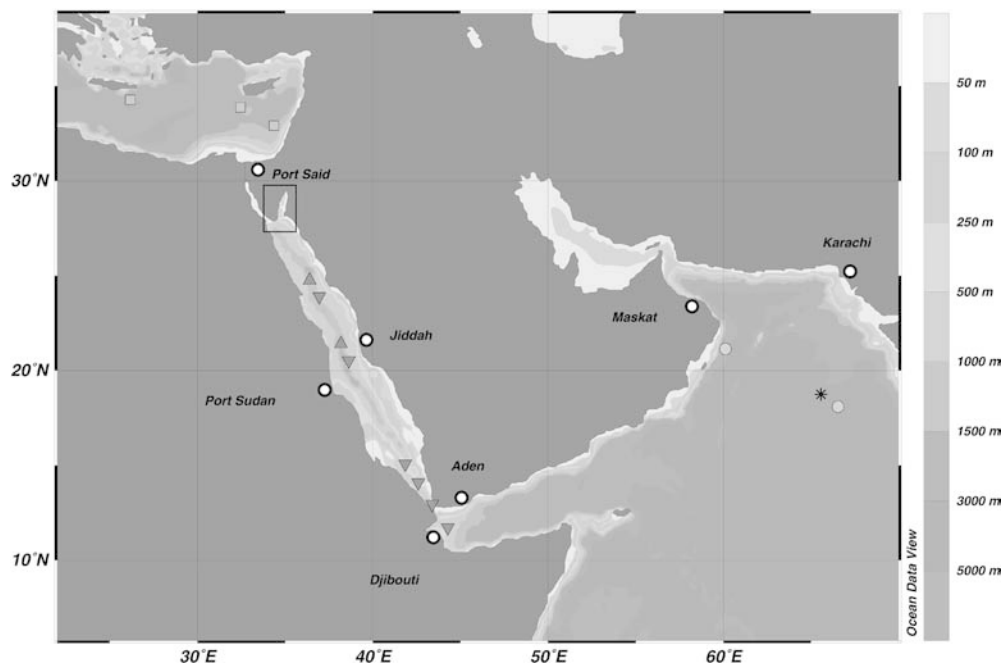
Species of Oncaeidae are difficult to identify, owing to the small size of the species, a very high species diversity, and the lack of fundamental taxonomic knowledge. The morphology of medium-sized and larger oncaeid species between 0.5 and 1.0 mm in length has been studied in more detail during the past two decades (e.g. Heron 1977; Heron et al. 1984; Boxshall and Böttger 1987; Heron and Bradford-Grieve 1995; Heron and Frost 2000), and many new species have been described. The number of known species has risen from about 70 (Malt 1983) to over 100 species in recent years (R. Böttger-Schnack, unpublished data). Many of the newly described species represent sibling species of well known,

abundant taxa, such as the *conifera* group of oncaeids, which presently contains 11 species differing only in very slight morphological details (Heron 1977; Heron and Bradford-Grieve 1995; Heron and Frost 2000). The taxonomy of smaller oncaeid species (<0.5 mm body length) was insufficiently known until recently. Species of this size spectrum have been found to represent one of the most abundant groups in the oceanic microcopepod communities of low latitudes (Böttger-Schnack 1994, 1995; Kršinić 1998).

To overcome the difficulties in species identification and resulting problems in the interpretation of ecological data on oncaeid copepods in the Red Sea, a detailed taxonomic study was started some years ago, focusing on 26 *Oncaea* species and morphotypes known at that time (Böttger-Schnack 1994). The taxonomic results of larger and medium-sized Red Sea oncaeids (Böttger-Schnack 1999, 2001; Böttger-Schnack and Huys 1997, 2001) and first data on the taxonomy of smaller species <0.5 mm in body length (Böttger-Schnack 2002, 2003) were published and further studies are in progress. Within the frame of a phylogenetic study, the diphyletic status of the family Oncaeidae sensu lato was recognized by Huys and Böttger-Schnack (1996), who proposed the new family Lubbockiidae to accommodate *Lubbockia* Claus, 1862 and related genera, retaining only *Oncaea* Philippi, 1843, *Conaea* Giesbrecht, 1891 and *Epicalymma* Heron, 1977 in the Oncaeidae. The large type genus *Oncaea* sensu lato was recognized as a paraphyletic assemblage (Huys and Böttger-Schnack 1996) and preliminary results of an ongoing phylogenetic study of the Oncaeidae sensu stricto at the species level identified about 20 monophyletic lineages, each of which may deserve a generic status (Böttger-Schnack and Huys 1998, 2001). In addition to the three genera retained in the revised family Oncaeidae s.str., four new oncaeid genera have been established to date: *Archioncaea* Böttger-Schnack & Huys, 1997, *Triconia* Böttger-Schnack, 1999, *Monothula* Böttger-Schnack & Huys, 2001, and *Spinoncaea* Böttger-Schnack, 2003.

The present paper focuses on the potential significance of an improved taxonomic resolution of oncaeids with respect to various ecological aspects of the Red Sea, such as indicator species, community analysis and vertical distribution. The progress in our knowledge of the diversity of Red Sea Oncaeidae is summarized, including latest findings on the taxonomy and zoogeography of the smaller species (<0.5 mm) many of which have been defined as new sibling species. New data on the abundance and vertical distribution of selected oncaeid siblings obtained during a recent cruise in the northernmost Red Sea and the Gulf of Aqaba are presented to exemplify the changes in the knowledge of oncaeid community structure attributable to the improved taxonomic resolution. The potential ecological importance of a more differentiated consideration of oncaeid species in marine microcopepod communities will be discussed.

Fig. 1 Plankton sampling stations in the Red Sea and adjacent areas; inset marks location of Gulf of Aqaba. ▲ VALDIVIA cruise 29: October 1980; February 1981; ■ METEOR cruise 5/1: January 1987; ○ METEOR cruise 5/3: April–May 1987; ▼ METEOR cruise 5/5: July–August 1987; * METEOR cruise 32/3: May 1995



Materials and methods

The compilation of taxonomic data of Red Sea Oncaidae is based on zooplankton samples from various regions of the open Red Sea collected between 1980 and 1987 during different seasons with a multiple opening–closing net (Weikert and John 1981) of 0.05-mm or 0.1-mm mesh size by stratified sampling down to a depth of 1850 m (Fig. 1). For details of sampling and evaluation methods see Böttger-Schnack (1990a, 1990b, 1995). At the beginning of the taxonomic study, 21 species of *Oncaea* s.l. and 5 provisionally classified species or forms were defined, which represented the species pool known at that time (Böttger-Schnack 1994; see also Table 1). Taxonomic analyses were conducted using a light- and (partly) scanning electron microscope following the methods described by Böttger-Schnack (1999, 2001). For several oncaeid species, specimens from the adjacent Arabian and eastern Mediterranean Seas (Fig. 1) as well as from various sites in the Atlantic, Indian, and Pacific Oceans were included in the morphological analyses, in order to demarcate their zoogeographical boundaries and detect endemic species in the Red Sea. The term “sibling species” denotes species which appeared to be monospecific at first sight, but could be distinguished morphologically once the appropriate character was considered. Other authors have used the term “pseudo-sibling species” for these (Knowlton 1993).

New data on the abundance and vertical distribution of selected oncaeid sibling species, considering the latest taxonomic findings, were taken from a current ecological study on the microcopepod fauna in the northern Red Sea. Samples had been collected during METEOR-cruise 44/2 (March/April 1999) by stratified vertical hauls with a multiple opening–closing net with 0.055-mm mesh size down to a maximum depth of 800 m (Böttger-Schnack et al. 2001) along a transect from the northernmost Red Sea to the Gulf of Aqaba (Fig. 2). Sample processing for the enumeration of oncaeid taxa and the evaluation of data followed the methods described by Böttger-Schnack (1990a). The study area represents two hydrologically different regimes: in the northernmost Red Sea (station 156), the water column was vertically stratified, with a shallow upper mixed layer extending from 0 to 50/100 m depth, and an extended oxygen-minimum zone occurred between 200/300 m and 600 m depth, whereas in the Gulf of Aqaba (stations 151, 152 and

164), deep vertical mixing occurred down to 300 m or even 400 m depth and the water column was well oxygenated (Pätzold et al. 2000; see also Cornils 2000).

Results

Review of progress in taxonomy and zoogeography of Red Sea Oncaidae

Twenty-three species of Red Sea Oncaidae were morphologically analysed and their taxonomic status has been fully determined to date. In addition to 21 *Oncaea* species and 5 provisionally classified species or forms (morphotypes) known from earlier ecological studies, 9 oncaeid species and 1 oncaeid genus (*Epicalymma*) have been newly recorded from the Red Sea since 1997, and the estimated number of morphotypes increased considerably to about 17 (Table 1). In total, the estimated number of oncaeid species in the Red Sea almost doubled, from about 26 to about 47 species and morphotypes.

