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Trophic interactions and life strategies of epi- to bathypelagic calanoid copepods in the tropical Atlantic Ocean

LENA TEUBER*, ANNA SCHUKAT, WILHELM HAGEN AND HOLGER AUEL

BREMARE BREMEN MARINE ECOLOGY, MARINE ZOOLOGY, UNIVERSITY OF BREMEN, PO BOX 330 440, BREMEN 28334, GERMANY

*CORRESPONDING AUTHOR: teuber@uni-bremen.de

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Copepods play central roles in pelagic food webs linking primary production to higher trophic levels. Biomarkers (lipids, stable isotopes) provide modern approaches to study dietary preferences and trophic interactions. A cluster analysis based on the fatty acid (FA) and fatty alcohol compositions of calanoid copepods (copepodids C4/C5 and adult stages) from the southeastern tropical Atlantic identified five distinct groups according to lipid composition and storage strategy, coinciding with differences in vertical distribution from the surface to 1800 m depth. Most epipelagic species were characterized by low lipid levels (~10% of dry mass, DM), low quantities of wax esters (WE) and low $\delta^{15}N$ ratios indicating low trophic positions. In contrast, surface-dwelling *Rhincalanus cornutus* had higher lipid levels (>29% DM) and stored WE (>90% of total lipid), whereas vertically migrating *Pleuromamma* species did not store WE. Most mesopelagic copepods belonged to another cluster, defined by high lipid level (max. 47% DM), high amounts of the FA 18:1(*n*-9) and high $\delta^{15}N$ ratios >9‰ indicating carnivorous feeding at a higher trophic level. Diapausing *Calanoides carinatus* (copepodids C5), collected at great depth, formed a separate cluster with low $\delta^{15}N$ ratios and high amounts of herbivory markers. The latter were apparently accumulated during active feeding on phytoplankton in surface waters and transferred to the deep sea during ontogenetic vertical migrations. In conclusion, these tropical calanoid copepod species from the surface to the deep sea have adopted diverse feeding strategies and occupy a wide range of ecological niches, affecting energy flux and carbon cycling in the tropical Atlantic.

KEYWORDS: plankton; lipids; fatty acids; stable isotopes; trophic markers; deep sea

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INTRODUCTION

Copepods are central components of marine pelagic food webs as they mediate the energy flow from phytoplankton to higher trophic levels. Species that undergo diel vertical migration (DVM) enhance vertical carbon flux by feeding at the surface at night and respiring and excreting in deeper layers during the day (Longhurst, 1991). Food webs in tropical oceans are characterized by a large proportion of omnivorous species and many opportunistic predators (Kleppel, 1993; Calbet and Saiz, 2005; Escribano and Pérez, 2010), reflecting the scarcity of pelagic primary production in these oligotrophic waters. Important food sources for small epipelagic copepods are typically microzooplankton such as ciliates and flagellates (Calbet and Landry, 1999; Gaudy *et al.*, 2003; Hernández-León *et al.*, 2007).

In tropical surface layers, phytoplankton production is too limited to support the accumulation of large lipid reserves in epipelagic copepods. Since low primary production is present year-round, lipid storage is not as crucial when compared with congeners from highly seasonal environments, such as polar oceans, where primary production is only temporarily available. Tropical epipelagic copepods are rather characterized by permanent feeding, high metabolic rates as well as fast growth, intense reproduction and short life cycles (Kattner and Hagen, 2009; Teuber *et al.*, 2013a). This is in stark contrast to the life strategies of deep-sea species, usually opportunistic omnivores or predators with lower metabolic rates and longer life cycles (Kattner and Hagen, 2009). Lipid deposition thus increases with increasing depth, as energy storage is a wide-spread strategy in deeper-living copepods worldwide that have to cope with a rather stochastic food supply (Lee *et al.*, 2006). A third group of copepods, mainly prevailing in polar, boreal and upwelling regions, perform seasonal or ontogenetic vertical migrations and enter dormancy to overcome unfavourable conditions (Verheye *et al.*, 2005; Shimode *et al.*, 2012). The presence of wax esters (WE) often characterizes these copepods, which developed adaptations to a temporarily fluctuating food supply such as energy storage and metabolic reduction (diapause) to endure long periods of starvation (Båmstedt *et al.*, 1990; Hagen and Schnack-Schiel, 1996). In the tropical Atlantic, this life strategy can be observed in *Calanoides carinatus*, a dominant copepod from the Benguela upwelling system, which also occurs in tropical regions.

In order to elucidate species-specific feeding behaviour and dietary preferences, the trophic biomarker approach has been applied to different zooplankton species (Auel *et al.*, 2002; Dalsgaard *et al.*, 2003; Schukat *et al.*, 2014). Trophic marker fatty acids (FAs) have commonly been used in marine food web studies to reveal major dietary components and thus indicate primarily herbivorous or carnivorous feeding (Dalsgaard *et al.*, 2003). In addition, stable isotopic ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) resolve the source of ingested organic carbon and the trophic position of a species in the food web, respectively (Minagawa and Wada, 1984; Post, 2002). Since the heavier ^{15}N isotope accumulates in the animal's body tissue, the isotopic composition of a consumer is enriched in ^{15}N by around 3.4‰ per trophic level (DeNiro and Epstein, 1978; Hobson and Welch, 1992; Bode and Alvarez-Ossorio, 2004).

Published data on lipid content and composition as well as trophic interactions of tropical Atlantic copepods are still very limited. The main objective of this study is therefore to elucidate dietary preferences and feeding strategies of various calanoid copepod species from the southeastern tropical Atlantic in relation to depth of occurrence and species-specific differences in life strategies. The study presents a comprehensive trophic data set of 32 copepod species (including copepodids C4/C5 and adult stages) from various stations throughout the southeastern tropical Atlantic, from the surface down to 1800 m.

METHOD

Zooplankton sampling

Zooplankton were sampled during three expeditions to the southeastern tropical Atlantic in September 2010 (RRS *Discovery*, D355), February/March 2011 (RV *Maria S. Merian*, MSM 17/3) and July/August 2011 (RV *Maria S. Merian*, MSM 18/4). Samples were retrieved between 3°S and 20°S by stratified vertical hauls from 1800 to 0 m with a Multinet Midi (HydroBios, Kiel, Germany, mouth opening 0.25 m^2, mesh size 300 μm) (Table I). Additional specimens were collected from a double (18 nets) and single (9 nets) MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System, mouth opening 1 m^2, mesh size 333 μm, Wiebe *et al.*, 1985). For a detailed description of the sampling method see Teuber *et al.* (Teuber *et al.*, 2013b). Data on phytoplankton biomass (Table I) was provided by Wasmund *et al.* (pers. comm.) for the assessment of food availability for herbivorous copepods.

Calanoid copepods were sorted from zooplankton samples and identified according to Bradford-Grieve *et al.* (Bradford-Grieve *et al.*, 1999). Live specimens of different species were deep-frozen at −80°C for lipid, FA and stable isotope analyses. In the home lab, frozen samples were lyophilized for 48 h and weighed for dry mass

Table I: Station data

Cruise	Station	Date (D/M/Y)	Time gear at depth (UTC)	Position latitude	Position longitude	Maximum sampling depth (m)	SST (°C)	Phytopl. biomass (mg C m^{-2})[a]
D 355	1	01.09.2010	15:43	7°15′S	0°45′W	800	n.d.	n.d.
	2	03.09.2010	14:30	12°42′S	4°26′E	800	n.d.	n.d.
MSM 17/3	275	13.02.2011	03:11	20°00′S	12°10′E	200	21.5	1020
	282	14.02.2011	05:29	19°00′S	12°15′E	100	19.7	360
	295	16.02.2011	15:11	19°05′S	11°01′E	1000	23.7	280
	298	17.02.2011	07:49	19°00′S	10°30′E	1000	23.8	n.d.
	306	19.02.2011	20:47	17°19′S	11°19′E	400	23.1	520
	308	20.02.2011	18:05	17°15′S	11°00′E	1000	23.9	1100
	309	21.02.2011	08:09	17°15′S	10°47′E	1000	23.0	180
	317	25.02.2011	22:50	10°00′S	8°00′E	1000	28.9	100
	318	28.02.2011	00:30	4°07′S	1°26′W	1000	28.4	50
MSM 18/4	782	25.07.2011	15:52	3°00′S	8°00′E	1800	22.1	120
	784	26.07.2011	06:43	5°00′S	8°00′E	1800	24.1	80
	787	27.07.2011	06:32	8°00′S	8°00′E	1800	22.9	80
	789	27.07.2011	21:48	10°00′S	8°03′E	1800	22.2	70
	791	28.07.2011	12:32	12°00′S	8°00′E	1800	20.7	40
	835	05.08.2011	17:49	14°00′S	9°06′E	1800	19.5	120
	840	07.08.2011	06:08	18°00′S	8°00′E	1800	17.9	60
	842	07.08.2011	16:42	17°00′S	8°34′E	1800	17.8	n.d.
	845	10.08.2011	23:08	13°00′S	9°05′E	1800	20.5	140
	847	12.08.2011	13:34	14°30′S	9°51′E	800	18.7	20

[a]Wasmund *et al.*, (pers. comm.)
D, *Discovery* cruise; MSM, *Maria S. Merian* cruises; D, day; M, month; Y, year; UTC, universal time code; SST, sea surface temperature; Phytopl. biomass, total phytoplankton biomass; n.d., no data.

determination. Eventually, individuals of the same species and stage collected at the same station were pooled to provide sufficient biomass for gravimetric total lipid (TL) measurements and stable isotope analyses.

