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[1,2]

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Abstract

Gut contents of 9 species and 4 forms of pelagic poecilostomatoid copepods of the genus *Oncaea* collected from the 0–250 m depth layer in the central Red Sea were examined with a differential interference and phase contrast microscope. Appendicularian houses were frequently detected in the guts irrespective of species, sex, time and depth of collection. Houses occurred on average more frequently in females (61%) than in males (42%), with *Oncaea venusta* f. *typica* and *O. clevei* showing the most extreme sex-related differences. Females of *O. conifera*, which is a strong vertical migrator, exhibited a corresponding daily feeding rhythm, with the highest feeding intensity during the night. Diatoms and unidentified minute particles were frequently found in the guts of all species, and these may have been derived indirectly from appendicularian houses or other detritus. Other zooplankters such as copepodids, copepod nauplii and chaetognaths were detected in the guts of relatively large species (>0.7 mm in body length) and rarely in smaller ones (<0.7 mm). The present and previous studies clearly reveal that attachment and feeding of both small and large species of *Oncaea* on appendicularian houses commonly occur in oligotrophic waters in tropical and subtropical regions and in the deep seas. The ecological role of *Oncaea* in these waters is discussed in comparison to that of calanoids.

Key words: *Oncaea*, appendicularian houses, copepodids, diatoms, Red Sea

The biology and ecology of the pelagic poecilostomatoid copepod families Corycaeidae, Oncaeidae and Sapphirinidae are poorly known compared with the calanoids. Recently the distribution and diel vertical migrations of pelagic poecilostomatoids such as *Copilia, Corycaeus, Oncaea* and *Sapphirina* have been intensively studied by Böttger (1985, 1987), Böttger-Schnack (1987, 1990a, b, 1992, 1994, 1995, 1996), Chae & Nishida (1995) and Metz (1995). The results showed that these copepods are distributed in markedly different vertical layers, from the epipelagic down to the bathypelagic zone. Corycaeids and most sapphirinids, which are characterized by a pair of well-developed eye lenses, are mainly restricted to the epipelagic zone (Böttger-Schnack 1990a, b, Chae & Nishida 1995). Presumably these lenses function to identify mating partners in *Copilia* and *Sapphirina* (Chae & Nishida 1995) and to detect prey in *Corycaeus* (Gophen & Harris 1981). Oncaeids, which do not possess eye lenses, exhibit much more extended vertical distribution patterns, ranging from the epipelagic to the bathypelagic zones (Böttger-Schnack 1994, 1995, 1996, in press, Metz 1995).

In general, the feeding ecology of poecilostomatoids is still enigmatic. Previous authors have observed both phytoplankton and zooplankton remains in the guts and in the fecal pellets of oncaeid and corycaeid species (Pasternak 1984, Turner 1986, Hopkins 1985, 1987). Alldredge (1972, 1976) first observed *Oncaea* feeding on phyto- and zooplankters remaining on discarded appendicularian houses. Both shallow- and deep-water *Oncaea* spp. occur on appendicularian houses, and these copepods use them as a food source (Ohtsuka & Kubo 1991, Ohtsuka et al. 1992, Steinberg et al. 1994). *Corycaeus* and *Sapphirina* gnaw tissues off juvenile fish and salps, respectively (Nishimura 1960, Heron 1973, Palomares & Vera 1995). Huys & Boxshall (1991) suggest that all pelagic poecilostomatoids are loosely associated with other zooplankters.

The present study reports on a light microscopic analysis of the gut contents of selected *Oncaea* species collected from a station in the central Red Sea. Special attention is paid to their feeding on appendicularian houses. The depth distributions and diel vertical migration patterns of the *Oncaea* species and their potential prey appendicularians at the same station are compared in the present paper.

Materials and Methods

Copepods were collected at a station in the central Red Sea above the Atlantis II Deep (21°23′ N, 38°04′ E) during the day (local time 1100–1500) and night (0000–0400) on 24 February 1981. An opening-closing net (mouth 0.25 m², mesh size 0.1 mm) was towed vertically and activated at 50 m intervals in the upper 450 m of the water column. In the present study only specimens from the upper 250 m samples were utilized. Copepod specimens were fixed with 4% buffered formaldehyde/seawater, and then transferred into a preservative of 5% propylenglycol, 0.5% propylenephenoxetol and 94.5% filtered seawater (Böttger-Schnack 1990b). The vertical profiles of temperature, salinity and dissolved oxygen at the station are described in Böttger-Schnack (see 1990b, Fig. 2). Copepods were sorted from size-

Table 1. *Oncaea* species examined in the present study. Species are listed in order of decreasing size. Distribution and migration pattern of each species and sex adapted from Böttger-Schnack (1990b). Distribution pattern: I, unimodal distribution in upper epipelagic zone (0–50 m); II, unimodal distribution in lower epipelagic zone (50–100/150 m); III, unimodal distribution in upper mesopelagic zone (100–250 m); IV, bimodal distribution in epi- and mesopelagic zones; V, variable distribution in epi- and/or mesopelagic zones. Migration: M, migrant; N, non-migrant; ?, migration not determined.