The greatest number of species (11) was found in the newly established genus *Triconia*, representing the *conifera/similis* group of oncaeids, which also included the greatest number of new species (5). Within this genus, three new pairs and one new triplet of sibling species were found: *T. hawii*–*T. recta*, *T. umerus*–*T. gonopleura*, *T. similis*–*T. parasimilis* and *T. dentipes*–*T. elongata*–*T. giesbrechti*. The species pairs exhibited different patterns of zoogeographical (regional) distribution along the south–north axis of the Red Sea: one pair, *T. hawii*–*T. recta*, and two species of the triplet, *T. dentipes*–*T. elongata*, co-occurred throughout the entire main basin,

Table 1 Updated species list of oncaeid copepods in the Red Sea, including the current state of taxonomic revision (A, B). Grouping of species (I–X.) follows preliminary results of a phylogenetic

analysis of total Oncaeidae (Böttger-Schnack and Huys 1998, 2001). Within a group or subgroup, species are listed chronologically (*, occurrence restricted to southern Red Sea; ?, uncertain)

Earlier ecological studies (up to 1997)	After taxonomic revision (after 1997)	
A. Taxonomical analysis completed		
Medium- to large-sized species (0.5–1.0 mm body length)		
	I. <i>Triconia</i> Böttger-Schnack, 1999	
	a. <i>conifera</i> -subgroup	
<i>Oncaea conifera</i>	<i>T. conifera</i> (Giesbrecht, 1891)	
<i>O. rufa</i>	<i>T. rufa</i> (Boxshall & Böttger, 1987)	
	b. <i>similis</i> -subgroup	
<i>O. minuta</i>	<i>T. minuta</i> (Giesbrecht, 1892)	
<i>O. hawii</i>	<i>T. hawii</i> (Böttger-Schnack & Boxshall, 1990)	
<i>O. umerus</i>	<i>T. umerus</i> (Böttger-Schnack & Boxshall, 1990)	
	<i>T. gonopleura</i> Böttger-Schnack, 1999*	
<i>O. similis</i>	<i>T. parasimilis</i> Böttger-Schnack, 1999*	
<i>O. hawii</i> long form	<i>T. recta</i> Böttger-Schnack, 1999	
	c. <i>dentipes</i> -subgroup	
<i>O. dentipes</i> form A (partim)	<i>T. dentipes</i> (Giesbrecht, 1891)	
	<i>T. elongata</i> Böttger-Schnack, 1999	
<i>O. dentipes</i> form B	<i>T. giesbrechti</i> Böttger-Schnack, 1999*	
	II. <i>Oncaea</i> s. str. (= <i>venusta</i> -group)	
	a. <i>venusta</i> -subgroup	
<i>O. venusta</i> f. <i>typica</i>	<i>O. venusta</i> Philippi, 1843 f. <i>typica</i> Farran, 1929*	
f. <i>venella</i>	f. <i>venella</i> Farran, 1929	
<i>O. mediterranea</i>	<i>O. mediterranea</i> (Claus, 1863)	
<i>O. media</i> f. <i>major</i>	<i>O. media</i> Giesbrecht, 1891	
<i>Oncaea</i> sp. AD	<i>O. waldemari</i> Bersano & Boxshall, 1994*	
<i>O. media</i> f. <i>minor</i>	<i>O. scottodicarloi</i> Heron & Bradford-Grieve, 1995	
<i>O. clevei</i>	b. <i>clevei</i> -subgroup	
	<i>O. clevei</i> Früchtl, 1923	
	<i>O. paraclevei</i> Böttger-Schnack, 1999*	
<i>Oncaea subtilis</i>	III. <i>Monothula</i> Böttger-Schnack & Huys, 2001	
Small-sized species (<0.5 mm)	<i>M. subtilis</i> (Giesbrecht, 1892)*	
<i>Oncaea ivlevi</i>	IV. <i>Spinoncaea</i> Böttger-Schnack, 2003	
	<i>S. ivlevi</i> (Shmeleva, 1966)	
	typical form sensu Böttger-Schnack, 2003	
	elongate form sensu Böttger-Schnack, 2003*	
<i>Oncaea ivlevi</i> / K (partim)	<i>S. humesi</i> Böttger-Schnack, 2003	
<i>Oncaea</i> sp. K	<i>S. tenuis</i> Böttger-Schnack, 2003	
<i>Oncaea zernovi</i>	V. <i>O. bispinosa</i> Böttger-Schnack, 2002	
B. Taxonomical analysis in progress		
<i>Oncaea ovalis</i>	VI. <i>Oncaea</i> sp. [new sibling species of <i>O. ovalis</i> Shmeleva 1968, to be described elsewhere]	
<i>O. tregoubovi</i>	VII. tentatively assigned to <i>O. tregoubovi</i> Shmeleva, 1968	
<i>O. atlantica</i>	VIII. <i>atlantica</i> -group	
	<i>O. atlantica</i> Shmeleva, 1967	
	+ 7 <i>atlantica</i> -morphotypes*?	
<i>O. platysetosa</i>	<i>O. platysetosa</i> Boxshall & Böttger, 1987	
	+ 5 <i>platysetosa</i> -morphotypes*?	
<i>O. vodjanitskii</i>	<i>O. vodjanitskii</i> Shmeleva & Delalo, 1965	
	+ 2 <i>vodjanitskii</i> -morphotypes*?	
	IX. <i>O. minima</i> Shmeleva, 1968, 2 morphotypes	
	X. <i>Epicalymma</i> sp.	
Total number of:		
Species (a)	21	30
Morphotypes (b)	5	17
Total of a + b	26	47

whereas the third species of the triplet, *T. giesbrechti*, and one species of another pair, the typological species *T. gonopleura*, were limited in regional distribution to the southern Red Sea (Table 1). Of the *T. similis*–*T.*

parasimilis siblings, only the newly described *T. parasimilis* was present in the area, recorded as a solitary find in the Strait of Bab al Mandab (southern Red Sea). The taxonomic study confirmed the occurrence of *T. conifera*

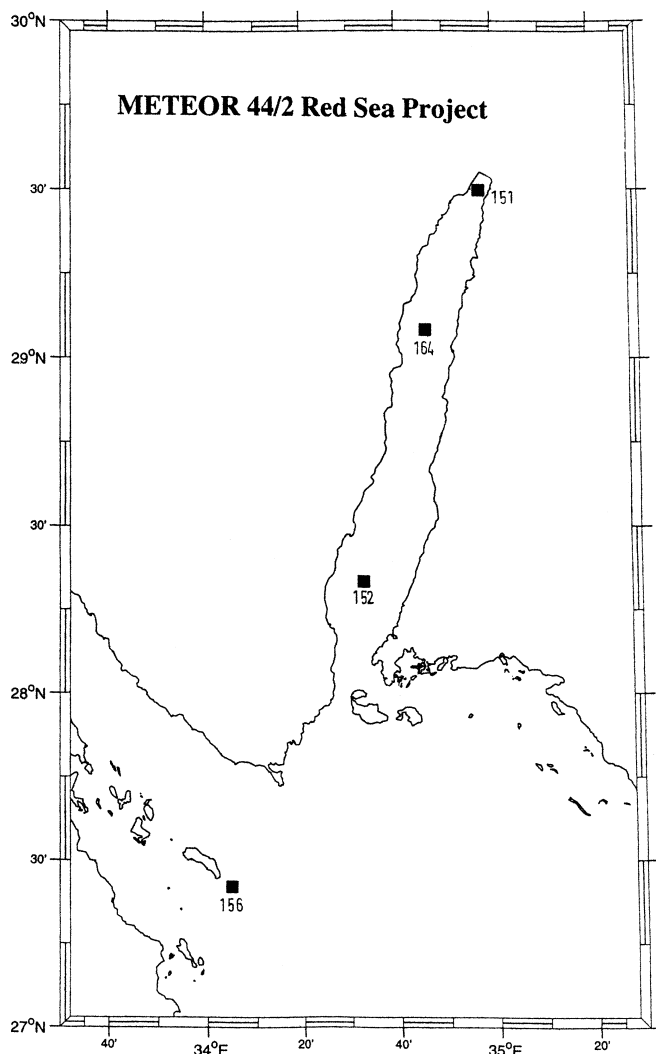


Fig. 2 Plankton sampling stations along a transect from the northernmost Red Sea to the Gulf of Aqaba (METEOR cruise 44/2: March–April 1999; after Böttger-Schnack et al. 2001)

(Giesbrecht) in the Red Sea basin, although very slight morphological differences in the anal somite and proportional lengths of spines on swimming leg 2 indicated that the Red Sea species might be regarded as a sibling of *T. conifera* (G. Heron, personal communication). Outside the Red Sea, however, the *conifera*-type oncaeid population in the Gulf of Aden belong to a morphologically different, yet closely related form which could not be assigned to any of the nine species of the *T. conifera* subgroup known at that time (Böttger-Schnack 1999). A continued revision of *conifera*-type oncaeids in the Red Sea and Gulf of Aden, including a detailed comparison with specimens from the type locality in the Mediterranean Sea and with recently described new species from the Pacific (Heron and Frost 2000), is necessary to fully elucidate their taxonomic status.