Lipid analysis

TL was extracted after Folch *et al.* (Folch *et al.*, 1957) as modified by Hagen (Hagen, 2000) with dichloromethane / methanol (2:1 per vol.). A Potter homogenizer (Braun, Potter S) and an ultrasonic cell disrupter (Bandelin electronic, UW 2070) were used to homogenize the samples. Lipid extracts were washed with aqueous KCl solution (0.88%) prior to centrifugation and phase separation.

After lipid extraction, subsamples were prepared for gas-chromatographic determination of FA and fatty alcohol (FAlc) composition after Kattner and Fricke (Kattner and Fricke, 1986). Subsamples of total FA were transesterified into methyl esters with hexane and methanol containing 3% concentrated sulphuric acid and heated at 80°C for 4 h. FA methyl esters were analyzed with a gas chromatograph (Agilent Technologies 7890A), equipped with a DB-FFAP column (30 m length, 0.25 mm diameter) and helium as carrier gas. FAs and FAlcs were detected by flame ionization and peaks were identified by comparing their retention times to those of a fish oil standard (Menhaden) and a natural copepod standard (*Calanus hyperboreus*) of known lipid composition. The WE percentage was estimated based on the FAlc content, assuming equal masses of the FA chain and the FAlc chain in the WE molecule (Kattner *et al.*, 2003).

The composition of FAs was analyzed by applying the trophic marker approach of Dalsgaard *et al.* (Dalsgaard *et al.*, 2003). The FAs 16:1(*n*-7), 16:4(*n*-1) and 18:1(*n*-7) were considered diatom markers, whereas 18:4(*n*-3) is found in high amounts in dinoflagellates (Sargent *et al.*, 1987; Graeve *et al.*, 1994a; Dalsgaard *et al.*, 2003) and thus served as an indicator of dinoflagellate feeding. The FAs 16:1(*n*-7) and 18:1(*n*-7) have also been suggested as bacterial markers (Cohen and Vonshak, 1991; Dalsgaard *et al.*, 2003; Brinis *et al.*, 2004). A typical marker FA indicating carnivorous feeding is 18:1(*n*-9) (Falk-Petersen *et al.*, 1990).

To evaluate the level of carnivory versus herbivory in copepods, two ratios were calculated; the traditional ratio 18:1(*n*-9)/18:1(*n*-7) (Auel *et al.*, 2002; Dalsgaard *et al.*, 2003) and the new and more specific ratio 18:1(*n*-9)/[16:1(*n*-7) + 16:4(*n*-1) + 18:1(*n*-7) + 18:4(*n*-3)], in the following named 18:1(*n*-9)/Σ herb. markers that includes additional diatom marker FAs as well as a dinoflagellate FA (Schukat *et al.*, 2014). Specific FAs comprising less than 2% of TFA composition were not included in the analyses and tables.

Stable isotope analysis

Dried individuals of different copepod species were transferred to tin capsules and sent to TÜV Rheinland

Agroisolab GmbH (Jülich, Germany) for stable isotope analysis. Stable isotopic ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were determined by mass spectrometry (Carlo Erba Instruments, EA NA1500 Series 2) with the standards IAEA-VPDB (IAEA-C1, Vienna) and AIR (atmospheric air; IAEA-N1, Vienna) as reference, respectively, and helium as carrier gas. Isotopic ratios of ^{13}C and ^{15}N are expressed in ‰, calculated by the formula described in Hodum and Hobson (Hodum and Hobson, 2000).

In this study, lipid levels varied greatly among tropical copepod species and according to Tieszen *et al.* (Tieszen *et al.*, 1983), differences in lipid content may affect the $\delta^{13}C$ ratio, since lipids are depleted in $\delta^{13}C$. To compensate for this variation and to obtain standardized lipid-corrected $\delta^{13}C$ values, a lipid-normalization model was applied to $\delta^{13}C$ ratios based on molar C/N ratios (valid if C/N $\geq$4), tested for several marine invertebrates (McConnaughey and McRoy, 1979) and for zooplankton in particular (Smyntek *et al.*, 2007). Lipid-corrected $\delta^{13}C$ ratios will be referred to as $\delta^{13}C'$ in the following.

Statistical analysis

Prior to statistical analyses, data were tested for normality. Species- and stage-specific differences were tested using two-tailed Man–Whitney *U*-tests as well as Kruskal–Wallis tests followed by Dunn's multiple comparison tests. All analyses were performed with GraphPad Prism 5.0 and considered significant if $P < 0.05$.

In order to identify similarities in FA and FAlc compositions between different copepod species, a cluster analysis based on a similarity matrix was performed applying the group average linkage technique (Primer v6 software, Clarke and Warwick, 1994). Prior to the cluster analysis, FA and FAlc concentrations were arcsine-square root-transformed in order to compensate for non-homogeneous variance of percentage data (Osborne, 2002). Similarity in FA and FAlc compositions among species was calculated by the Bray–Curtis similarity index. The results of the cluster analysis are presented in a dendrogram.

RESULTS

TL content

TL contents of tropical Atlantic copepods ranged from 5.1% dry mass (DM) in *Temora stylifera* to 47% DM in *Paraeuchaeta hansenii* (Table II, Fig. 1A). In general, TL contents increased with increasing depth of occurrence. Typical epipelagic species such as *T. stylifera*, *Undinula vulgaris* and *Scolecithrix danae* had TL contents <10% DM, while species from mesopelagic depths showed increased lipid levels of usually >20% DM or even >30% DM, as in *Paraeuchaeta aequatorialis* and *P. hansenii* or copepodids C5 of *Calanoides carinatus*. Exceptionally high lipid contents of up to 43.5% DM were found in females and copepodids C5 of *Rhincalanus cornutus* from the surface (Table II, Fig. 1A). Diel vertical migrants (DVM) such as *Pleuromamma* spp. had TL contents of around 10% DM.

Megacalanus princeps males displayed much higher TL contents (27.7 ± 3.9% DM) when compared with females (12.7 ± 4.9% DM) and copepodids C5 (13.9% DM) (Table II). Males of *Gaussia princeps* had lower TL contents (16.7 ± 3% DM) than females (21.3/23.4% DM), while TL in C5s was rather variable (12.5/36.3% DM). In contrast, *R. cornutus* did not display major differences in TL contents between adult females and copepodids C5 (29–44% DM).

FA and FAlc composition and WE content

The composition of FAs and FAlcs in tropical calanoid copepods is summarized in Table II and was further analyzed by cluster analysis applying the Bray–Curtis similarity index (Fig. 2). Only FAs and FAlcs with maximum values of ≥2% of total fatty acids (TFAs) and total fatty alcohols (TFAlcs), respectively, were included in the analyses. Cluster analysis mainly differentiated between genera and identified different subgroups of species that were distinct in their FA and FAlc compositions. WE contents, as calculated from FAlcs, are shown in Fig. 1B.

Females and copepodids C5 of *R. cornutus* from the surface differed from all other species and formed a separated cluster (Fig. 2). *Rhincalanus cornutus* displayed the highest quantities of the short-chain saturated FAs 14:0 and 16:0 (Table II) and contained extremely high amounts of WE (up to 96.8% TL, Fig. 1B) that were dominated by the monounsaturated FAlcs 16:1(*n*-7) and 18:1(*n*-9), together comprising ca. 90% of TFAlc (Table II).

Several other epipelagic species (*Euchaeta marina*, *S. danae, T. stylifera* and *U. vulgaris*) formed a large cluster together with *Pleuromamma* spp. and *Euchirella* spp., which were characterized by little or no WE.

The epipelagic copepods formed a separate subgroup and contained high quantities of the FA 16:0, together with the long-chain polyunsaturated FAs 20:5(*n*-3) and 22:6(*n*-3) (Table II). *Euchaeta marina* and *S. danae* were also high in 18:1(*n*-9) with 14–15% TFA. All these species contained lower amounts of WE (2.9–29.5% TL, Fig. 1B). While the shorter-chain saturated FAlc 16:0 represented the major component of TFAlc in *E. marina*, FAlcs in the other three species mainly consisted of 14:0, 16:0 and 22:1(*n*-11) (Table II).