Species	Sex	Body length* (mm)	Time	Depth (m)	Number of individuals examined	Distribution pattern*	Migration*
O. venusta f. *typica*	♀	1.00–1.23	Day	0–50	20	I	N
			Night	0–50	20		
	♂	0.88–0.95	Day	0–50	20	I	N
			Night	0–50	19		
O. conifera	♀	0.98–1.06	Day	100–150	5	III	M
				150–200	5		
				200–250	10		
			Night	0–50	18		
	♂	0.62–0.70	Day	50–100	10	II	M
			Night	0–50	17		
O. mediterranea	♀	0.90–1.03	Day	50–100	18	II	M
				200–250	10		
			Night	0–50	20		
	♂	0.70–0.78	Day	50–100	19	II	M
			Night	0–50	19		
O. venusta f. *venella*	♀	0.75–0.88	Day	0–50	20	I	N
			Night	0–50	14		
	♂	0.55–0.65	Day	0–50	19	I	N
			Night	0–50	20		
O. clevei	♀	0.62–0.68	Day	0–50	15	I	N
			Night	0–50	20		
	♂	0.49–0.57	Night	0–50	9	I	N
O. media f. *major*	♀	0.65–0.77	Day	0–50	13	I	N
O. umerus	♀	0.57–0.62	Day	50–100	20	II	?
			Night	0–50	18		
O. minuta	♀	0.50–0.56	Day	0–50	9	V	?
				50–100	8		
			Night	0–50	18		
				200–250	18		
O. hawii	♀	0.49–0.56	Night	200–250	8	V	?
O. media f. *minor*	♀	0.48–0.52	Day	0–50	20	IV	?
			Night	0–50	19		
	♂	0.41–0.44	Day	0–50	8	I	?
				50–100	20		
			Night	0–50	19		
O. dentipes	♀	0.44–0.49	Day	50–100	13	II	?
			Night	50–100	13		

*from Böttger-Schnack (1988, unpubl. data), Böttger-Schnack et al. (1989) and Böttger-Schnack & Boxshall (1990).

fractionated samples or subsamples as described by Böttger-Schnack (1990b). Up to 20 specimens of each species were examined. The taxonomy of *Oncaea* follows Böttger-Schnack (1990b); however, *O. umerus* and *O. hawii* have only recently been described as new species (Böttger-Schnack & Boxshall 1990). They correspond to *Oncaea* sp. F and E/F of the previous study, respectively. The 9 species and 4 forms

of *Oncaea* examined in the present study are shown in Table 1.

The gut was dissected out of the prosome with a pair of fine needles after immersion of the copepods in distilled water for several hours. The gut was then transferred into gum-chloral medium on a glass slide, and covered with a cover slip. After drying for 4–5 days at a temperature of ca. 50 ℃ on a hot plate (Sakura, model PS51), gut contents were analyzed with a differential interference and phase contrast microscope (Nikon Optiphoto). When a sample contained less than 20 copepods, all individuals were analyzed.

Gut contents of some specimens were stained by 0.03% toluidine blue buffered with Sörensen-Gomori sodium phosphate buffer solution (cf. Mochioka & Iwamizu 1996). This staining method was employed to detect the presence of metachromatically-stained mucopolysaccharide which composes the outer membrane of appendicularian houses (Alldredge 1977).

Results

Items detected in guts

Gut contents are shown in Figures 1 to 4. All species consumed appendicularian houses, which were provisionally identified by their unique characters including the fibers of the incurrent filters (Figure 1), and/or a large amount of packed translucent mucus (house membranes) (Figure 2). The transluscent mucus was partly or entirely stained metachromatically in red, strongly suggesting the presence of mucopolysaccharides from appendicularian houses (Figure 3). In addition, the packed mucus contained neither cells nor special structures such as cnidarian nematocysts, radiolarian needles or minipellets (cf. Riemann 1989); the mucus was almost always accompanied with numerous minute particles including broken and/or intact frustules of diatoms, which may have been trapped on the incurrent and/or food-concentrating filters or packed within appendicularian fecal pellets not expelled from the houses (Figure 2A–C). Although it is hard to measure the diameter of fibers in the copepod guts precisely under the light microscope, they seem to be about 0.5–1.0 μm based on Figure 1, which approximately coincides with that of the mesh fibers of the incurrent filter of *Oikopleura labradoriensis* (Flood 1991).