The revised genus *Oncaea* s.str. worldwide includes seven species, all of which occur in the Red Sea

Table 2 Abundance of two pairs of oncaeid sibling species on a transect from the northernmost Red Sea to the Gulf of Aqaba obtained during March 1999. Values are number of female individuals beneath 0.25 m² in the depth layer sampled (*DLS*) (*TWD*, total water depth; +, solitary find)

Species	Northern Red Sea	Gulf of Aqaba		
		South	Central	North
<i>DLS</i> (m)	0–750	0–750	0–800	0–450
<i>TWD</i> (m)	800	860	820	600
Epipelagic siblings				
<i>Spinoncaea ivlevi</i>	3000	1300 ^a	4400	2500
<i>S. humesi</i>	1500	96 ^a	100	< 50
Mesopelagic siblings				
<i>Triconia hawii</i>	300	180	66	140 ^b
<i>T. recta</i>	48	42	20	+

^aunderestimated (data from depth layer 100–150 m missing)

^bunderestimated (depth layers below 450 m not sampled)

(Table 1). Within the genus, one triplet of sibling species is known (*O. media*–*O. scottodicarloi*–*O. waldemari*) and a new species pair, *O. clevei*–*O. paraclevei*, has been described. Morphological differences of the two form variants of *O. venusta*, which differ mainly in size and in a few minor characters, were not regarded as being sufficient to warrant separation of them as different species (Böttger-Schnack 2001), although this may be regarded as a point of discussion (Heron 2002; Böttger-Schnack and Huys in press). An application of alternative taxonomic methods on *O. venusta* size variants using molecular-genetic analyses is currently in progress (D. Elvers and W. Hagen, personal communication). Within each group of siblings or form variants of *Oncaea* s.str., a different distribution pattern along the south–north axis of the Red Sea was recorded, with *O. venusta* f. *typica*, *O. paraclevei* and *O. waldemari* being limited to the southern part, while their corresponding siblings were distributed throughout the entire Red Sea (Table 1). All species are also found outside the Red Sea.

The three *Spinoncaea* siblings, two of which are new to science, co-occurred throughout the Red Sea main basin, but one of them, *S. humesi*, did not penetrate farther north into the Gulf of Aqaba in substantial numbers (Table 2). Outside the Red Sea, each *Spinoncaea* species was recorded from distant localities at low latitudes in all the major oceans (Böttger-Schnack 2003). However, several specimens of *S. ivlevi* and *S. tenuis* displayed some morphological differences; thus, further taxonomic studies are needed to clarify whether these morphs represent distinct, though closely related, species.

The *zernovi*-type oncaeid in the Red Sea was described as a new species, *Oncaea bispinosa*, which is closely related to *O. zernovi* Shmeleva, but can readily be distinguished by differences in the leg armature (Böttger-Schnack 2002). In contrast to other small-sized oncaeid siblings, which often co-occur throughout their zoogeographical ranges (e.g. *O. scottodicarloi*–*O. waldemari*, *Spinoncaea ivlevi*–*S. humesi*), the *O. zernovi*–*O. bispinosa* siblings were found to

differ in zoogeographical distribution: *O. bispinosa* seems to be provincial to the northern and equatorial Indian Ocean, including the Red Sea, whereas *O. zernovi* occurs in all the major oceans at low latitudes (Böttger-Schnack 2002). The two species did not co-occur in any area. This is the first pair of sibling species among the smaller oncaeids for which a distinct zoogeographical separation could be demonstrated.

For the remaining 5 oncaeid species and 17 morphotypes listed in Table 1, taxonomical analyses are still in progress. Preliminary results indicate that they can be classified into 5 species groups (i.e. genera) as defined by Böttger-Schnack and Huys (1998, 2001) within the Oncaeidae s.str.: the *ovalis*-type oncaeid in the Red Sea represents a new species and is a sibling of *Oncaea ovalis* Shmeleva, which will be described elsewhere. The new species has so far been recorded only from the Red Sea, but subsequent zoogeographical studies might show a wider geographical distribution. Oncaeid copepods of the *ovalis* complex have been found to be widely distributed in the Indo-Pacific region (R. Böttger-Schnack, unpublished data) and *O. ovalis*, which originally was known only from the Mediterranean, was recently recorded from the NE Pacific (Heron and Frost 2000). The *tregoubovi*-type in the Red Sea was tentatively assigned to *O. tregoubovi* Shmeleva, which is a sister taxon of *Spinoncaea* and, together with *Monothula subtilis*, *O. prendeli* Shmeleva and *O. curvata* Giesbrecht, these species were found to form a robust clade within the phylogenetic tree of Oncaeidae (Böttger-Schnack and Huys 2001). The *atlantica* group, which comprises very small species of about 0.25 mm in length, appears to be extremely speciose. In addition to the 3 known species, to date about 14 different morphotypes, based on the presence or absence of a modified, flattened outer basal seta on swimming legs 1–4, were recognized from the Red Sea (Table 1). The modified setae, which are also found on the antenna and sometimes on leg 5 and the caudal rami (*platysetosa* subgroup; see Boxshall and Böttger 1987), represent a unique character and can be used to separate the *atlantica* type from all other oncaeid groups. Whether the observed modifications of the basal setae on the swimming legs warrants the identification of all morphs as distinct species or has to be viewed as intraspecific variation in setal morphology can only be judged after detailed analyses of all morphotypes, including mouthparts and antennae, which is yet to be completed. The first record of an as yet unidentified species of *Epicalymma* is noteworthy, because the genus had previously been assumed to be absent from the Red Sea (Böttger-Schnack 1994, as *Oncaea* sp. 5). In the adjacent Arabian Sea, species of *Epicalymma* display a great diversity in the meso- and bathypelagic zone (Böttger-Schnack 1996, as species group 1), whereas the *Epicalymma* type in the Red Sea was monotypic and occurred from the epipelagic zone down to mesopelagic depths. The morphology of the minute species in the *minima* group, which represent the smallest oncaeid copepods yet discovered (0.18–0.2 mm body length), has not yet been examined in detail.

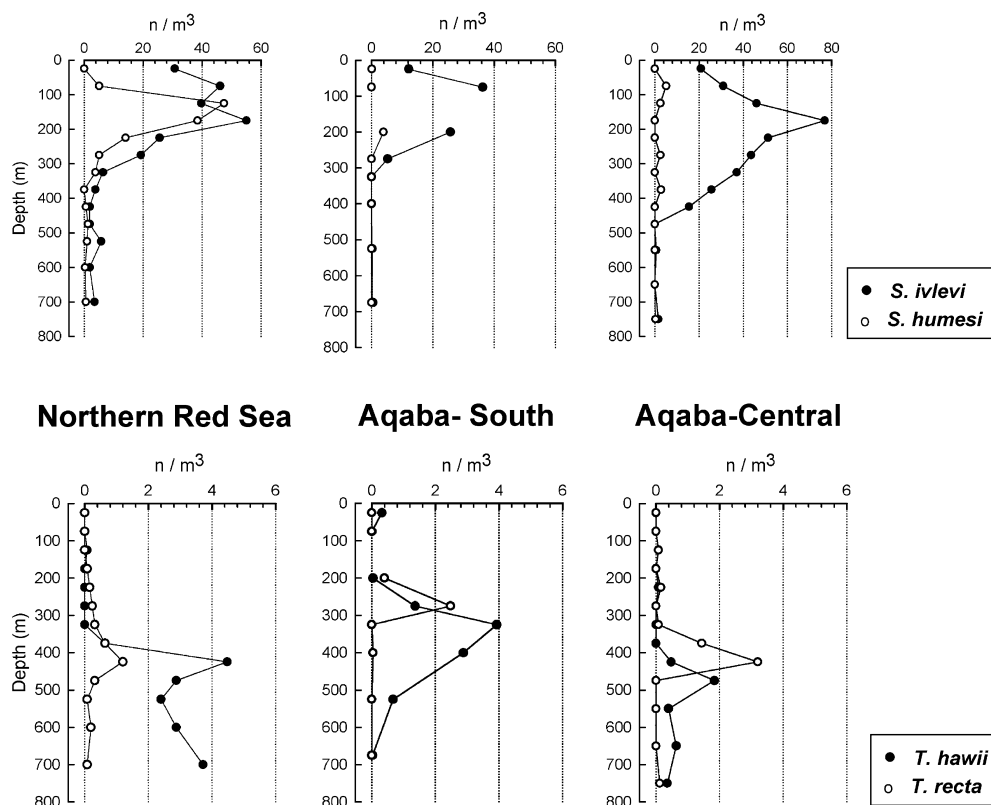
New results on abundance and vertical distribution of oncaeid sibling species