Table II: Total lipid and wax ester contents (calculated from fatty alcohols), fatty acid and fatty alcohol compositions

Species	*Undinula vulgaris*	*Temora stylifera*	*Scolecithrix danae*	*Euchaeta marina*	*Neocalanus gracilis*	*Rhincalanus cornutus*	*Rhincalanus cornutus*	*Pleuromamma robusta*	*Pleuromamma xiphias*	*Pleuromamma quadrungulata*	*Euchirella splendens*	*Euchirella similis*
Stage	f	f	f	f (ripe)	f	f	C5	f	f	f	f	f
Depth (m)	50–0	50–0	25–0	40–0	80–0	50–0	50–0	100–50	500–150	600–400	250–0	600–400
Dry mass (mg ind^{-1})	0.16/0.15	0.03	0.20	0.30	0.47 ± 0.05	0.16/0.21	0.13	0.31 ± 0.01	0.72 ± 0.02	0.48	1.31	1.34
n (ind)	2 (40)	1 (56)	1 (15)	1 (9)	3 (17)	2 (22)	1 (19)	3 (23)	3 (11)	1 (8)	1 (2)	1 (2)
Total lipid (% DM)	6.5/7.4	5.1	9.6	10.3	14.9 ± 0.4	28.8/40.0	43.5	9.3 ± 0.9	9.9 ± 1.6	15.4	18.3	17.0
Wax ester (% TL)	2.9/4.6	3.1	13.7	29.5	59.4 ± 9.9	79.8/86.4	96.8	–	–	–	–	–
Fatty acids (% TFA)												
14:0	0.1/–	0.4	0.5	–	0.4 ± 0.1	24.2/20.3	20.3	0.7 ± 0.4	–	–	0.5	0.3
16:0	16.3/15.6	19.1	23.9	14.1	17.1 ± 1.1	43.4/43.9	47.1	19.1 ± 0.4	14.0 ± 1.1	16.0	25.0	24.8
17:0	2.3/2.4	1.9	1.2	0.8	2.0 ± 0.1	0.4/–	–	1.7 ± 0.1	1.7 ± 0.0	0.9	1.6	1.3
18:0	9.7/9.8	8.7	4.7	4.2	4.1 ± 0.6	5.3/6.6	6.1	3.1 ± 0.1	3.9 ± 0.1	2.0	4.2	3.7
16:1(*n*-7)	0.7/0.5	0.4	4.7	2.2	1.1 ± 0.3	1.7/3.5	2.4	2.1 ± 0.2	1.3 ± 1.0	3.1	3.3	2.8
16:2(*n*-4)	–	–	0.5	0.3	0.1 ± 0.2	0.3/2.4	2.0	0.2 ± 0.2	0.2 ± 0.2	0.2	0.9	0.6
16:4(*n*-1)	–	–	–	–	–	0.8/0.7	–	–	–	–	–	–
18:1(*n*-7)	1.3/1.2	2.5	2.4	1.9	2.1 ± 0.1	1.0/1.0	1.1	2.0 ± 0.1	1.5 ± 0.2	3.4	2.5	2.4
18:1(*n*-9)	3.9/4.4	2.0	14.3	14.8	8.6 ± 0.6	5.9/7.4	5.1	4.7 ± 0.3	5.3 ± 1.3	20.8	13.7	15.0
18:2(*n*-6)	1.4/1.4	1.3	1.8	2.2	1.7 ± 0.4	0.5/0.5	0.6	1.5 ± 0.1	1.4 ± 0.2	1.2	1.5	1.8
18:4(*n*-3)	–	0.3	0.5	2.1	1.1 ± 0.1	0.4/-	–	1.7 ± 0.2	1.4 ± 0.3	0.3	1.4	2.1
20:1(*n*-9)	0.3/0.4	0.3	1.7	0.6	1.0 ± 0.2	–	–	1.2 ± 0.0	1.2 ± 0.2	3.9	0.9	1.2
20:4(*n*-3)	–	0.3	0.4	0.6	1.9 ± 0.5	–	–	0.8 ± 0.1	1.3 ± 0.3	0.4	0.5	0.4
20:4(*n*-6)	0.9/0.9	1.5	1.0	1.0	1.0 ± 0.1	0.7/0.8	0.9	1.2 ± 0.1	1.2 ± 0.0	0.9	1.4	1.0
20:5(*n*-3)	13.2/13.0	11.9	11.9	12.6	12.6 ± 1.1	4.4/4.1	4.1	14.7 ± 1.2	13.5 ± 0.5	7.4	10.6	10.8
22:1(*n*-9)	–	0.3	0.2	–	1.0 ± 0.2	–	–	0.7 ± 0.2	0.1 ± 0.1	2.8	0.2	0.2
22:1(*n*-11)	–	–	1.8	0.3	5.4 ± 2.3	–	–	–	–	3.2	0.3	0.3
22:5(*n*-3)	0.5/0.6	1.4	0.2	0.6	1.0 ± 0.2	–	–	0.8 ± 0.0	0.4 ± 0.4	0.7	1.0	0.7
22:6(*n*-3)	42.1/42.2	43.1	22.9	34.7	29.3 ± 2.0	5.7/3.3	5.1	34.0 ± 0.5	40.3 ± 4.7	16.5	21.4	20.9
24:1(*n*-9)	4.9/5.0	2.7	2.7	3.1	3.1 ± 0.3	0.7/0.7	0.8	5.2 ± 0.2	7.7 ± 1.4	10.9	2.2	2.2
18:1(*n*-9)/ 18:1(*n*-7)	3.0/3.6	0.8	5.9	7.6	4.1 ± 0.3	5.7/7.2	4.7	2.3 ± 0.1	3.6 ± 0.4	6.1	5.4	6.2
18:1(*n*-9)/Σ herb. markers	1.9/2.5	0.6	1.9	2.4	2.0 ± 0.2	1.5/1.4	1.4	0.8 ± 0.0	1.3 ± 0.2	3.1	1.9	2.1
Fatty alcohols (% TFAlc)												
14:0	24.0/15.1	16.1	15.7	3.0	0.8 ± 0.7	–	–	–	–	–	–	–
16:0	37.5/30.7	27.2	41.1	92.3	1.1 ± 0.4	6.0/3.5	z3.9	–	–	–	–	–
18:0	–	–	4.6	4.7	–	–	–	–	–	–	–	–
16:1(*n*-7)	–	–	–	–	–	20.4/21.2	21.7	–	–	–	–	–
18:1(*n*-7)	–	–	–	–	–	1.5/2.4	3.1	–	–	–	–	–
18:1(*n*-9)	–	–	–	–	–	68.8/71.1	68.4	–	–	–	–	–
20:1(*n*-7)	–	–	–	–	0.7 ± 0.6	–	–	–	–	–	–	–
20:1(*n*-9)	–	–	6.1	–	2.4 ± 1.3	–	–	–	–	–	–	–
22:1(*n*-7)	–	–	–	–	4.8 ± 0.2	–	–	–	–	–	–	–
22:1(*n*-9)	–	–	–	–	18.8 ± 2.4	–	–	–	–	–	–	–
22:1(*n*-11)	38.5/54.2	56.7	32.6	–	71.5 ± 3.3	3.4/1.9	2.9	–	–	–	–	–