Guts also contained solitary and chain-forming diatoms (Figures 1B, 4D–F) and thecate dinoflagellates (Figure 1D). Intact frustules of both centric and pennate diatoms and thecal plates of dinoflagellates in the guts of females ranged from 4 to 25 μm in largest dimension. Zooplankters such as radiolarians (Figure 1A), copepodids (Figures 2A, 4A, B), copepod nauplii and unidentified crustaceans were also found in the guts. Copepodid bodies of almost perfect condition were found only in females of some of the larger species including *Oncaea venusta* f. *typica*, *O. conifera* and *O. venusta* f. *venella*. Grasping spines from chaetognaths were detected in a female of *O. venusta* f. *typica*. Cnidarian nematocysts (Figure 4C) were found infrequently in the guts. Unidentified minute particles (Figure 4F) were discovered in almost all guts.
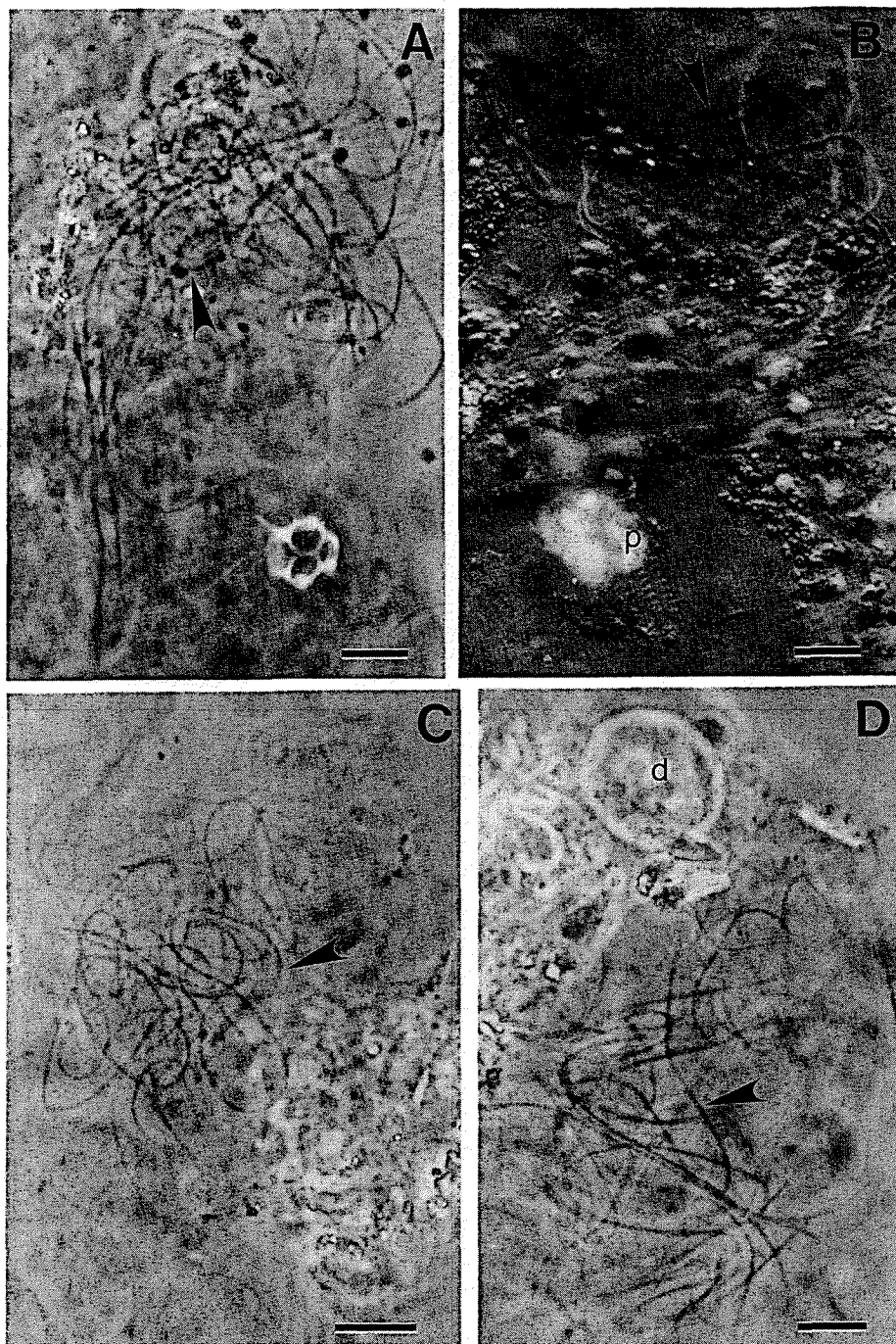