Four pairs and one triplet of oncaeid siblings, which were newly recorded during the taxonomic studies, had not been recognized as separate species during the earlier ecological investigations. For these species, which are *Triconia hawii*–*T. recta*, *T. umerus*–*T. gonopleura*, *T. dentipes*–*T. elongata*–*T. giesbrechti*, *Oncaea clevei*–*O. paraclevei*, and *Spinoncaea ivlevi*–*S. humesi*, additional quantitative investigations are required to estimate their abundance and species-specific vertical distribution in the Red Sea. New data on the abundance and vertical distribution of oncaeid species that were obtained during a current study on the microcopepod fauna in the northernmost Red Sea and the Gulf of Aqaba, including latest taxonomic findings, provide an opportunity to test the significance of the improved taxonomic resolution of oncaeids in ecological investigations. Selected examples are the abundance of females and the vertical distribution of two pairs of sibling species: the epipelagic *Spinoncaea ivlevi*–*S. humesi* pair and the mesopelagic *Triconia hawii*–*T. recta* pair. Females of the two *Spinoncaea* siblings differ in numerical abundance and in regional distribution between the Red Sea basin and the Gulf, with *S. ivlevi* being much more numerous and regionally extended than *S. humesi* (Table 2). The vertical distribution of the two siblings appears to be similar, since both species inhabit the same upper-300-m depth layer, though *S. humesi* seems to avoid the near-surface layer (Fig. 3). Females of the mesopelagic siblings *T. hawii*–*T. recta*, on the other hand, show less marked differences in regional distribution and numerical proportions (except for the northernmost Gulf), with *T. hawii* being two to four times more abundant than *T. recta* (Table 2). The two *Triconia* siblings differ in their vertical distribution: *T. recta* occurs shallower in the water column, at 200–450 m, than *T. hawii*, which is distributed between 300 and 600 m depth or even deeper (Fig. 3).

Discussion

The progress in the taxonomy of oncaeid copepods appears to be of significance with respect to various aspects of the earlier ecological studies from the Red Sea. The most important parameters to be checked include: (1) species diversity and zoogeographical distribution; (2) species-specific vertical distribution; (3) regional and seasonal differences of species abundances and the resulting spatio-temporal differences in the community structure of oncaeids. Several of the earlier hypotheses and conclusions need to be revised, as will be discussed, taking into consideration the latest findings in oncaeid species differentiation.

Fig. 3 Vertical distribution of two pairs of oncaeid sibling species in the northern Red Sea and Gulf of Aqaba during spring 1999: females of the epipelagic *Spinoncaea ivlevi* and *S. humesi* (upper row) and the mesopelagic *Triconia hawii* and *T. recta* (lower row). Note the differences in density scales



Species diversity and gradients along the south–north axis in the Red Sea

The species diversity of oncaeid copepods in the Red Sea has been considerably underestimated so far: at present it appears to be about twice as high as was assumed earlier (e.g. Böttger-Schnack 1994, 1995). The greatest increase in species numbers was found in the genus *Triconia*, all of which represent new siblings of known species, and probably in the *atlantica* group, for which the greatest number of new morphotypes was recorded but not yet completely described.

Regional differences in the numbers of oncaeid species between the south and the north in the Red Sea during summer appear to be more pronounced than was estimated previously (Böttger-Schnack 1995), because four of the newly described species (*Triconia gonopleura*, *T. parasimilis*, *T. giesbrechti* and *Oncaea paraclevei*) were mainly or completely restricted to the southern part. During summer, the invasion of the Red Sea basin by Gulf of Aden plankton is regarded as being at its lowest (Beckmann 1996), because surface currents in the Red Sea are directed southwards during this period, flowing over the Strait of Bab al Mandab into the Gulf (Morcos 1970; Patzert 1974; Maillard and Soliman 1986). During winter and spring, when the NE monsoons prevail over this area, the reversed surface currents flow northwards from the Gulf of Aden into the Red Sea, and copepod species of southern origin have successfully been used to trace the monsoon-driven inflow of Gulf of Aden surface water into the central Red Sea during this period

(Beckmann 1984; Böttger-Schnack 1990b). The new oncaeid species of southern origin could therefore be used as additional indicator species in future ecological studies.

Triconia recta, on the other hand, which previously had been regarded as being confined to the southern Red Sea (Böttger-Schnack 1999), was recently recorded from the northernmost area, including the Gulf of Aqaba (Böttger-Schnack et al. 2001), thereby demonstrating the difficulties in establishing zoogeographical boundaries of sibling species (see Knowlton 1993, and literature cited therein). The area north of 27°N, which had not been investigated during the earlier studies, showed a further reduction in species numbers of oncauids (Böttger-Schnack et al. 2001). On the whole, the south–north gradient in oncaeid species numbers in the Red Sea increased considerably now, from 31 species in the south (~13°N) to 23 species in the region north of 27°N (Böttger-Schnack et al. 2001). It is presumed that this ratio will increase further, as soon as the taxonomic status of the numerous new morphotypes of the *atlantica* group is clarified, most of which seem to be confined to the southern Red Sea. Thus the earlier hypothesis that Oncaeidae do not follow the general northward trend of reduced species diversity in the Red Sea has to be revised and the south–north gradient observed for this family now appears to be similar to that of other zooplankton taxa, such as chaetognaths (J.-P. Casanova 1985, 1990), pteropods (Rampal 1988, 1990), euphausiids (B. Casanova 1990) and various non-calanooid copepod families (Halim 1969; Böttger-Schnack 1995). Compared to

(larger) calanoid copepods, however, the regional decrease in oncaeid species numbers still appears to be somewhat lower, since only about half the numbers of calanoid species found in the southern Red Sea extend to the northern parts and the Gulf of Aqaba (Almeida Prado-Por 1983; Weikert 1987). Therefore it may still be assumed that oncaeid species are less sensitive to the strong horizontal gradients in the Red Sea, in particular the increasing salinity, than larger (calanoid) taxa, which may be related to their different mode of life (see below).

The latitudinal differences in the species numbers of oncaeids are most marked in the epi- and upper mesopelagic zones, where there is high environmental variability, as opposed to the rather uniform deeper layers. Deep-living oncaeids did not show a marked south-north gradient in species numbers and only a few additional species were newly recorded during the taxonomic analyses, which extend down to the lower mesopelagic zone (e.g. *Triconia recta*). Typical mesopelagic and/or deep-sea oncaeids, such as the genus *Conaea* sensu Heron or species of the *notopus* and the *ornata* groups are absent from the Red Sea (Böttger-Schnack 1994). Also, the newly recorded *Epicalymma* type in the Red Sea was monotypic and occurred at shallower depth than in the adjacent Arabian Sea, where this genus displays a great species diversity in the meso- and bathypelagic zones (Böttger-Schnack 1996, as species group 1). The lack of a special deep-sea fauna in Red Sea Oncaeidae corresponds to observations on various other zooplankton taxa (Weikert 1982, 1987) and has been explained by the extremely limited downward transport of organic matter to the bathypelagic zone caused by the unusually high deep-sea temperatures and correspondingly high remineralization (Wishner 1980; Weikert 1982).

Zoogeographical distribution of oncaeids outside the Red Sea

None of the newly recorded oncaeid species was restricted in its distribution to the Red Sea, except for *Triconia gonopleura*, which was a solitary find in the Strait of Bab al Mandab. *T. parasimilis*, another solitary find from the Straits (Böttger-Schnack 1999), was recently recorded from the NW Pacific (Y. Nishibe, personal communication) thus indicating a wider geographical distribution outside the Red Sea. Also, the record of *T. rufa* as an endemic Red Sea species (Böttger-Schnack 1994) is revised, since it was reported from the northern Arabian Sea later (Böttger-Schnack 1999). Thus the proportion of endemic species among oncaeid copepods in the Red Sea appears to be very low, which is similar to calanoid copepods, for which only 5 out of more than 60 species occurring in the Red Sea have been assumed to be endemic in this area (Halim 1969). A low proportion of endemic species in the Red Sea, which was isolated during Pleistocene glacial stages, seems to be the rule rather than the exception. This is also indicated by

the low number of endemic pteropods and benthic foraminiferans even in the northernmost extension of the Red Sea, the Gulf of Aqaba (Reiss and Hottinger 1984). Many faunal elements may have been extinguished over the past 75,000 years by rapid environmental changes, when the Basin's connection with the Gulf of Aden was recurrently interrupted by the 137-m-shallow Hanish Sill (Por 1978). Speciation rates of mixed-layer calanoid copepods at low latitudes are suggested as falling between 10^6 and 10^4 years (Fleminger 1986). This time span is apparently too long to allow for a rich speciation in zooplankton in general, when the recolonization by Indian Ocean species started about 10,000 years ago.