Continued

Table II: Continued

Species	*Gaetanus brevicornis*	*Gaetanus pileatus*	*Megacalanus princeps*	*Megacalanus princeps*	*Megacalanus princeps*	*Gaussia princeps*	*Gaussia princeps*	*Gaussia princeps*	*Paraeuchaeta aequatorialis*	*Paraeuchaeta hansenii*	*Paraeuchaeta gracilis*	*Calanoides carinatus*
Stage	f	f	f	m	C4/C5	f	m	C5	f	f	f	C5
Depth (m)	600–400	1000–150	1000–250	600–400	600–400	800–200	600–200	600–200	1000–500	600–400	600–400	1800–1000
Dry mass (mg ind^{-1})	1.14/1.15	1.44	5.94 ± 0.63	4.24 ± 0.39	1.24	8.54/9.39	6.32 ± 0.93	2.39/4.54	1.92/1.51	5.97/5.89	1.78	0.14/0.12
n (ind)	2 (4)	1 (3)	3 (3)	3 (3)	1 (3)	2 (2)	3 (3)	2 (2)	2 (2)	2 (2)	1 (1)	2 (54)
Total lipid (% DM)	6.5/8.2	14.9	12.7 ± 4.9	27.7 ± 3.9	13.9	21.3/23.4	16.7 ± 3.0	12.5/36.3	46.0/38.0	47.0/44.5	25.4	45.4/39.3
Wax ester (% TL)	13.8/16.2	49.9	42.3 ± 6.1	69.9 ± 1.2	54.7	60.4/45.2	65.7 ± 2.6	52.7/69.3	62.6/73.2	78.2/69.4	60.6	90.9/84.4
Fatty acids (% TFA)												
14:0	0.5/0.2	–	–	–	–	–	–	–	1.2/–	–/0.5	–	6.2/7.2
16:0	11.5/13.5	5.4	7.4 ± 1.9	1.3 ± 0.6	4.6	2.5/9.5	1.4 ± 0.1	3.8/0.6	5.9/0.4	0.8/4.2	6.9	6.2/5.7
17:0	1.0/0.8	0.5	0.4 ± 0.1	–	0.3	0.5/0.3	–	–	–	–	–	–
18:0	3.8/2.7	1.2	1.1 ± 0.3	–	1.0	0.7/1.1	0.8 ± 0.0	2.0/0.7	–	–	0.7	1.4/1.3
16:1(*n*-7)	2.1/4.1	3.9	3.1 ± 0.8	5.0 ± 0.4	3.0	4.9/5.0	6.5 ± 1.8	4.5/5.8	22.5/24.7	19.3/16.8	12.5	15.6/14.6
16:2(*n*-4)	–/0.4	0.9	0.3 ± 0.1	–	–	0.4/0.4	0.1 ± 0.2	–/0.4	1.2/0.9	1.7/1.5	1.4	1.4/1.7
16:4(*n*-1)	–	0.5	0.4 ± 0.1	0.9 ± 0.1	0.3	1.3/0.3	1.3 ± 0.2	1.6/1.5	–/0.5	0.7/0.5	1.0	1.8/2.7
18:1(*n*-7)	2.4/2.7	2.7	4.3 ± 0.6	3.5 ± 0.2	3.0	1.8/2.8	1.9 ± 0.4	2.5/2.0	1.3/0.5	1.4/1.1	1.4	0.6/0.7
18:1(*n*-9)	9.6/20.4	30.9	39.4 ± 6.9	45.6 ± 1.5	49.7	51.3/45.5	55.0 ± 1.2	39.6/46.5	38.8/53.6	51.0/56.9	35.8	4.4/4.9
18:2(*n*-6)	1.1/1.2	0.9	1.0 ± 0.2	1.5 ± 0.1	1.1	1.2/1.1	1.5 ± 0.2	1.9/1.1	1.2/0.6	1.9/0.9	1.4	1.6/1.2
18:4(*n*-3)	–/0.3	0.6	0.4 ± 0.1	0.9 ± 0.1	–	0.5/0.3	0.1 ± 0.2	–/0.7	–	1.3/0.3	1.5	1.9/1.7
20:1(*n*-9)	1.9/2.5	3.3	2.0 ± 0.4	2.4 ± 0.8	1.7	3.5/4.2	3.0 ± 0.5	3.5/3.4	5.2/2.5	3.9/1.5	2.3	11.0/10.7
20:4(*n*-3)	–/0.3	0.7	0.3 ± 0.1	0.3 ± 0.5	–	0.8/0.6	0.7 ± 0.2	–/0.7	–	–	0.5	0.8/0.4
20:4(*n*-6)	1.1/1.1	1.2	0.9 ± 0.2	1.5 ± 0.1	0.4	1.5/0.9	1.3 ± 0.4	1.5/1.8	–	0.5/–	0.8	2.0/3.3
20:5(*n*-3)	9.2/7.4	8.4	6.6 ± 2.0	9.2 ± 0.3	5.3	8.2/7.3	8.1 ± 1.1	8.8/12.0	2.3/1.8	4.3/2.0	9.7	12.8/16.6
22:1(*n*-9)	2.2/3.1	2.4	0.3 ± 0.2	–	0.3	0.6/1.7	–		1.0/0.4	0.5/0.9	0.5	1.3/0.8
22:1(*n*-11)	1.5/1.7	1.1	3.7 ± 1.2	3.1 ± 0.5	3.0	1.8/2.9	1.5 ± 0.1	1.1/0.8	9.8/5.4	4.8/3.2	4.7	17.9/11.7
22:5(*n*-3)	1.8/0.9	1.5	0.6 ± 0.3	0.4 ± 0.7	0.4	0.8/0.5	–	–/1.2	–	–	0.6	2.1/1.9
22:6(*n*-3)	40.6/27.8	27.5	20.4 ± 4.4	20.7 ± 1.3	19.2	12.7/10.1	11.9 ± 0.5	22.2/17.4	4.8/4.6	2.2/4.2	12.4	6.0/8.1
24:1(*n*-9)	7.1/5.1	2.7	2.5 ± 0.6	0.9 ± 0.2	3.0	1.4/1.6	1.9 ± 0.4	4.7/0.7	1.5/0.8	0.6/1.2	1.6	0.7/0.7
18:1(*n*-9)/18:1(*n*-7)	4.0/7.5	11.2	9.4 ± 2.5	13.2 ± 0.5	16.5	27.9/16.0	30.5 ± 8.3	15.6/23.3	30.1/108.6	37.3/51.6	25.6	6.9/6.7
18:1(*n*-9)/Σ herb. markers	2.2/2.9	4.0	4.8 ± 0.6	4.4 ± 0.1	7.8	6.0/5.4	5.8 ± 1.2	4.6/4.7	1.6/2.1	2.3/3.0	2.2	0.2/0.2
Fatty alcohols (% TFAlc)												
14:0	8.5/6.6	4.1	5.1 ± 2.2	10.0 ± 0.9	6.4	10.1/10.4	7.8 ± 0.6	10.4/9.0	27.7/30.4	29.4/29.2	27.4	9.7/15.5
16:0	6.7/8.9	48.8	62.8 ± 8.5	65.8 ± 2.5	60.3	71.4/55.3	61.0 ± 1.0	59.6/65.5	36.6/37.3	54.0/52.8	48.1	14.2/18.1
18:0	–	–	–	4.5 ± 0.8	4.2	–/2.7	3.7 ± 0.2	3.4/3.6	–/1.0	1.3/1.1	2.4	1.2/1.8
16:1(*n*-7)	–	–	1.2 ± 1.1	2.9 ± 0.7	2.2	1.5/1.1	1.7 ± 0.2	2.5/1.4	4.7/4.9	1.7/3.1	1.3	1.6/2.3
18:1(*n*-7)	–	–	–	4.0 ± 0.3	4.6	–/4.9	5.5 ± 0.8	6.4/5.1	4.3/4.0	3.0/3.0	–	–
18:1(*n*-9)	–	2.4	2.8 ± 0.9	3.4 ± 0.2	4.8	4.0/4.3	4.5 ± 0.3	4.2/3.2	2.6/3.4	–/0.5	0.6	0.6/0.8
20:1(*n*-7)	–	1.2	3.0 ± 1.6	–	1.8	0.9/1.0	0.7 ± 0.6	–/0.9	–/0.5	–	0.6	–/0.8
20:1(*n*-9)	–/3.5	2.0	2.2 ± 0.9	0.9 ± 0.8	1.7	7.4/8.8	7.6 ± 1.5	7.4/6.9	4.8/3.5	2.4/1.9	4.6	15.8/19.1
22:1(*n*-7)	14.2/9.8	3.8	2.4 ± 0.7	–	–	–	–	–	–/0.9	–	1.1	–
22:1(*n*-9)	70.7/60.7	35.9	11.5 ± 4.5	5.3 ± 1.8	7.9	2.4/5.3	3.5 ± 1.2	3.0/2.1	6.6/5.7	3.1/4.8	3.8	1.8/2.8
22:1(*n*-11)	–/10.6	1.9	8.9 ± 2.1	3.2 ± 0.8	6.3	2.3/6.1	4.0 ± 0.6	3.1/2.1	12.8/8.4	5.1/3.7	10.1	55.0/39.0

DM, dry mass; TL, total lipid; TFA, total fatty acids; TFAlc, total fatty alcohols; *n* (ind), number of samples (total number of individuals); f, female; m, male; C4/C5, copepodids 4 and 5. Σ herb. markers, sum of 16:1(*n*-7); 16:4(*n*-1), 18,1(*n*-7); 18:4(*n*-3). Values are given as mean ± standard deviation for $n \geq 3$, if $n = 2$; values are arranged according to the scheme: sample 1 data/sample 2 data.

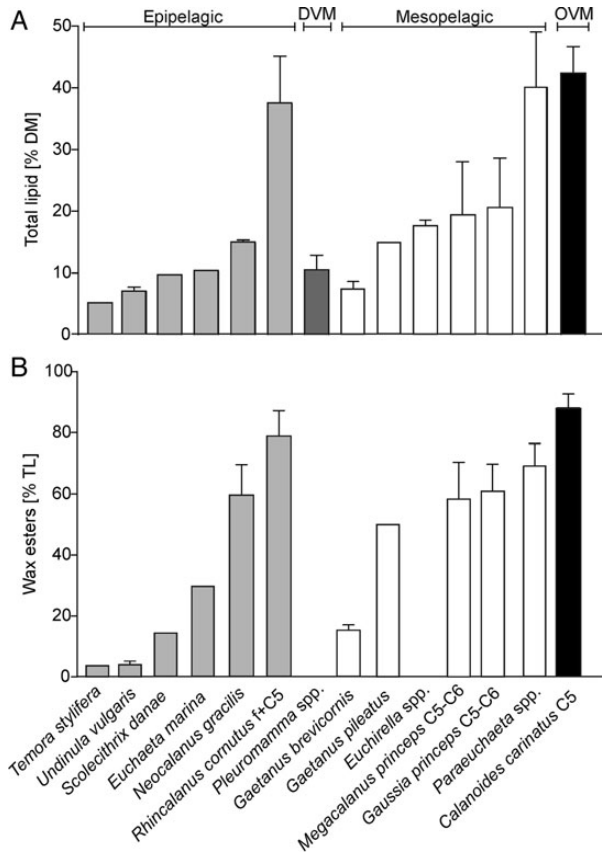

Fig. 1. Total lipid (**A**, in % dry mass) and wax ester contents (**B**, in % total lipid, as calculated from fatty alcohols) of calanoid copepods from the tropical Atlantic. Bars are arranged according to increasing depth of occurrence from epi- to mesopelagic depths and increasing total lipid content within each group (light grey: epipelagic species, dark grey: diel vertical migrants, white: mesopelagic species, black: ontogenetic vertical migrants). The majority of copepods analyzed were adult females, if not indicated otherwise. DM, dry mass; TL, total lipid; WE, wax ester; DVM, diel vertical migration; OVM, ontogenetic vertical migration; f, female; C5, copepodid 5; C6, adult stages (male and female). See Table II for the number of replicates.