Fig. 1. Fibers of incurrent filters of appendicularian houses in the guts of *Oncaea* species, arrowed. A, *O. venusta* f. *venella*, female, night, 0–50 m, r: radiolarian; B, *O. venusta* f. *typica*, female, night, 0–50 m, p: pennate diatom frustles; C, *O. mediterranea*, male, day, 50–100 m; D, *O. conifera*, female, night, 0–50 m, d: dinoflagellate. Scale bars = 10 μm (A, B, D); 50 μm (C).
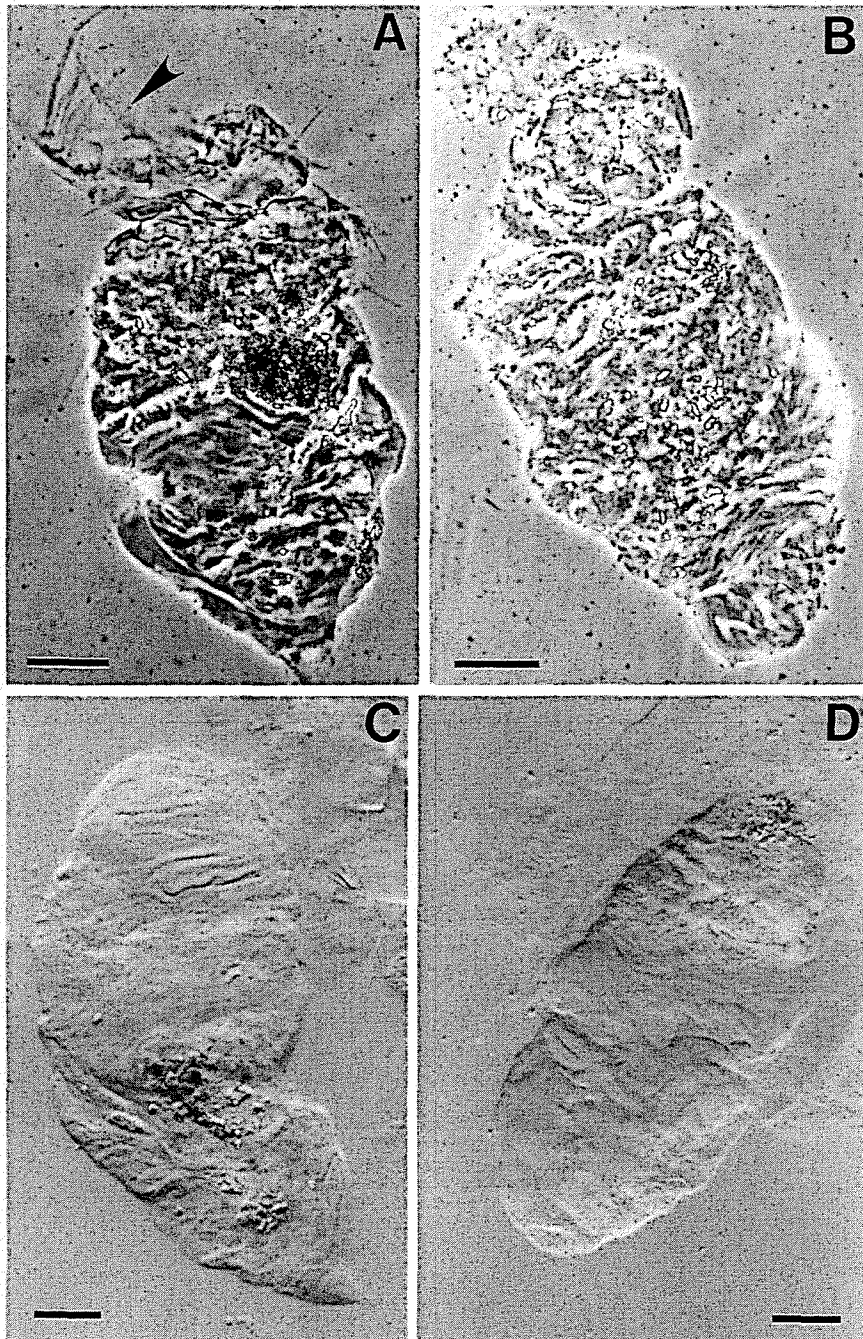
Fig. 2. Packed house membranes of appendicularians detected in the guts of *Oncaea* species. A, *O. venusta* f. *typica*, female, day, 0–50 m, copepodid fragments arrowed; B, *O. mediterranea*, female, night, 0–50 m; C, *O. minuta*, female, night, 0–50 m; D, *O. media* f. *minor*, male, day, 50–100 m. Scale bars = 50 μm (A, B); 20 μm (C, D).
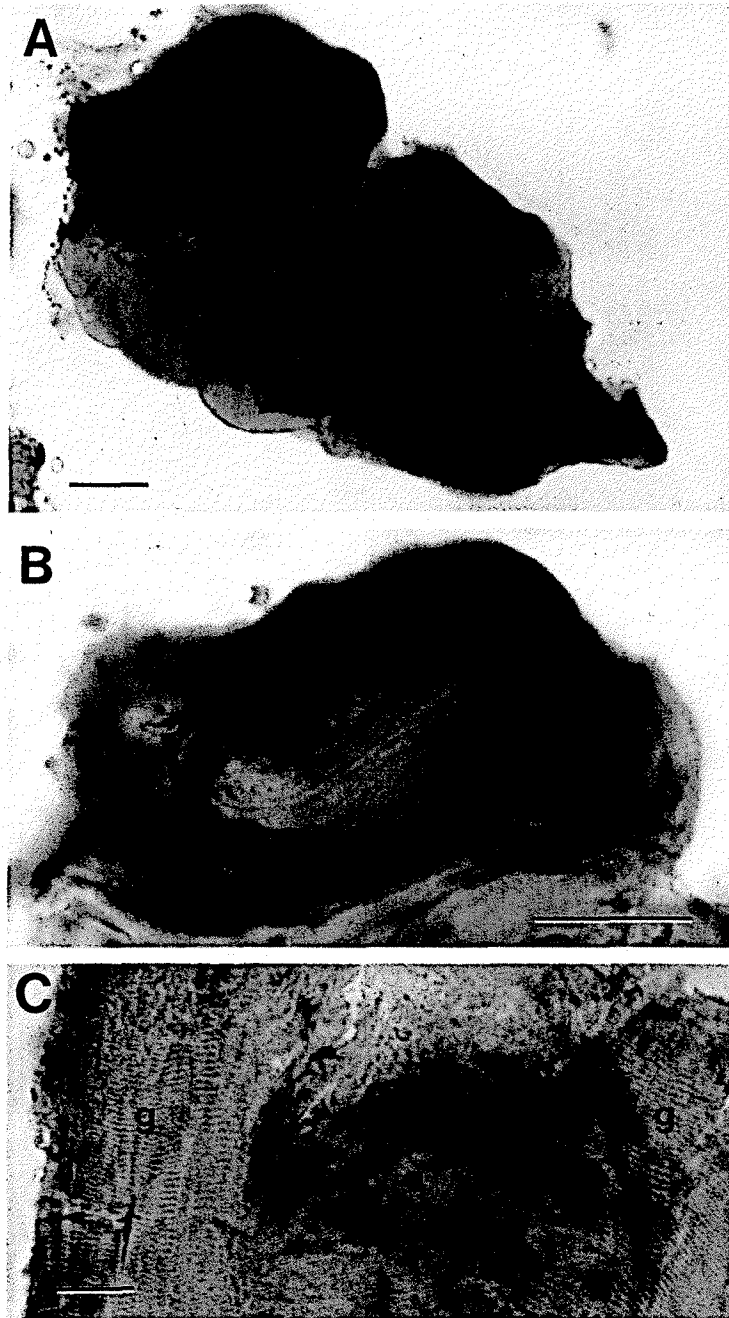
Fig. 3. Appendicularian houses detected in the guts of *Oncaea* species, and metachromatically stained. Note the difference in color: parts containing