However, the absolute number of endemic species among Red Sea oncaeids might be underestimated, since taxonomic studies in the adjacent areas are not yet complete. Some *Triconia* species, for instance, are assumed to be represented by different morphotypes in these neighbouring areas (Böttger-Schnack 1999). This was most conspicuous for the population of *T. conifera* in the Gulf of Aden, compared to the morphologically distinct population from the Red Sea. In the earlier ecological studies it had been found that *T. conifera* displays a conspicuous regional distribution, with minimal numbers in the southern Red Sea and higher numbers to the south (Gulf of Aden) as well as to the north (central Red Sea) (Böttger-Schnack 1995). This unusual pattern of horizontal distribution can now be explained by the existence of two morphologically different species or forms, which seem to be geographically separated. The results further substantiate the significant changes in the species composition and community structure of oncaeids between the Red Sea and the Gulf of Aden reported by Böttger-Schnack (1995). A sharp change in population structure has also been reported for the large calanoid copepod *Pleuromamma indica*. This species undergoes a significant change in the asymmetry of the dark organ on the second thoracic somite, between the Red Sea population, with about 50% right-sided specimens, and populations in the Gulf of Aden and the northern Arabian Sea, with less than 20% right-sided specimens (Beckmann 1996). The significance and maintenance of such a sharp morphological cline within a copepod population, perhaps one of the sharpest in marine waters, still remains a point of debate (Beckmann 1996).

Species-specific vertical distribution

The earlier ecological results on the abundance and vertical distribution of oncaeid species in the Red Sea (Böttger-Schnack 1988, 1990a, 1990b, 1995) can now be confirmed for those 20 species or form variants which had been treated separately during the quantitative studies (e.g. *Oncaea media*, *O. scottodicaloi*, *O. venusta* f. *typica* and f. *venella*). Earlier quantitative data will have to be revised, however, for another five species,

owing to the existence of sibling species which had not been separated during the quantitative studies. The examples given in the present paper indicate that in some cases considerable changes to the earlier data can be expected. Females of the mesopelagic siblings *Triconia hawaii*–*T. recta*, for instance, clearly differ in their depth distribution. The vertical segregation of closely related species is regarded as one possibility for marine copepods to avoid competition, e.g. for food, since they are assumed to use similar resources (Harris 1987). When two sibling species occupy almost the same depth layer, such as in the epipelagic *Spinoncaea ivlevi*–*S. humesi* pair, habitat selection may occur on an even finer vertical scale than had been previously examined. Small-scale vertical peaks of abundances are typically found in epipelagic zooplankton taxa (Longhurst 1976, 1985), but could not be detected during the present study based on integrated samples over depth intervals of 50 m. Thus, a vertical separation of the two *Spinoncaea* species might possibly be found once the adequate sampling strategy is employed. In addition, differences in horizontal distribution are obvious between the two species (*S. humesi* does not penetrate farther north into the Gulf of Aqaba). Horizontal separation of closely related species has been repeatedly observed in marine copepod communities, as for instance in the Candaciidae (Lawson 1977), congeners of *Centropages* (cf. Halsband-Lenk et al. 2002) or sibling species of *Pseudocalanus* (cf. Bucklin et al. 1998). Co-occurring sibling species may also exhibit differences in population dynamics and species life-histories. An excellent example for this has been reported by Yamaguchi et al. (1998) for the co-occurring calanoid copepods *Pseudocalanus minutus* and *P. newmani* in the southern Japan Sea, which were found to differ significantly in seasonal abundance and population structure. From these data, differences in generation times and life cycles were derived for the two sibling species (Yamaguchi et al. 1998).

Several oncaeid species had a bimodal vertical distribution in the Red Sea main basin. This was most conspicuous for *Oncaea scottodicalloi*, which exhibited a population peak in both the lower epipelagic and the upper mesopelagic zone (Böttger-Schnack 1990a). It was uncertain whether this pattern could have resulted from the existence of two different forms (or species) that are vertically separated. The taxonomic results now confirm that both populations are conspecific. Temporary bimodal vertical distributions of marine copepods may be caused by partial vertical migration (Andersen et al. 2001), which is regarded as a mechanism to increase intraspecific diversity of a copepod population (Hattori 1989), but this is not the case in *O. scottodicalloi*, which exhibited a permanent separation of the two populations, and only parts of the shallow-living population migrated vertically (Böttger-Schnack 1990a). Another explanation might be that the copepods avoid strong environmental gradients, created by temperature, salinity or oxygen, which can be reinforced by current shears (Angel 1968). Minimal concentrations of *O. scottodi-*

carloi in the central Red Sea coincided with strong oxygen gradients occurring between 100 and 250 m depth in this area (Edwards 1987; Böttger-Schnack 1990a) which seems to be avoided by the species. The same explanation might be applied to other poecilostomatoid species with a bimodal vertical distribution, such as *Lubbockia squillimana* and *O. bispinosa* (cf. Böttger-Schnack 1990a, 1990b, 2002). Generally, the depth layers of oxygen gradients are known to be avoided by zooplankton organisms in the Red Sea (Weikert 1980; Beckmann 1996), but no bimodality has been observed for other zooplankton species so far. Future investigations of Red Sea populations of *O. scottodicalloi* are envisaged in the Gulf of Aqaba, where no oxygen gradient is found, to obtain further information on the reactions of this ubiquitous species to local hydrographical conditions.

Species abundances and community structure of oncaeid copepods

The significance of the improved taxonomic resolution for the species abundances and community structure of oncaeid microcopepods in the Red Sea can only be assessed by subsequent ecological studies. This could be achieved either by re-evaluating the earlier data, as has been done before for the separation of a single *Spinoncaea* species, *S. tenuis*, in the Red Sea (Böttger-Schnack 1992, as *Oncaea* sp. K), or by providing new data on the copepod community by taking into consideration the latest findings in oncaeid species differentiation. Examples from the current Aqaba study presented herein demonstrate that major changes will have to be expected in the community structure of epipelagic microcopepods as a result of the detection of a new sibling species among the most common epipelagic oncaeid, *Spinoncaea ivlevi*. The combined species accounted for up to 40% of the total number of oncaeids in the upper 250 m of the water column in the past (e.g. Böttger-Schnack 1995), which is equivalent to up to 15% of all copepods in this layer. The previously unknown sibling *S. humesi* now proved to be numerically very important (at least in the Red Sea main basin), contributing as much as 30% to the total number of the two species combined (Table 2). As for the community structure of meso- and bathypelagic microcopepods, on the other hand, less conspicuous changes will have to be expected, because the newly described oncaeid siblings from deeper layers are less abundant (e.g. *Triconia recta*), and the dominant species (e.g. *Oncaea tregoubovi*, *S. tenuis* and the new *ovalis*-type oncaeid) are confirmed to be monospecific by the taxonomic analyses.

Potential ecological significance of oncaeid species and perspectives of future studies

The progress in the taxonomy of Red Sea Oncaeidae, derived so far from morphological documentation and

classification of 23 species, has indicated a much higher complexity of this microcopepod community than was previously known. The species complexity of Oncaeidae, as demonstrated in the Red Sea, indicates a corresponding complexity in the ecological interactions within this copepod family. At present, the ecological significance of the improved taxonomic resolution can only be hypothesized, since the ecology of oncaeid species is still poorly known. However, the few published data on habitat preference, feeding and reproduction of oncaeids already point to a very different mode of life of this poecilostomatoid taxon as compared to similar-sized calanoid and cyclopoid microcopepod taxa.

Regarding habitat preference, Oncaeid copepods show a “creeping” swimming behaviour (Hwang and Turner 1995) and are partly pseudopelagic, being loosely associated with marine snow in surface waters (Green and Dagg 1997) and gelatinous matter, such as houses of appendicularians (e.g. Alldredge 1976). Whether this habitat preference is a general characteristic of the family or occurs only in certain species is unknown, since no attempt has been made to identify the species community of associated oncaeids so far. The numerous deep-living oncaeids from the meso- and bathypelagic zones may also be associated with gelatinous plankton and/or mucous material, because giant appendicularians and their houses occur at these depths as well (e.g. Davoll and Youngbluth 1990; Steinberg et al. 1997).