The genera *Pleuromamma* and *Euchirella* formed the second subgroup within this cluster (Fig. 2), characterized by the absence of WE (Table II, Fig. 1B). Their FA composition was dominated by higher levels of 16:0, 20:5(*n*-3) and 22:6(*n*-3). *Pleuromamma quadrungulata* and *Euchirella* spp. additionally contained higher amounts of 18:1(*n*-9) (Table II).

Gaetanus brevicornis and *Neocalanus gracilis* formed a different cluster (Fig. 2). The FA and FAlc compositions of *G. brevicornis* were similar to those of epipelagic species, with generally low amounts of WE (Table II, Fig. 1B). Nevertheless, *G. brevicornis* was clearly enriched in the FA 18:1(*n*-9), while the long-chain monounsaturated FAlcs 22:1(*n*-7) and 22:1(*n*-9) dominated its FAlc composition (Table II). *Neocalanus gracilis* differed from the other typical surface species due to its higher WE levels (~60% TL) (Table II, Fig. 1B). The FA composition was similar to those of other epipelagic copepods, whereas the FAlcs were dominated by the long-chain FAlcs 22:1(*n*-11) and 22:1(*n*-9).

The largest cluster was formed by the deeper-living copepods, which could be further separated into three subgroups. Copepodids C5 of *C. carinatus* were distinct from all other mesopelagic copepods (Table II, Fig. 2) due to their substantially higher WE levels (up to 90.9% TL) and different FA pattern (Table II, Fig. 1B). Their FA composition was dominated by 16:1(*n*-7) as well as by the two long-chain monounsaturates 20:1(*n*-9) and 22:1(*n*-11) (Table II). Likewise, the FAlc composition mainly consisted of the long-chain monounsaturates 20:1(*n*-9) and 22:1(*n*-11).

Paraeuchaeta aequatorialis and *P. hansenii* formed another subgroup within the mesopelagic species cluster, due to their high concentrations of the FA 16:1(*n*-7) (Table II).

The large cluster of all other mesopelagic copepods contained species from different genera (Fig. 2) characterized by high amounts of WE (up to 78% TL) (Table II, Fig. 1B). In contrast to all other species, the dominant FA in the mesopelagic *Gaetanus pileatus*, *M. princeps*, *G. princeps* and *Paraeuchaeta* spp. was the carnivory marker FA 18:1(*n*-9) with up to 56.9% of TFA. The FAlc composition was characterized by highest concentrations of the short-chain moiety 16:0. The FAlc 14:0 was also prominent in *M. princeps*, *G. princeps* and *Paraeuchaeta* spp., whereas *G. pileatus* contained high portions of 22:1(*n*-9) (Table II).

Trophic marker FA ratios

The trophic marker FA ratios (carnivory/herbivory ratios), in particular 18:1(*n*-9)/Σ herb. markers, serve as indices of the degree of carnivory in marine invertebrates (Table II, Fig. 3). The copepods *T. stylifera*, *Pleuromamma robusta* and *C. carinatus* exhibited the lowest degree of carnivory with ratios <1 (Table II, Fig. 3). While *T. stylifera* and *P. robusta* came from the epipelagic layer, copepodids C5 of *C. carinatus* were sampled between 1000 and 1800 m and showed the lowest ratio of all species investigated with 0.2. The majority of copepods distributed from the surface to mesopelagic waters displayed intermediate ratios between 1 and 3. A higher degree of carnivory (ratio >3) was determined in deeper-living species such as *M. princeps*, *G. princeps* and *G. pileatus*. *Megacalanus princeps* copepodids displayed the highest ratio of 7.8 (Table II, Fig. 3).

The regression analysis showed (Fig. 4A) that the carnivory/herbivory ratio essentially increased with increasing depth of occurrence. Due to special features of the FA composition of *Paraeuchaeta* spp. (open circles) and due to the deviating life-cycle strategy of *C. carinatus* (open triangles), these data points were not included in the

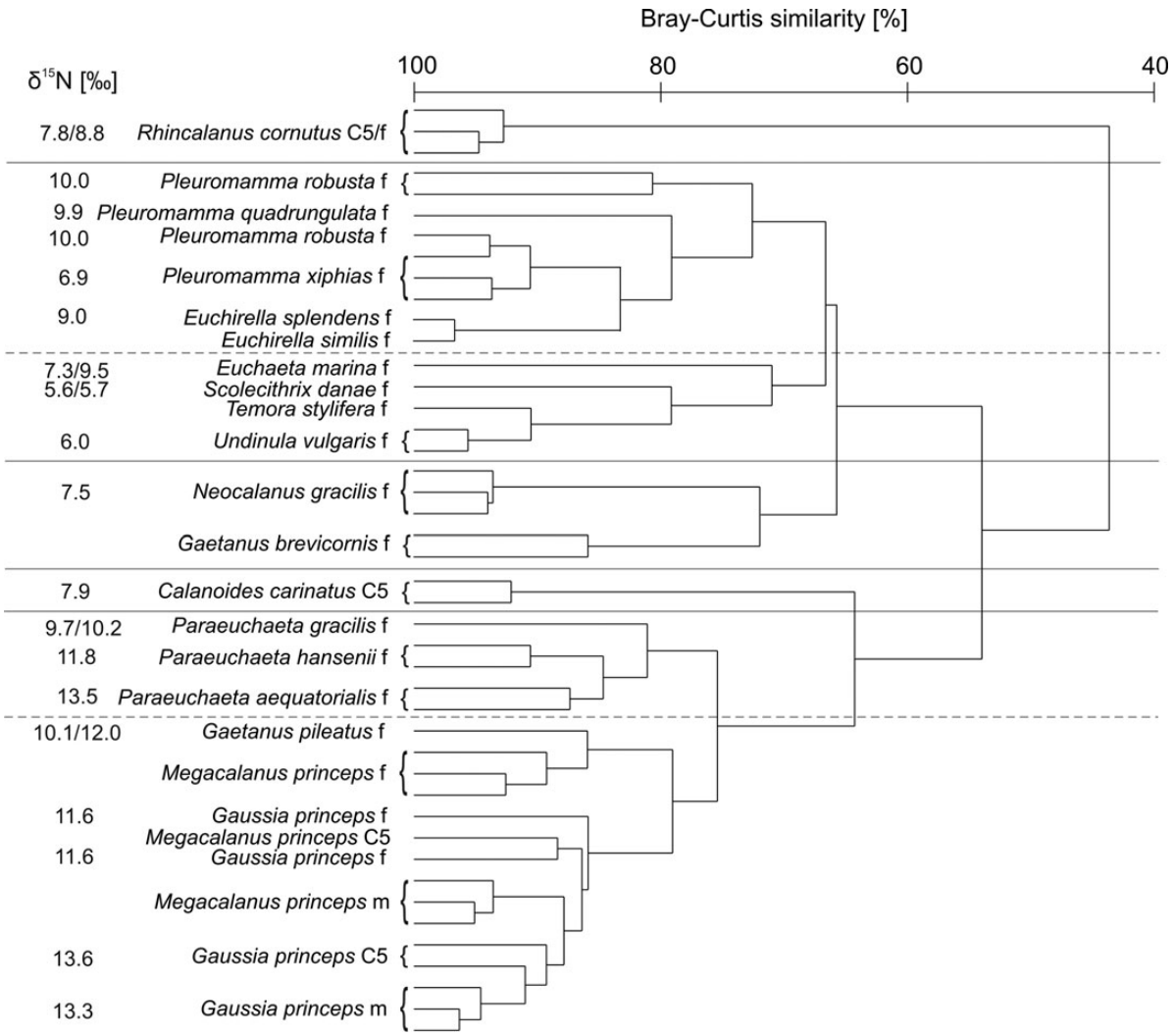

Fig. 2. Clusters of calanoid copepods from the tropical southeastern Atlantic with similar patterns in fatty acid and fatty alcohol composition illustrated as a dendrogram. $\delta^{15}N$ ratios (‰), if available, are indicated on the left as mean values. f, female; m, male; C5, copepodid 5.

calculation of the regression coefficient in Fig. 4A. In *Paraeuchaeta* spp., high amounts of the FA 16:1(*n*-7) result in a low carnivory/herbivory ratio, which does not reflect their actual carnivorous feeding behaviour. In copepodids C5 of *C. carinatus*, it does not make sense to relate the low carnivory/herbivory ratio to its sampling depth, since high amounts of herbivory markers were incorporated by *C. carinatus* after feeding on phytoplankton in surface layers. At greater depth, *C. carinatus* rests in diapause and does not feed.