mucopolysaccharides are stained in reddish purple while others are stained in blue. A, *O. conifera*, female, night, 0–50 m; B, magnification of A; C, *O. venusta* f. *venella*, female, night, 0–50 m, g: gut tissue of copepod, a: appendicularian house remain in gut. Scale bars = 20 μm.
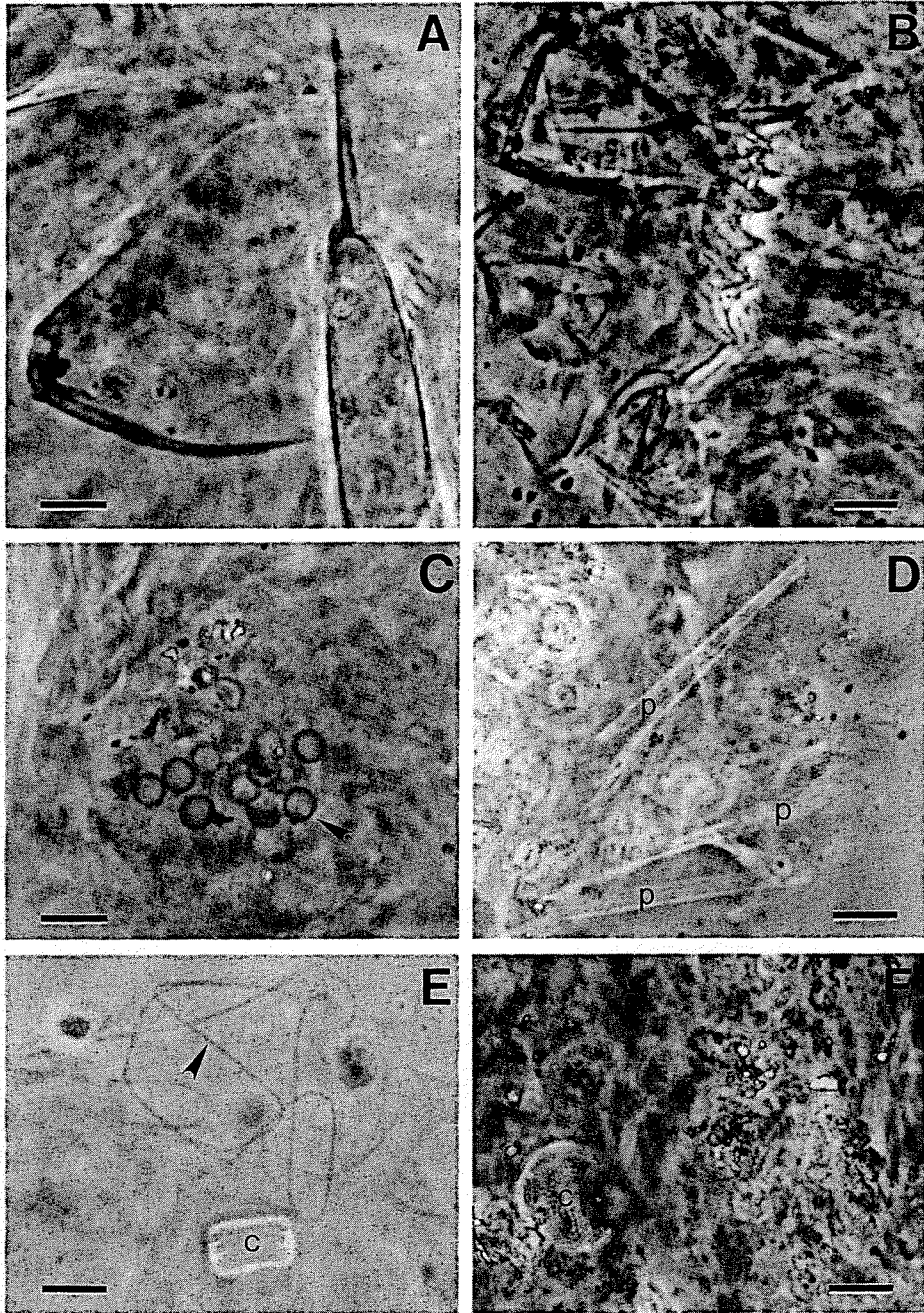
Fig. 4. Gut contents of *Oncaea* species. A, maxilliped and leg of copepodids, *O. venusta* f. *typica*, female, day, 0–50 m; B, calanoid mandible, *O. venusta* f. *typica*, female, night, 0–50 m; C, nematocysts (arrowed), *O. venusta* f. *venella*, female, night, 0–50 m; D, pennate diatoms (p), *O. venusta* f. *typica*, female, day, 0–50 m; E, centric diatom (c) and fibers of the incurrent filter of an appendicularian house (arrowed), *O. conifera*, female, night, 0–50 m; F, centric diatom (c) and unidentified minute particles, *O. media* f. *major*, female, day, 0–50 m. Scale bars = 10 μm (A–F).