Regarding food and feeding, the oncaeid diet includes a wide spectrum of prey, ranging from phytoplankton cells, flagellates, to crustacean plankton and appendicularians (e.g. Pasternak 1984; Turner 1986; Ohtsuka et al. 1996). The substrate-feeding modus of oncaeid copepods enables them to utilize colonial phytoplankton cells (*Phaeocystis* spp.) as a preferred food (Metz 1998), which escape filter-feeding copepods by their large size and have thus been regarded as “nuisance algae” by some marine ecologists (Sommer and Stibor 2002). Gut-fluorescence measurements of oncaeids showed that they exhibit higher weight-specific chlorophyll contents than similar-sized calanoid filter-feeders (Arinardi et al. 1990) and their ingestion rates were calculated to be similar to or even higher than those of small calanoids (Dagg 1995). On the other hand, oncaeids have been observed to attack large prey, such as chaetognaths (Go et al. 1998; B.-C. Oh, personal communication) and large copepods, cutting off the antennules or the urosome (S. Schnack-Schiel, personal communication; see also Metz 1998). Traditionally, the entire group is regarded as food generalists or “omnivore” (Timonin 1971), and this classification has been adopted also for studies on the trophic structure of Red Sea zooplankton (Beckmann 1996), but they have also been classified as “carnivore” (e.g. Arinardi 1990) or “detritivore” (Yamaguchi et al. 2002). Published data on the food of oncaeids are still restricted to a few larger species feeding in the upper water (surface) layers, such as the epipelagic *Oncaea venusta* (Turner 1986) or the vertically migrating *Triconia conifera* (Ohtsuka et al. 1996) and *O. curvata* (Metz

1998), but interspecific differences between oncaeid species, as indicated in a recent study in the Red Sea (Ohtsuka et al. 1996), have not been investigated in sufficient detail yet. Virtually nothing is known about the food requirements of the smaller species of less than 0.5 mm in length and of those in the meso- and bathypelagic zones. If oncaeid copepods are viewed in toto as substrate feeders, they may contribute substantially to a rapid remineralization of particulate organic matter in the water column (e.g. Gonzalez et al. 2000), a pathway which has not yet been sufficiently considered in marine pelagic food-web studies and estimations of vertical carbon flux (Kjørboe 1998; but see Yamaguchi et al. 2002). Stable isotope tracing may be an important tool to discriminate between trophic levels, as exemplified for size-class-based mesozooplankton communities at mid-water and abyssopelagic depths (Koppelman and Weikert 2000). Analyses of lipid composition might also be helpful to study the food sources of deep-living oncaeids, which are often densely filled with oil droplets, such as *ovalis*-type oncaeids in the Red Sea (R. Böttger-Schnack, personal observation) or *Triconia canadensis* in the Pacific (Y. Nishibe, personal communication), and appear to survive extremely long starvation times (Y. Nishibe, personal communication). For calanoid copepod species, determination of the lipid composition has been successfully used to shed light on their food selection (e.g. Bühring and Christiansen 2001) and life-histories (e.g. Hagen and Schnack-Schiel 1996).

Regarding reproduction, the reproductive biology of oncaeids is another important parameter to be investigated in the future, since it is crucial for the assessment of differences between taxonomic (species, subspecies) as well as ecological (populations) groups. So far, oncaeid species (which are egg-carriers) have not been successfully reared from the egg to the adult, which is mainly due to the insufficient knowledge of their food requirements (e.g. Paffenhöfer 1993), and only scattered information is available on the morphology and stage duration of their developmental stages (e.g. Malt 1982; Webber and Roff 1995; Metz 1996). Adult females appear to be long-lived in laboratory cultures (Paffenhöfer 1993; Metz 1996) even under starvation conditions (Y. Nishibe, personal communication), and their longevity has been viewed as a mechanism to compensate for a relatively low-egg production rate of oncaeids compared to free-spawning calanoid microcopepods (Paffenhöfer 1993). Production estimates have only been obtained for a few large oncaeids, such as *Oncaea mediterranea* (Paffenhöfer 1993; Webber and Roff 1995) and *O. venusta* (Hirakawa 1995), which possibly are not representative of the entire family. These large oncaeid species have a high number of relatively small eggs per female and thus may exhibit a different reproduction strategy from that of smaller oncaeids of <0.5 mm in size, which carry only few, large eggs per female (Böttger-Schnack et al. 1989; Böttger-Schnack 2003).

In the future, besides a continued effort to study the spatio-temporal distributions and population dynamics

of oncaeid species in the field, more information on biological and ecological parameters, in particular food requirements and reproduction, are needed from experimental and field studies. For these studies, a profound knowledge of the taxonomy of oncaeids appears essential in view of the great number of sibling species in this copepod family. Uncertainties in species resolution for Oncaeidae and for marine microcopepods in general require great care in the interpretation of results from previous ecological studies. There are numerous examples in the literature, in which closely related oncaeid species have been confounded with each other, such as the *media* complex, which presently includes three species (Heron and Bradford-Grieve 1995; Böttger-Schnack 2001). *Oncaea media* has been reported as a dominant copepod species from a wide range of localities, such as the Mediterranean Sea (e.g. Mazzocchi and Ribera d'Alcala 1995; Böttger-Schnack 1997), the open and neritic NE Pacific (Star and Mullin 1981), the Inland Sea of Japan (Madhupratap and Onbé 1986; Checkley et al. 1992) and the NW Pacific (Noda et al. 1998); however, in view of the identification problems, it remains uncertain whether different species of the *media* complex had been mistakenly combined in these studies. For instance, specimens of *O. media* examined during a study of seasonal body-length variation in the Lagoon of Venice (Riccardi and Mariotto 2000) were assigned solely to *O. waldemari* upon a recent taxonomic re-examination (R. Böttger-Schnack, unpublished data), whereas the specimens recorded as *O. media* f. *minor* in the eastern Mediterranean (Böttger-Schnack 1997) were found to include two species, *O. scottodicarloi* and *O. waldemari* (R. Böttger-Schnack, unpublished data). The copepod material of *O. media* from the northern Aegean Sea used for feeding experiments (Zervoudaki et al. 2002) obviously consisted of a mixture of all three species of the *media* complex (R. Böttger-Schnack, unpublished data). The key question asked by the ecologists: "At what level are we safe in lumping species versus splitting species?" Or: "To what extent are taxonomically very similar species (sibling species) different in their ecological interaction?" cannot yet be answered for marine microcopepods. A concerted action of taxonomists and ecologists is required to assess the ecological significance of the complex taxonomic structure of oncaeid microcopepods, which for a long time have been known to be numerically important in the world ocean, but have rarely been investigated ecologically.

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References

- Allredge AL (1976) Discarded appendicularian houses as source of food, surface habitat and particulate organic matter in planktonic environments. *Limnol Oceanogr* 21:14–23
- Almeida Prado-Por MS (1983) The diversity and dynamics of Calanoida (Copepoda) in the northern Gulf of Elat (Aqaba), Red Sea. *Oceanol Acta* 6:139–145
- Andersen V, Gubanova A, Nival P, Ruellet T (2001) Zooplankton community during the transition from spring bloom to oligotrophy in the open NW Mediterranean and effects of wind events. 2. Vertical distributions and migrations. *J Plankton Res* 23:243–261
- Angel MV (1968) The thermocline as an ecological boundary. *Sarsia* 34:299–312
- Arinardi OH, Baars MA, Osterhuis SS (1990) Grazing in tropical copepods, measured by gut fluorescence, in relation to seasonal upwelling in the Banda Sea (Indonesia). *Neth J Sea Res* 25:545–560
- Beckmann W (1984) Mesozooplankton distribution on a transect from the Gulf of Aden to the central Red Sea during the winter monsoon. *Oceanol Acta* 7:87–102
- Beckmann W (1996) Der Einfluß der großräumigen Wasser-austauschvorgänge auf den Zooplanktonbestand des Roten Meeres und sein trophisches Gefüge. Dissertation thesis, University of Hamburg
- Böttger R (1987) The vertical distribution of micro- and small mesozooplankton in the central Red Sea. *Biol Oceanogr* 4:383–402
- Böttger-Schnack R (1988) Observations on the taxonomic composition and vertical distribution of cyclopoid copepods in the central Red Sea. *Hydrobiologia* 167/168:311–318
- Böttger-Schnack R (1990a) Community structure and vertical distribution of cyclopoid copepods in the Red Sea. I. Central Red Sea autumn 1980. *Mar Biol* 106:473–485
- Böttger-Schnack R (1990b) Community structure and vertical distribution of cyclopoid copepods in the Red Sea. II. Aspects of regional and seasonal differences. *Mar Biol* 106:487–501
- Böttger-Schnack R (1992) Community structure and vertical distribution of cyclopoid and poecilostomatoid copepods in the Red Sea. III. Re-evaluation for separating a new species of *Oncaea*. *Mar Ecol Prog Ser* 80:301–304
- Böttger-Schnack R (1994) The microcopepod fauna in the eastern Mediterranean and Arabian Seas: a comparison with the Red Sea fauna. *Hydrobiologia* 292/293:271–282
- Böttger-Schnack R (1995) Summer distribution of micro- and small mesozooplankton in the Red Sea and Gulf of Aden, with special reference to non-calanoïd copepods. *Mar Ecol Prog Ser* 118:81–102
- Böttger-Schnack R (1996) Vertical structure of small metazoan plankton, especially non-calanoïd copepods. I. Deep Arabian Sea. *J Plankton Res* 18:1073–1101
- Böttger-Schnack R (1997) Vertical structure of small metazoan plankton, especially non-calanoïd copepods. II. Deep eastern Mediterranean (Levantine Sea). *Oceanol Acta* 20:399–419
- Böttger-Schnack R (1999) Taxonomy of Oncaeidae (Copepoda:Poecilostomatoida) from the Red Sea. I. 11 species of