Stable isotope ratios

Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic signatures of different calanoid copepod species displayed a wide range of values (Table III). Lipid-corrected $\delta^{13}C'$ ranged from −25.4‰ in females of *Pareucalanus sewelli* to −17.1‰ in females of *Candacia bipinnata*, although the majority of lipid-corrected $\delta^{13}C'$ were between −22 and −18‰. $\delta^{15}N$ varied from 5.6‰ in females of *S. danae* to 13.6 ± 0.7‰ in C5s of *G. princeps* (Table III). Among species with low $\delta^{15}N$ ratios of around 6‰ were the epipelagic copepods *S. danae*, *U. vulgaris* and *Candacia* spp. as well as *Pleuromamma abdominalis* (Table III). The other *Pleuromamma* species displayed $\delta^{15}N$ signatures between 6.9 and 11.1‰. The majority of mesopelagic copepods exhibited intermediate $\delta^{15}N$ ratios ranging from 7 to 10‰ (Table III), while high $\delta^{15}N$ ratios above 10‰ were found in deeper-living species such as *Paraeuchaeta* spp., *G. pileatus* and *G. princeps* (Table III, Fig. 3).

The $\delta^{15}N$ ratios of various species were related to their vertical distribution as well as to their degree of carnivory (Fig. 4B and C). The regression analyses showed that $\delta^{15}N$ ratios generally increased with increasing depth of

occurrence (Fig. 4B) and that $\delta^{15}N$ ratios also correlate well with the degree of carnivory as quantified based on FA patterns (Fig. 4C). Again, *Paraeuchaeta* spp. (open circles) were excluded from the calculation of the regression coefficient in Fig. 4C for reasons mentioned earlier.

DISCUSSION

This study presents a comprehensive set of lipid and stable isotope data reflecting dietary preferences as well as trophic interactions of tropical calanoid copepods from the southeastern Atlantic Ocean. FA and stable isotope biomarkers are extensively used for trophic studies in the world oceans and provide reliable estimates of dietary relationships and trophic levels (Graeve *et al.*, 1994a; Auel *et al.*, 2002; Dalsgaard *et al.*, 2003; Schukat *et al.*, 2014). Trophic biomarkers integrate dietary signals over longer time periods of days to several weeks depending on the species (Graeve *et al.*, 1994a; Gentsch *et al.*, 2009). Since lipid storage plays a rather minor role in tropical epipelagic zooplankton, certain concerns as to the applicability of trophic biomarkers in tropical ecosystems have been raised. Lipid and FA compositions are highly dependent on the TL content of marine organisms and dietary signals are usually reflected best in depot (neutral) lipids (Hagen and Kattner, 1998; Hagen *et al.*, 2001; Lee *et al.*, 2006). Tropical epipelagic copepods are characterized by constant feeding, rapid turnover and high metabolic rates (Kattner and Hagen, 2009; Teuber *et al.*, 2013a) and thus tend to contain rather low amounts of storage lipid, potentially limiting the validity of FA biomarkers.

Diatoms and dinoflagellates, which represent the typical primary producers in higher latitudes and eutrophic systems and for which characteristic marker FAs are available, are less abundant in oligotrophic tropical environments (Calbet and Landry, 1999; Gaudy *et al.*, 2003). In contrast, cyanobacteria, e.g. *Prochlorococcus* or *Trichodesmium*, may contribute up to 60% of total primary production in tropical offshore regions (Platt *et al.*, 1983; Carpenter *et al.*, 2004). *Trichodesmium* is the only cyanobacterium, of which a unique trophic marker is known, the FA 22:2(*n*-6) (Post *et al.*, 2002). However, neither this FA nor other typical bacteria markers, e.g. FAs with an odd number of carbon atoms, were detected in significant amounts in the tropical copepods. Therefore, we assume that 16:1(*n*-7) and 18:1(*n*-7), which are typical components of both, cyanobacteria and diatoms (Cohen and

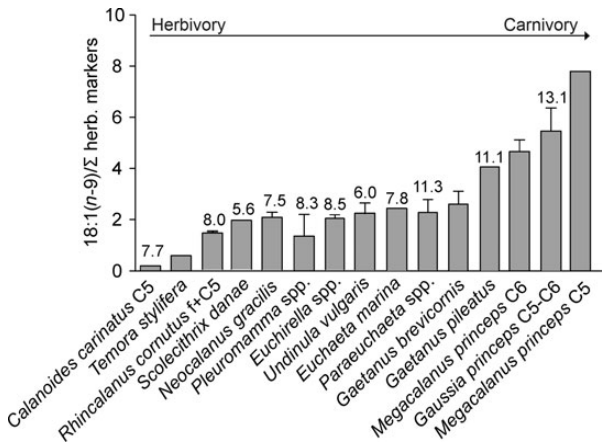

Fig. 3. Carnivory/herbivory ratio 18:1(*n*-9)/Σ herb. markers of tropical calanoid copepods in order of increasing degree of carnivory. $\delta^{15}N$ ratios [‰] are indicated above each bar as mean values. The majority of copepods analyzed were adult females, if not indicated otherwise. f, female; C5, copepodid 5; C6, adult stages (male and female). See Tables II and III for number of replicates.

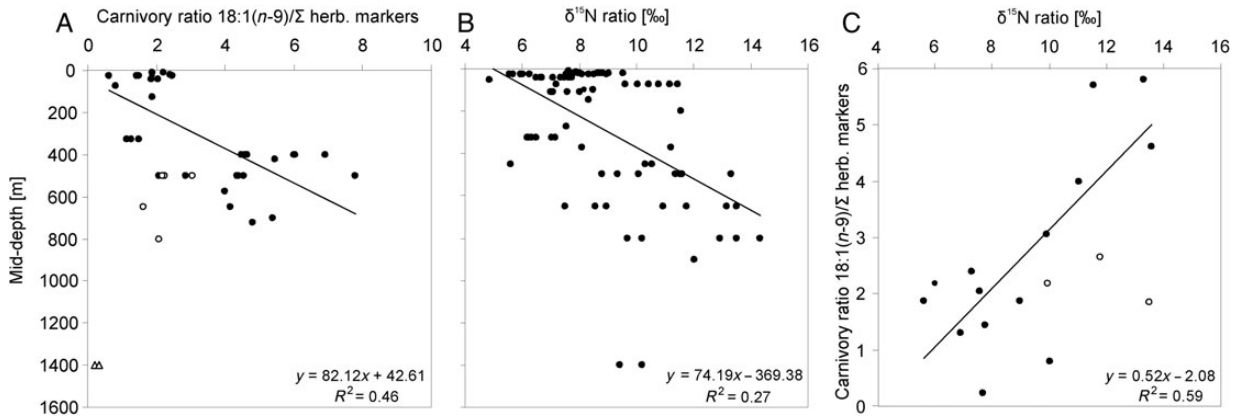

Fig. 4. Regression analyses of (**A**) habitat depth (mid-depth of the sampling interval) and carnivory ratio, (**B**) habitat depth and $\delta^{15}N$ ratio and (**C**) carnivory ratio and $\delta^{15}N$ ratio of calanoid copepods from the tropical Atlantic. Black circles: majority of copepods used to calculate the regression equations, open circles: *Paraeuchaeta* spp., open triangles: copepodids C5 of *Calanoides carinatus*.

Table III: Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic ratios as well as molar C/N ratios of calanoid copepods from the southeastern tropical Atlantic