Table 2. Frequency of occurrence of appendicularian houses in guts of *Oncaea*.

Species	Sex	No. of individuals examined	Frequency of occurrence of appendicularian houses (%)
O. venusta f. *typica*	♀	40	82.5
	♂	39	28.2
O. conifera	♀	38	68.4
	♂	27	59.3
O. mediterranea	♀	48	60.4
	♂	38	42.1
O. venusta f. *venella*	♀	34	64.7
	♂	39	48.7
O. clevei	♀	35	68.6
	♂	9	33.3
O. media f. *major*	♀	13	100.0
O. umerus	♀	38	60.5
O. minuta	♀	53	50.9
O. hawii	♀	8	37.5
O. media f. *minor*	♀	39	53.9
	♂	47	42.6
O. dentipes	♀	26	23.1

Sporozoans and parasitic flagellates were rarely found in the guts of *O. venusta* f. *typica*, *O. venusta* f. *venella*, *O. mediterranea*, *O. clevei* and *O. media* f. *major*.

Frequency of occurrence of each item in guts

The frequency of occurrence of food items found in the guts of the 9 species and 4 forms of *Oncaea* are outlined in Tables 2 and 3. Appendicularian houses were detected in all species (Table 2) with a frequency range of 23.1–100.0% (mean 54.4%, n=17). On the average, females showed a higher frequency of the occurrence of appendicularian houses in the guts (mean 61.0%, n=11) than males (mean 42.4%, n=6); the most prominent sexual difference occurred in *O. venusta* f. *typica* and *O. clevei* (Table 2). The frequencies of occurrences of the incurrent filter fibers (IF) and packed house membranes (HM) of appendicularians in the guts are shown separately for each time and depth in Table 3. Although appendicularian house membranes were usually accompanied with incurrent filter fibers in the guts, occasionally either one was detected singly. The occurrence of appendicularian houses in the guts did not correlate with time or depth in any of the species examined (Table 3). The only exception was in the vertically migrating *O. conifera* females, which had a much higher frequency of appendicularian house occurrence · in their guts during the night in the epipelagic zone (94%) compared to their daytime residence in the mesopelagic zone (20 or 40%). This is a statistically significant difference (χ^2–test, $P<0.01$).

Copepodids and copepod nauplii (CO) only occurred in the guts of larger species (>0.7 mm), being present in the guts of up to 40–45% of female *O. venusta* f. *typica* (0–50 m depth) and in 80% of *O. conifera* females at night (100–150 m depth). Radiolarians (RA) and cnidarian nematocysts (NC) were rarely detected in the guts excepting very high occurrences (60%) of radiolarians in *O. conifera* (female, day, 100–150 m). Unidentified remains (UM), consisting mainly of minute

Table 3. Frequency of occurrence of items detected in guts of *Oncaea* species. AH: Appendicularian houses identified by either incurrent filter fibers or packed transluscent matter; IF: fibers of incurrent filter of appendicularian houses; HM: appendicularian house membrane with incurrent filter fibers not contained (only packed transluscent matter); DI: diatoms; DF: dinoflagellates; SF: silicoflagellates; CO: copepodids & copepod nauplii; CR: unidentified crustaceans; RA: radiolarians; NC: cnidarian nematocysts; CH: chaetognaths; UM: unidentified remains; EG: empty gut.