- Triconia* gen. nov., and a redescription of *T. similis* (Sars) from Norwegian waters. Mitt Hamb Zool Mus Inst 96:39–128
- Böttger-Schnack R (2001) Taxonomy of Oncaeiidae (Copepoda:Poecilostomatoida) from the Red Sea. II. Seven species of *Oncaea* s. str. Bull Nat Hist Mus London (Zool) 67:25–84
- Böttger-Schnack R (2002) Taxonomy of Oncaeiidae (Copepoda:Poecilostomatoida) from the Red Sea. VI. Morphology and zoogeography of *Oncaea bispinosa* sp.nov., a sister taxon of *O. zernovi* Shmeleva. J Plankton Res 24:1107–1129
- Böttger-Schnack R (2003) Taxonomy of Oncaeiidae (Copepoda:Poecilostomatoida) from the Red Sea. V. Three species of *Spinoncaea* gen. nov. (*ivlevi*-group), with notes on zoogeographical distribution. Zool J Linn Soc 137:187–226
- Böttger-Schnack R, Huys R (1997) Morphological observations on *Oncaea mediterranea* (Claus, 1863) (Copepoda, Poecilostomatoida) with a comparison of Red Sea and eastern Mediterranean populations. Bull Nat Hist Mus London (Zool) 63:137–147
- Böttger-Schnack R, Huys R (1998) Species groups within the genus *Oncaea* (Copepoda, Poecilostomatoida). J Mar Syst 15:369–371
- Böttger-Schnack R, Huys R (2001) Taxonomy of Oncaeiidae (Copepoda, Poecilostomatoida) from the Red Sea. III. Morphology and phylogenetic position of *Oncaea subtilis* Giesbrecht, 1892. Hydrobiologia 453/454:467–481
- Böttger-Schnack R, Huys H (2003) Size polymorphism in *Oncaea venusta* Philippi, 1843 and the validity of *O. frosti* Heron, 2002: a commentary. Hydrobiologia (in press)
- Böttger-Schnack R, Schnack D, Weikert H (1989) Biological observations on small cyclopoid copepods in the Red Sea. J Plankton Res 11:1089–1101
- Böttger-Schnack R, Hagen H, Schnack-Schiel SB (2001) The microcopepod fauna in the Gulf of Aqaba, northern Red Sea: species diversity and distribution of Oncaeiidae (Poecilostomatoida). J Plankton Res 23:1029–1035
- Boxshall GA, Böttger R (1987) Two new species of *Oncaea* (Copepoda:Poecilostomatoida) from the Red Sea and redescription of *O. atlantica* Shmeleva. J Plankton Res 9:553–564
- Bucklin A, Buckley AM, Franzen SP (1998) Distribution and relative abundance of *Pseudocalanus moultoni* and *P. newmani* (Copepoda:Calanoida) on Georges Bank using molecular identification of sibling species. Mar Biol 132:97–106
- Bühning SI, Christiansen C (2001) Lipids in selected abyssal benthopelagic animals: links to the epipelagic zone? Prog Oceanogr 50:369–382
- Casanova B (1990) Biologie et biogéographie des euphausiacés de la mer Rouge. Relations avec les mers voisines. In: Godeaux J (ed) A propos des migrations lessepsiennes. Bull Inst Océanogr Monaco no spéc 7:117–129
- Casanova J-P (1985) Les chaetognathes de la mer Rouge. Remarques morphologiques et biogéographiques. Description de *Sagitta erythraea* sp.n. Rapp P-v Réun Comm Int Explor Scient Mer Méditer 29:269–274
- Casanova J-P (1990) Taxonomie et biogéographie des chaetognathes de la mer Rouge. Comparaison avec les mers voisines. In: Godeaux J (ed) A propos des migrations lessepsiennes. Bull Inst Océanogr Monaco no spéc 7:89–102
- Checkley DM Jr, Uye S, Dagg MJ, Mullin MM, Omori M, Onbé T, Zhy M-Y (1992) Diel variation of the zooplankton and its environment at neritic stations in the Inland Sea of Japan and the north-west Gulf of Mexico. J Plankton Res 14:1–40
- Cornils A (2001) Räumliche Verbreitung von Phyto- und Zooplankton im nördlichen Roten Meer. Diplomarbeit Universität Kiel
- Cowles TJ, Roman MR, Gauzens AL, Copley NJ (1987) Short-term changes in the biology of a warm-core ring: zooplankton biomass and grazing. Limnol Oceanogr 32:653–664
- Dagg MJ (1995) Copepod grazing and the fate of phytoplankton in the northern Gulf of Mexico. Cont Shelf Res 15:1303–1317
- Davoll PJ, Youngbluth MJ (1990) Heterotrophic activity on appendicularian (Tunicata:Appendicularia) houses in mesopelagic regions and their potential contribution to particle flux. Deep-Sea Res 37:285–294
- Edwards FJ (1987) Climate and oceanography. In: Edwards AJ, SM Head (eds) Red Sea. Key environments. Pergamon Press, Oxford, pp 45–69
- Fleminger A (1986) The pleistocene equatorial barrier between the Indian and Pacific Oceans and a likely cause for Wallace's Line. In: Pierrot-Bults AC, van der Spoel S, Zahuranec BJ, Johnson RK (eds) Pelagic biogeography. Proceedings of an international conference. The Netherlands 29 May–5 June 1985. Unesco Tech Pap Mar Sci 49:84–97
- Go Y-B, Oh B-C, Terazaki M (1998) Feeding behaviour of the poecilostomatoid copepods *Oncaea* spp. on chaetognaths. J Mar Syst 15:475–482
- Gonzalez HE, Ortiz VC, Sobarzo M (2000) The role of faecal material in the particulate organic carbon flux in the northern Humboldt Current, Chile (23°C), before and during the 1997–1998 El Niño. J Plankton Res 22:499–529
- Green EP, Dagg MJ (1997) Mesozooplankton associations with medium to large marine snow aggregates in the northern Gulf of Mexico. J Plankton Res 19:435–447
- Hagen W, Schnack-Schiel SB (1996) Seasonal lipid dynamics in dominant Antarctic copepods: energy for overwintering or reproduction? Deep-Sea Res 43:139–158
- Halim Y (1969) Plankton of the Red Sea. Oceanogr Mar Biol Annu Rev 7:231–275
- Halsband-Lenk C, Hirche H-J, Carlotti F (2002) Temperature impact on reproduction and development of congener copepod populations. J Exp Mar Biol Ecol 271:121–153
- Harris RP (1987) Spatial and temporal organization in marine plankton communities. In: Gee JHR, Giller PS (eds) Organization of communities past and present. Blackwell, Palo Alto, pp 327–346
- Hattori H (1989) Bimodal vertical distribution and diel migration of the copepods *Metridia pacifica*, *M. okhotensis* and *Pleuromamma scutellata* in the western North Pacific Ocean. Mar Biol 103:39–50
- Head SM (1987) Introduction. In: Edwards AJ, Head SM (eds) Red Sea. Key environments. Pergamon Press, Oxford, pp 1–21
- Heron GA (1977) Twenty-six species of Oncaeiidae (Copepoda: Cyclopoida) from the southwest Pacific–Antarctic area. In: Pawson DL (ed) Biology of the Antarctic Seas. VI. Antarct Res Ser 26:37–96
- Heron GA (2002) *Oncaea frosti*, a new species (Copepoda: Poecilostomatoida) from the Liberian coast and the Gulf of Mexico. Hydrobiologia 480:145–154
- Heron GA, Bradford-Grieve JM (1995) The marine fauna of New Zealand: pelagic Copepoda: Poecilostomatoida: Oncaeiidae. NZ Oceanogr Inst Mem104:1–57
- Heron GA, Frost BW (2000) Copepods of the family Oncaeiidae (Crustacea: Poecilostomatoida) in the northeast Pacific Ocean and inland coastal waters of Washington State. Proc Biol Soc Wash 113:1015–1063
- Heron GA, English TS, Damkaer DM (1984) Arctic Ocean Copepoda of the genera *Lubbockia*, *Oncaea* and *Epicalymma* (Poecilostomatoida: Oncaeiidae), with remarks on distributions. J Crustac Biol 4:448–490
- Hirakawa K (1995) Effects of temperature on egg production of a warm-water copepod *Oncaea venusta* Philippi (Poecilostomatoida) (in Japanese, English abstract). Bull Jpn Sea Natl Fish Resour Inst 45:39–45
- Hopcroft RR, Roff JC, Lombard D (1998) Production of tropical copepods in Kingston Harbour, Jamaica: the importance of small species. Mar Biol 130:593–604
- Hopcroft RR, Roff JC, Chavez FP (2001) Size paradigms in copepod communities: a re-examination. Hydrobiologia 453/454:133–141