Species	Stage	Depth (m)	$\delta^{13}C$ (‰)	$\delta^{13}C'$ (‰)	$\delta^{15}N$ (‰)	C/N	*n* (ind)
Undinula vulgaris	f	50–0	−20.0	−20.6	6.0 ± 0.1	3.5	3 (16)
	m	50–0	−20.2	−20.8	6.3	3.5	1 (4)
Scolecithrix danae	f	50–0	−20.0/−19.7	−20.5/−20.1	5.7/5.6	3.6/3.6	2 (9)
Candacia bipinnata	f	50–0	−16.8/−16.8	−17.1/−17.2	8.9/8.8	3.7/3.7	2 (9)
Candacia curta	f	50–0	−18.3/−16.9	−18.6/−17.3	8.6/8.3	3.7/3.7	2 (8)
Candacia pachydactyla	m	30–0	−19.9	−20.4	7.9	3.6	1 (4)
Calanoides carinatus	f	40–0	−18.9 ± 1.0	−17.9 ± 0.5	7.9 ± 0.1	5.2 ± 0.7	3 (20)
	m	40–0	−20.8 ± 1.2	−18.6 ± 1.3	8.8 ± 0.2	7.6 ± 0.4	3 (21)
	C5	600–400	−20.0 ± 0.3	−17.5 ± 0.2	7.7 ± 1.1	8.8 ± 0.4	3 (44)
Arietellus aculeatus	f	120–80	−21.1/−20.7	−21.5/−21.2	8.2/8.5	3.7/3.6	2 (2)
Euchaeta marina	f	220–0	−21.3 ± 0.3	−21.8 ± 0.2	7.3 ± 0.4	3.6 ± 0.1	3 (8)
	f (eggs)	40–0	−18.9	−18.8	9.5	4.0	1 (3)
	C5	80–0	−21.8	−21.6	7.6	4.2	1 (4)
Neocalanus gracilis	f	220–0	−21.2 ± 0.5	−21.6 ± 0.3	7.5 ± 1.0	3.7 ± 0.2	3 (6)
Neocalanus robustior	f	220–0	−20.9 ± 0.3	−21.3 ± 0.3	7.6 ± 0.5	3.7 ± 0.4	3 (6)
Pareucalanus sewelli	f	40–0	−25.0/−18.4	−25.4/−18.2	7.6/7.6	3.7/4.2	2 (5)
Pareucalanus langae	f	220–0	−19.7 ± 0.1	−20.2 ± 0.1	7.2 ± 0.7	3.7	4 (8)
Rhincalanus cornutus	f	150–0	−21.4 ± 0.5	−19.2 ± 0.5	7.8 ± 0.7	7.7 ± 0.1	3 (16)
	C5	800–200	−22.1	−19.7	8.8	8.5	1 (7)
Pleuromamma abdominalis	f	400–300	−20.1	−20.6	5.6	3.6	1 (3)
	m	500–150	−21.6	−22.2	6.2	3.5	1 (2)
Pleuromamma quadrungulata	f	500–150	−18.7 ± 0.7	−18.9 ± 0.7	9.9 ± 1.6	3.9 ± 0.1	4 (9)
Pleuromamma robusta	f	100–50	−19.6 ± 0.6	−19.9 ± 0.5	10.0 ± 0.4	3.8 ± 0.1	3 (10)
	m	100–50	−19.8 ± 0.2	−19.7	11.1 ± 0.3	4.2 ± 0.2	3 (10)
Pleuromamma xiphias	f	600–150	−21.6 ± 0.3	−22.1 ± 0.2	6.9 ± 1.1	3.6	3 (8)
	m	500–150	−21.8 ± 0.5	−22.3 ± 0.4	6.9 ± 0.4	3.6 ± 0.1	3 (6)
Euchirella pulchra	f	800–220	−20.3/−20.1	−21.1/−20.9	7.5/9.3	3.4/3.4	2 (4)
Euchirella rostrata	f	250–40	−22.4	−21.7	8.3	4.7	1 (2)
Euchirella splendens	f	800–500	−21.0	−21.7	9.0	3.4	1 (1)
Gaetanus pileatus	f	1000–400	−19.3/−21.9	−19.8/−20.3	10.1/12.0	3.6/6.1	2 (2)
Gaussia princeps	f	300–100	−21.4	−21.1	11.6	4.3	1 (1)
	m	600–400	−20.2	−19.6	13.3	4.7	1 (1)
	C5	1000–600	−21.2 ± 1.1	−20.3 ± 0.4	13.6 ± 0.7	5.2 ± 1.3	3 (3)
Metridia princeps	f	800–500	−20.7	−19.2	13.2	5.9	1 (2)
Paraeuchaeta aequatorialis	f	800–500	−21.9	−19.4	13.5	8.9	1 (1)
Paraeuchaeta gracilis	f	1000–600	−22.6/−22.5	−21.5/−21.2	10.2/9.7	5.3/5.6	2 (2)
	C5	600–400	−21.7 ± 0.2	−19.2 ± 0.2	11.5 ± 0.1	9.1	3 (3)
Paraeuchaeta hansenii	f	800–500	−23.2	−20.9	11.8	8.4	1 (1)
Chirundina streetsii	f	800–500	−20.4	−20.7	10.9	3.8	1 (1)
Lucicutia sp.	f	1800–1000	−21.8	−21.0	9.4	4.8	1 (1)
	m	1800–1000	−22.3	−20.9	10.2	5.6	1 (1)

$\delta^{13}C'$, lipid-corrected $\delta^{13}C$ ratio; f, female; f (eggs), female carrying egg sac; m, male; C5, copepodid 5; *n* (ind), number of samples (total number of individuals). Values are given as mean ± standard deviation for $n \geq 3$, if $n = 2$; values are arranged according to the scheme: sample 1 data/sample 2 data.

Vonshak, 1991; Dalsgaard *et al.*, 2003; Brinis *et al.*, 2004), are largely of algal origin.

Although certain limitations exist in the use of the trophic biomarker approach for tropical copepods, the results of this study confirm its applicability even in tropical species. In the present study, indices of carnivory derived from FA compositions (Table II, Fig. 3) agreed quite well with trophic positions determined by nitrogen stable isotope analysis, supporting the validity of the lipid biomarker concept (compare Fig. 4C). In addition, the long-chain monounsaturated FAs and FAlcs 20:1 and 22:1, which are only synthesized by calanid copepods (see *C. carinatus* in Table II), were also present in the carnivorous mesopelagic *Gaussia princeps* and *Paraeuchaeta* spp. This finding can be used as unambiguous evidence to reveal predator–prey relationships, indicating predation on *C. carinatus* by carnivorous copepods (Table II) (Lee, 1975; Kattner and Hagen, 1995; Dalsgaard *et al.*, 2003; Laakmann *et al.*, 2009a,b).

Furthermore, cluster analysis grouped copepod species with similar FA and FAlc compositions in broad clusters that were often characterized by similarities in vertical distribution and lipid storage, hence similar life strategies. Within each broader cluster, FA and FAlc compositions largely reflected taxonomic relationships (Fig. 2), as clusters based on similarities in lipid composition often coincided with genera. This is obvious in the close clustering of the *Pleuromamma* species which rather reflects their

taxonomic relationship, since these species conduct DVMs and cannot be related to a certain depth layer. In contrast, some other closely related species such as *Paraeuchaeta* spp. and *Euchaeta marina* or the two *Gaetanus* species were separated by cluster analysis and were predominantly grouped according to their habitat depth.

The parallel use of the two complementary and independent methods in the present study confirms that the FA trophic marker concept is largely supported by similar results derived from stable nitrogen isotope analysis. Hence, this approach proved to be successful for tropical copepods.

Epipelagic copepods showed a primarily herbivorous to omnivorous feeding mode, which is consistent with studies on other tropical surface zooplankton (Madhupratap and Haridas, 1990; Kleppel *et al.*, 1996; Escribano and Pérez, 2010). Phytoplankton biomass (Table I), an indicator reflecting food availability for herbivorous copepods, was higher at the sampling sites in the eastern tropical Atlantic (this study) than previously measured in the central tropical Atlantic (Marañón *et al.*, 2000). Huskin *et al.* (Huskin *et al.*, 2001) calculated a copepod community ingestion rate of 49 mg C m^{-2} day^{-1} for the eastern tropical Atlantic, which suggests that existing phytoplankton biomass (compare Table I) might be sufficient for herbivorous copepod consumption. Nevertheless, phytoplankton alone usually does not cover carbon demand in oligotrophic tropical regions (Zhang *et al.*, 1995). The potentially limited availability of phytoplankton is therefore often compensated by feeding on microzooplankton (Kleppel, 1993; Calbet and Landry, 1999; Calbet and Saiz, 2005), which results in a rather mixed diet and a more opportunistic and omnivorous feeding mode.

Most tropical copepods typically do not accumulate extensive lipid stores (e.g. Lee *et al.*, 2006). They stay active throughout the year in this non-seasonal environment with a low but reliable food supply, which does not support but also does not require provisions for overwintering or resting phases (Lee and Hirota, 1973). The absence or near absence of WE in most epipelagic species suggests the limited storage of triacylglycerols as short-term energy reserves (not WE, known as long-term energy depots), corresponding to faster turnover rates and shorter generation times (Lee and Hirota, 1973; Hagen *et al.*, 1993; Kattner and Hagen, 2009). The dominant FAs in many epipelagic species were 16:0, 20:5(*n*-3) and 22:6(*n*-3), which are principal components of biomembranes (Lee *et al.*, 2006; Kattner and Hagen, 2009). Rather low levels of diatom and dinoflagellate biomarker FAs reflect the scarcity and rapid catabolism of these primary producers in tropical waters. While *S. danae* and *U. vulgaris* had rather low $\delta^{15}N$ ratios indicating lower trophic positions, *E. marina* showed intermediate $\delta^{15}N$ values, reflecting its carnivorous feeding mode (Morris and Hopkins, 1983).