Species	Sex	Time	Depth (m)	AH Total	AH IF	HM	DI	DF	SF	CO	CR	RA	NC	CH	UM	EG
O. venusta f. *typica*	♀	Day	0–50	90.0	55.0	70.0	95.0	10.0	0.0	45.0	20.0	10.0	10.0	0.0	100.0	0.0
		Night	0–50	75.0	60.0	75.0	90.0	15.0	10.0	40.0	25.0	5.0	0.0	5.0	100.0	0.0
	♂	Day	0–50	15.0	15.0	10.0	20.0	5.0	0.0	0.0	5.0	0.0	5.0	0.0	35.0	55.0
		Night	0–50	42.1	21.1	31.6	68.4	5.3	0.0	0.0	31.6	0.0	5.3	0.0	84.2	15.8
O. conifera	♀	Day	100–150	100.0	60.0	100.0	100.0	0.0	0.0	80.0	20.0	60.0	0.0	0.0	100.0	0.0
		Day	150–200	40.0	20.0	40.0	60.0	0.0	20.0	0.0	20.0	0.0	20.0	0.0	60.0	40.0
		Day	200–250	20.0	10.0	10.0	30.0	0.0	0.0	0.0	10.0	0.0	0.0	0.0	50.0	50.0
		Night	0–50	94.4	61.1	77.8	100.0	27.8	0.0	11.1	33.3	5.6	5.6	0.0	100.0	0.0
	♂	Day	50–100	70.0	0.0	70.0	70.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0
		Night	0–50	52.9	35.3	35.3	47.0	5.5	0.0	0.0	0.0	0.0	5.9	0.0	70.6	23.5
O. mediterranea	♀	Day	50–100	66.7	44.4	55.6	66.7	5.5	0.0	0.0	0.0	5.5	0.0	0.0	94.4	5.5
		Day	200–250	40.0	30.0	10.0	30.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	80.0	20.0
		Night	0–50	65.0	35.0	10.0	85.0	25.0	0.0	0.0	10.0	0.0	0.0	0.0	85.0	15.0
	♂	Day	50–100	42.1	31.6	21.1	42.1	0.0	0.0	0.0	0.0	5.3	0.0	0.0	84.2	15.8
		Night	0–50	42.1	26.3	36.8	52.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	78.9	21.1
O. venusta f. *venella*	♀	Day	0–50	75.0	40.0	75.0	85.0	5.0	5.0	20.0	15.0	10.0	0.0	0.0	85.0	10.0
		Night	0–50	50.0	28.6	50.0	92.9	7.1	0.0	14.3	7.1	14.3	7.1	0.0	92.8	7.1
	♂	Day	0–50	31.6	0.0	31.6	47.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	73.7	26.3
		Night	0–50	65.0	40.0	30.0	35.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0	80.0	20.0
O. clevei	♀	Day	0–50	73.3	53.3	60.0	73.3	0.0	0.0	13.3	13.3	0.0	0.0	0.0	93.3	6.7
		Night	0–50	65.0	30.0	50.0	60.0	5.0	0.0	0.0	10.0	0.0	0.0	0.0	90.0	10.0
	♂♀	Night	0–50	33.3	11.1	33.3	44.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	66.7	11.1
O. media f. *major*	♀♀	Day	0–50	100.0	38.5	100.0	84.6	15.4	0.0	7.7	46.2	15.4	7.7	0.0	100.0	0.0
O. umerus	♀	Day	50–100	65.0	20.0	60.0	60.0	5.0	0.0	0.0	0.0	5.0	5.0	0.0	95.0	5.0
		Night	0–50	55.6	11.1	55.6	77.8	0.0	0.0	0.0	11.1	5.6	0.0	0.0	100.0	0.0
O. minuta	♀	Day	0–50	55.6	33.3	55.6	55.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	77.8	22.2
		Day	50–100	50.0	25.0	25.0	50.0	0.0	0.0	0.0	12.5	0.0	0.0	0.0	87.5	12.5
		Night	50–100	38.9	16.7	33.3	55.6	0.0	0.0	5.6	0.0	0.0	0.0	0.0	77.8	22.2
		Night	200–250	61.1	22.2	55.6	66.7	0.0	0.0	5.6	16.7	0.0	0.0	0.0	94.4	5.6
O. haurii	♀♂	Night	200–250	37.5	0.0	37.5	50.0	0.0	0.0	0.0	12.5	0.0	0.0	0.0	75.0	25.0
O. media f. *minor*	♀	Day	0–50	70.0	25.0	70.0	40.0	0.0	0.0	0.0	5.0	0.0	5.0	0.0	80.0	20.0
		Night	0–50	36.8	5.3	36.8	42.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	57.9	31.6
	♂	Day	0–50	37.5	0.0	37.5	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	62.5	37.5
		Day	50–100	55.0	20.0	45.0	35.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	65.0	35.0
O. dentipes	♀	Night	50–100	31.6	10.5	26.3	15.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	63.2	36.8
		Day	50–100	15.4	7.7	15.4	15.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	76.9	23.1
		Night	50–100	30.8	7.7	23.1	46.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	84.6	15.4

Table 4. Numerical abundance of·all *Oncaea* spp. and appendicularians during daytime in the upper 250 m of the central Red Sea in February 1981 (adapted from Böttger 1985). X: average number of individuals m⁻³, based on 3 sampling series; R: range.

Depth(m)	*Oncaea* spp.		Appendicularians	
	X	R	X	R
0–50	480	290–640	520	400–740
50–100	330	170–440	240	130–350
100–150	200	100–310	120	30–200
150–200	100	81–130	8.3	4.2–12
200–250	110	92–140	1.2	0.4–2.6

particles (see Figures 1A–D, 4F), were the most frequent items found in the guts (mean 81.1%, n=37). Identification of these remains was impossible using light microscopy. Less than about half the individuals of any given species or sex had empty guts (Table 3).