- Huys R, Böttger-Schnack R (1996/1997) On the diphyletic origin of the Oncaeidae Giesbrecht, 1892 (Copepoda: Poecilostomatoida) with a phylogenetic analysis of the Lubbockiidae fam. nov. *Zool Anz* 235:243–261
- Hwang J-S, Turner JT (1995) Behaviour of cyclopoid, harpacticoid and calanoid copepods from coastal waters of Taiwan. *PSZNI Mar Ecol* 16:201–216
- Judkins DC (1980) Vertical distribution of zooplankton in relation to the oxygen minimum off Peru. *Deep-Sea Res* 27A:475–487
- Kjørboe T (1998) Population regulation and role of mesozooplankton in shaping marine pelagic food webs. In: Tamminen T, Kuosa H (eds) Eutrophication in planktonic ecosystems: food web dynamics and elemental cycling. *Hydrobiologia* 363:13–27
- Knowlton N (1993) Sibling species in the sea. *Annu Rev Ecol Syst* 24:189–216
- Koppelman R, Weikert H (2000) Transfer of organic matter in the deep Arabian Sea zooplankton community: insights from ¹⁵N analysis. *Deep-Sea Res II* 47:2653–2672
- Kršinić F (1998) Vertical distribution of protozoan and microcopepod communities in the South Adriatic pit. *J Plankton Res* 20:1033–1060
- Lawson TJ (1977) Community interactions and zoogeography of the Indian Ocean Candaciidae (Copepoda: Calanoida). *Mar Biol* 43:71–92
- LeBrasseur RJ, Kennedy OD (1972) Microzooplankton in coastal and oceanic areas of the Pacific subarctic water mass: a preliminary report. In: Takenouti AY (ed) Biological oceanography of the northern North Pacific Ocean. Idemitsu Shoten, Tokyo, Japan, pp 355–365
- Lenz J, Schneider G, El Haq AGD, Gradinger R, Fritsche P, Moigis A, Pillen T, Rolke M, Weisse T (1988) Planktological data from the central Red Sea and the Gulf of Aden. R.V. "Meteor", cruise No. 5/2, January-March 1987. *Ber Inst Meeresk Kiel* 180:1–200
- Longhurst AR (1976) Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean. *Deep-Sea Res* 23:729–754
- Longhurst AR (1985) Relationship between diversity and the vertical structure of the upper ocean. *Deep-Sea Res* 32:1535–1570
- Madhupratap M, Onbé T (1986) Structure and species diversity of the zooplankton community of the Inland Sea of Japan. *Estuar Coast Shelf Sci* 23:725–737
- Maillard C, Soliman GF (1986) Hydrography of the Red Sea and exchanges with the Indian Ocean in summer. *Oceanol Acta* 9:249–269
- Malt SJ (1982) Developmental stages of *Oncaea media* Giesbrecht, 1891 and *Oncaea subtilis* Giesbrecht, 1892. *Bull Brit Mus (Nat Hist)* Zool 43:129–151
- Malt SJ (1983) Studies on the taxonomy and ecology of the marine copepod genus *Oncaea* Philippi. PhD dissertation, University of London
- Mazzocchi MG, Ribera D'Alcala M (1995) Recurrent patterns in zooplankton structure and succession in a variable coastal environment. *ICES J Mar Sci* 52:679–692
- Metz C (1996) Life strategies of dominant Antarctic Oithonidae (Cyclopoida, Copepoda) and Oncaeidae (Poecilostomatoida, Copepoda) in the Bellingshausen Sea (in German, English abstract). *Ber Polarforsch/Rep Polar Res* 207:1–123
- Metz C (1998) Feeding of *Oncaea curvata* (Poecilostomatoida, Copepoda). *Mar Ecol Prog Ser* 169:229–235
- Morcos SA (1970) Physical and chemical oceanography of the Red Sea. *Oceanogr Mar Biol Annu Rev* 8:73–202
- Noda M, Ikeda I, Ueno S, Hashimoto H, Gushima K (1998) Enrichment of coastal zooplankton communities by drifting zooplankton patches from the Kuroshio front. *Mar Ecol Prog Ser* 170:55–65
- Ohtsuka S, Böttger-Schnack R, Okada M, Onbé T (1996) In situ feeding habits of *Oncaea* (Copepoda: Poecilostomatoida) from the upper 250 m of the central Red Sea, with special reference to consumption of appendicularian houses. *Bull Plankton Soc Jpn* 43:89–105
- Paffenhöfer G-A (1993) On the ecology of marine cyclopoid copepods (Crustacea, Copepoda, Cyclopoida). *J Plankton Res* 15:37–55
- Pasternak AF (1984) Feeding of copepods of genus *Oncaea* (Cyclopoida) in the southeastern Pacific Ocean. *Oceanology* 24:609–612
- Patzert WC (1974) Wind-induced reversal in the Red Sea circulation. *Deep-Sea Res* 21:109–121
- Pätzold J, Halbach PE, Hempel G, Weikert H (2000) Östliches Mittelmeer–Nördliches Rotes Meer [eastern Mediterranean–northern Red Sea] 1999, Cruise No. 44, 22 January–16 May 1999. Meteor-Berichte 00–3, Universität Hamburg
- Por FD (1978) Lessepsian migration. *Ecological Studies* 23. Springer, Berlin Heidelberg New York
- Rampal J (1988) Les thécosomes de la mer Rouge. *Rapp P-v Réunion Comm Int Explor Sci Mer Méditer* 31:300
- Rampal J (1990) Les thécosomes de la mer Rouge. In: Godeaux J (ed) A propos des migrations lessepsiennes. *Bull Inst Océanogr Monaco no spéc* 7:103–107
- Reiss Z, Hottinger L (1984) The Gulf of Aqaba. *Ecological micropaleontology*. Springer, Berlin Heidelberg New York
- Riccardi N, Mariotto L (2000) Seasonal variations in copepod body length: a comparison between different species in the Lagoon of Venice. *Aquat Ecol* 34:243–252
- Schneider G, Lenz J (1991) Zooplankton community metabolism in the upper 200 m of the central Red Sea and the Gulf of Aden. *Mar Ecol Prog Ser* 77:301–306
- Schneider G, Lenz J, Rolke M (1991) Zum Bestand und Stoffumsatz des Ultra-, Mikro- und Mesoplanktons im Roten Meer und im Golf von Aden. *Ber Inst Meeresk Kiel* 205:1–167
- Schneider G, Lenz J, Rolke M (1994) Zooplankton standing stock and community size structure within the epipelagic zone: a comparison between the central Red Sea and the Gulf of Aden. *Mar Biol* 119:191–198
- Sommer U, Stibor H (2002) Copepoda–Cladocera–Tunicata: the role of three major mesozooplankton groups in pelagic food webs. *Ecol Res* 17:161–174
- Star JL, Mullin MM (1981) Zooplankton assemblages in three areas of the North Pacific as revealed by continuous horizontal transects. *Deep-Sea Res* 28A:1303–1322
- Steinberg DK, Silver MW, Pilskaln CH (1997) Role of mesopelagic zooplankton in the community metabolism of giant larvacean house detritus in Monterey Bay, California, USA. *Mar Ecol Prog Ser* 147:167–179
- Sutton T, Hopkins T, Remsen A, Burghart S (2001) Multisensor sampling of pelagic ecosystem variables in a coastal environment to estimate zooplankton grazing impact. *Cont Shelf Res* 21:67–87
- Timonin AG (1971) The structure of plankton communities of the Indian Ocean. *Mar Biol* 9:281–289
- Turner JT (1986) Zooplankton feeding ecology: contents of fecal pellets of the cyclopoid copepods *Oncaea venusta*, *Corycaeus amazonicus*, *Oithona plumifera*, and *O. simplex* from the northern Gulf of Mexico. *PSZNI Mar Ecol* 7:289–302
- Webber MK, Roff JC (1995) Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. *Mar Biol* 123:481–495
- Weikert H (1980) The oxygen-minimum layer in the Red Sea: ecological implications of the zooplankton occurrence in the area of the Atlantis II Deep. *Meeresforsch* 28:1–9
- Weikert H (1982) The vertical distribution of zooplankton in relation to habitat zones in the area of the Atlantis II Deep central, Red Sea. *Mar Ecol Prog Ser* 8:129–143
- Weikert H (1987) Plankton and the pelagic environment. In: Edwards AJ, Head SM (eds) Red Sea. Key environments. Pergamon Press, Oxford, pp. 90–111
- Weikert H, John H-C (1981) Experiences with a modified Bé multiple opening-closing plankton net. *J Plankton Res* 3:167–176
- Wishner KF (1980) The biomass of the deep-sea benthopelagic plankton. *Deep-Sea Res* 27(A):203–216

- Yamaguchi A, Ikeda T, Shiga N (1998) Population structure and life cycle of *Pseudocalanus minutus* and *Pseudocalanus newmani* (Copepoda:Calanoida) in Toyama Bay, southern Japan Sea. *Plankton Biol Ecol* 45:183–193
- Yamaguchi A, Watanabe Y, Ishida H, Harimoto T, Furusawa K, Suzuki S, Ishizaka J, Ikeda T, Takahashi M (2002) Community and trophic structures of pelagic copepods down to greater depths in the western subarctic Pacific (WEST-COSMIC). *Deep-Sea Res I* 49:1007–1025
- Zervoudaki S, Christou ED, Siokou-Frangou I, Nielsen TG (2002) Distribution and feeding of small pelagic copepods in an oligotrophic area (N. Aegean Sea). Abstract presented at 8th Int Conf Copepoda 122. 21–26 July 2002, Keelung, Taiwan