The lipid composition of *Rhincalanus cornutus* from the surface was considerably different from that of all other copepods and strongly deviated from the general characteristics of tropical epipelagic copepods as described above. *Rhincalanus cornutus* contained very high amounts of lipid with up to 43.5% DM in copepodids C5, as well as remarkably high WE levels (80–97% TL), indicating the massive deposition of WE as important long-term lipid reserves (Lee and Hirota, 1973; Cass *et al.*, 2011). Its FA composition was dominated by the shorter-chain, saturated FAs 14:0 and 16:0, while the monounsaturated FAlcs 16:1(*n*-7) and 18:1(*n*-9) represented the major WE moieties. *Rhincalanus cornutus* is able to synthesize these FAlcs via reduction from the corresponding FAs (Cass *et al.*, 2011). The FA and FAlc pattern of *R. cornutus* is similar to that of congeners from the Gulf of Mexico (Cass *et al.*, 2011). According to its $\delta^{15}N$ ratios (females 7.7‰, C5 8.5‰), *R. cornutus* occupies an intermediate trophic position in our study area, characterized by herbivorous to omnivorous feeding, which is also supported by its low carnivory/herbivory ratio. The storage of large amounts of lipid, especially as WE, is evident by its prominent oil sac, comprising most of its body volume. Females of other *Rhincalanus* species (*R. gigas*, *R. nasutus*) are assumed to undergo ontogenetic vertical migrations and enter a dormant stage in deeper waters (Schnack-Schiel *et al.*, 2008; Shimode *et al.*, 2012; Schukat *et al.*, 2014), where they do not feed and rely on their extensive energy reserves accumulated at the surface. Dormancy has never been demonstrated for *R. cornutus*, but possibly females of *R. cornutus* (this study) were about to enter their resting phase or had just terminated it. Along with the observed sluggish movement, high lipid and WE levels may also help contribute to neutral buoyancy (Jónasdóttir, 1999) and save extra energy otherwise lost in constant locomotion to avoid sinking. These characteristics are also reflected in reduced metabolic rates in *R. cornutus* and other eucalanid species (Flint *et al.*, 1991; Teuber *et al.*, 2013a,b). Hence, Flint *et al.* (Flint *et al.*, 1991) classified the special life style of *Eucalanus* spp. as 'lethargic'.

Pleuromamma and *Euchirella* formed a separate subcluster, characterized by the absence of WE. *Pleuromamma* spp. are active DVM (Morris and Hopkins, 1983; Madhupratap and Haridas, 1990; Auel and Verheye, 2007) and follow a different life strategy in terms of energy metabolism (Teuber *et al.*, 2013b). *Pleuromamma* spp. migrate to the surface at night to benefit from a richer food supply in epipelagic layers. The low C/N ratio implies a high protein content, which is necessary to support a strong musculature in DVM species (Morris

and Hopkins, 1983). These species occupy various trophic positions (Morris and Hopkins, 1983; Longhurst, 1985; Morales *et al.*, 1993), as verified by their wide range of $\delta^{15}N$ ratios (6–11‰). While the FA compositions of *Pleuromamma xiphias* and *P. robusta* point towards herbivorous feeding, *P. quadrungulata* was characterized by a more carnivorous diet also reflected in its higher carnivory/herbivory ratio.

Mesopelagic copepods showed distinct lipid compositions. Both TL and WE levels increased with increasing depth of occurrence (present study; Lee and Hirota, 1973; Kattner and Hagen, 2009). This coincides with a higher degree of carnivory in deep-sea species, as indicated by a high carnivory/herbivory ratio (3–8) and high amounts (>30% TFA) of the carnivory biomarker FA 18:1(*n*-9) (Falk-Petersen *et al.*, 1990; Hagen *et al.*, 1995). The FA 18:1(*n*-9) may also be synthesized *de novo* via desaturation of 18:0 (Kattner and Hagen, 1995), but it seems rather unlikely as long as enough dietary resources of this FA are available (Dalsgaard *et al.*, 2003). Supporting this view, higher $\delta^{15}N$ ratios of above 10‰ (maximum of 13.6‰) also underline carnivory as the dominant feeding type in *Paraeuchaeta* spp., *Megacalanus princeps* and *Gaussia princeps* from lower mesopelagic depths (Laakmann *et al.*, 2009a,b). Predatory feeding in *Paraeuchaeta* spp. was also confirmed from feeding experiments, stomach contents and from mouthparts morphology (Yen, 1991; Øresland and Ward, 1993; Olsen *et al.*, 2000; Michels and Schnack-Schiel, 2005). Most deep-sea copepods contain large amounts of lipids, especially FAlcs (as WE moieties, usually >20% TL) (Lee and Hirota, 1973; Hagen *et al.*, 1995; Lee *et al.*, 2006). They are enriched in the short-chain FAlcs 14:0 and 16:0, which typically point to a more opportunistic feeding mode (Graeve *et al.*, 1994b; Kattner and Hagen, 2009). In addition, large lipid stores serve as buoyancy aids (Sargent and Henderson, 1986) to support the 'float and wait' feeding strategy of large-size deep-sea copepods (Auel and Hagen, 2005; Laakmann *et al.*, 2009a). Comparatively high amounts of the FA 16:1(*n*-7) were found in *Paraeuchaeta* spp., which has also been recorded in earlier studies (Hagen *et al.*, 1995; Laakmann *et al.*, 2009a). *Paraeuchaeta* probably accumulates this FA when feeding on herbivores with a high concentration of 16:1(*n*-7) as in *Calanoides carinatus*. Therefore, *de novo* synthesis is not very likely (Hagen *et al.*, 1995; Laakmann *et al.*, 2009a,b). Furthermore, higher quantities of the calanoid marker FAs 20:1 and 22:1 (Hopkins *et al.*, 1993) were detected in some carnivorous deep-sea species (e.g. *Paraeuchaeta aequatorialis*, *Paraeuchaeta hansenii*), indicating predation on diapausing copepodids of *C. carinatus*, the only species synthesizing these long-chain monounsaturated FAs in the region (present study; Schukat *et al.*, 2014).

In the present study, *C. carinatus* occurred in large numbers as copepodids C5 at great depths between 1800 and 1000 m. This finding agrees well with the known ontogenetic vertical migration of the species, where non-feeding copepodids C5 descend to the deep sea and survive in diapause with severely reduced locomotion and metabolism suppressed by 82% (Auel *et al.*, 2005; Schukat *et al.*, 2014). The high WE levels in C5s are advantageous for survival during periods of food shortage (Lee *et al.*, 2006). Nevertheless, in this extreme resting stage, *C. carinatus* probably utilizes very little of its enormous lipid reserves previously accumulated during feeding in surface waters (Verheye *et al.*, 2005). It is suggested that instead of fuelling maintenance, these energy depots are primarily invested in gonad maturation and reproductive processes towards termination of diapause and re-ascent to the surface. Freshly moulted females will be able to quickly produce new off-spring, which can make full use of the next phytoplankton bloom (Verheye *et al.*, 1991). Herbivorous feeding in *C. carinatus* is supported by high amounts of diatom biomarker FAs, especially 16:1(*n*-7) (present study; Verheye *et al.*, 2005; Schukat *et al.*, 2014). Although *de novo* synthesis of the FA 16:1(*n*-7) is possible in many marine animals, it has been confirmed that 16:1(*n*-7) in herbivorous calanoid copepods predominantly derives from dietary sources, i.e. diatoms (Graeve *et al.*, 1994a; Dalsgaard *et al.*, 2003). An herbivorous diet in *C. carinatus* is also supported by its rather low $\delta^{15}N$ ratio (7.7‰) and lowest FA carnivory/herbivory ratio of all copepods (0.2). Besides large quantities of diatom biomarkers, the composition of its TL is characterized by the long-chain monounsaturated FAs 20:1(*n*-9) and 22:1(*n*-11), which are typical of calanoid copepods, as they may synthesize these FAs *de novo* (Hopkins *et al.*, 1993; Kattner and Hagen, 1995). Since these FAs were also quite often found in considerable quantities in deep-sea species such as *Paraeuchaeta* spp. and *G. princeps*, this suggests *C. carinatus* C5s as possible prey items at depth. Applying an enrichment factor of around 3.4‰ per trophic level (Peterson and Fry, 1987; Hobson and Welch, 1992), deep-sea copepods with $\delta^{15}N$ ratios of around 11‰ may represent potential predators on *C. carinatus* copepodids. Similar interactions have been reported between *Paraeuchaeta* and *Calanus* species in other regions (Øresland and Ward, 1993; Fleddum *et al.*, 2001; Laakmann *et al.*, 2009a).

In conclusion, the present study revealed a high diversity of species-specific life strategies with regard to feeding preferences and lipid storage mechanisms in tropical copepods from epipelagic to bathypelagic depths. Feeding modes and dietary preferences depend to a great extent on depth of occurrence, prey availability as well as individual metabolic strategy. Nevertheless, omnivory was

the prevailing feeding mode, demonstrating a high degree of opportunistic feeding in tropical copepods. The two complementary trophic biomarker approaches, i.e. based on FAs and stable isotopes, lead to similar results and emphasize the applicability of lipid trophic biomarkers even in tropical regions, albeit with certain limitations. Studies on zooplankton feeding strategies and dietary preferences are crucial to trace energy pathways in marine food webs and to identify trophic relationships. These data will improve our understanding of energy fluxes from the surface to the deep sea in tropical pelagic food webs, which are still poorly investigated.

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