Discussion

Zooplankton composition and vertical distribution of Oncaea *species in the central Red Sea*

Copepods (including nauplii) were the dominant zooplankton fraction in the central Red Sea during February, 1981, accounting on average for 82% of total zooplankton density by number in the upper 450 m of the water column (Böttger 1985). Appendicularians ranked next to copepods, accounting for about 8% of the total zooplankton in that layer. The species composition of appendicularians was not evaluated from the present material, and information in the literature on their community structure in the central Red Sea is scarce. According to Lohmann (1931) *Oikopleura longicauda* (Vogt) is the most abundant oikopleurid species, followed in number by *O. fusiformis* Fol and *O. rufescence* Fol. *Fritillaria* species seem to be rare. Similar results were reported by Fenaux & Godeaux (1970) and Vaissire & Seguin (1984) from the Gulf of Aqaba, in the northernmost part of the Red Sea. Among the copepodids, oncaeids comprised 25% of the total standing stock in the upper 450 m (Böttger 1985). Maximum concentrations of oncaeids and appendicularians were always found in the upper 50 m, showing average values of ca. 500 ind. m⁻³ for both taxa (Table 4). Below 150 m depth, the density of appendicularians decreased substantially, while the corresponding density gradient· for oncaeids was less pronounced. This pattern is seen in Table 4 where the 9 species and 4 forms of *Oncaea* that were used for the gut content analysis are combined. Most of the species are epipelagic, occurring mainly in the upper 100 m.

Oncaea media f. minor was numerically dominant in that layer, accounting for 15% of the total number of oncaeids (Böttger-Schnack 1990b). Females of this species also had a secondary concentration peak in the mesopelagic zone. Some of the lower epipelagic species or sexes, such as the males of *O. conifera* and both sexes of *O. mediterranea* showed diel vertical migration and concentrated in the upper 50 m during the night (Table 1). The most extended diel vertical migration was

found for females of *O. conifera*, which migrated from their daytime depth in the upper mesopelagic zone (200–300 m) up to the upper epipelagic zone (0–50 m) during the night. For smaller mesopelagic species such as *O. hawii* and *O. minuta*, the vertical migration pattern was not investigated for the winter material. However, investigations in the same area during autumn indicated that they undertook no or even reverse diel vertical migration (Böttger-Schnack 1990b).

Feeding habits of Oncaea

The feeding ecology of pelagic poecilostomatoids is poorly understood compared with that of calanoid copepods. Direct observations of their feeding behavior suggests they are loosely associated with other pelagic zooplankters or detrital matter (Nishimura 1960, Heron 1973, Alldredge 1972, 1976, Landry & Fagerness 1988, Ohtsuka & Kubo 1991, Ohtsuka et al. 1993, Steinberg et al. 1994). The association of relatively large species of *Oncaea* (ca. 1 mm in body length) with both discarded and occupied appendicularian houses is commonly observed in subtropical and tropical waters (Alldredge 1972, 1976, Ohtsuka & Kubo 1991, Ohtsuka et al. 1993, Steinberg et al. 1994). The present study reveals that small species of *Oncaea* of less than 0.5 mm in body length also utilize appendicularian houses as a food source. In addition, Lampitt et al. (1993) have found that *Oncaea conifera* consumes amorphous marine snow. As suggested by Huys & Boxshall (1991), both small and large species of *Oncaea* seem to need relatively large-sized detrital matter such as appendicularian houses or other marine snow as food. The mouthpart structure and feeding behavior of *Oncaea* also support this possibility: chelate maxillipeds are used for the capture and grasping of relatively large food items (Ohtsuka & Kubo 1991); antennae are also used for clinging to appendicularian houses (Ohtsuka et al. 1993); maxillules and maxillae are rather reduced (see Giesbrecht 1892, plate 47), and seem to play a role only in the scraping of food. Nanophytoplankters (<10 μm) found in the guts of *Oncaea* spp. (Turner 1986, present study) were possibly derived indirectly from such large detrital matter. Although the feeding habits of related poecilostomatoids such as *Lubbockia* and *Paralubbockia* are unknown, they may be associated with other zooplankters or relatively large detrital matter because their mouthpart structures are similar to those of *Oncaea* (cf. Boxshall 1977).

Ohtsuka et al. (1993) speculated that since species of *Oncaea* have similar mouthparts, irrespective of size, they may employ similar feeding behavior or habits. The present study also supports this inference because of the absence of obvious differences in the gut contents among the species examined, with the exception of stronger carnivory on copepodids and appendicularians in the larger species (Ohtsuka & Kubo 1991, present study). It is uncertain in the present study whether these larger species catch living copepodids or feed on their carcasses and/or exuviae. However, the almost intact bodies of copepodids detected in some guts point to their direct predation on living individuals.

The present study strongly supports the association of *Oncaea* with appendicularian houses in the epipelagic and upper mesopelagic zones. Discarded

appendicularian houses may be an important constituent of detritus and a food source for copepods in the mesopelagic zone, as suggested by Steinberg et al. (1994). Large mesopelagic species such as *O. conifera*, with a strong vertical migration pattern, exhibited a corresponding daily feeding rhythm, with the highest feeding intensity during the night in the upper 50 m, where the maximum concentration of appendicularians was found. According to Weikert (1987), chlorophyll *a* was almost confined to the upper 150 m with the highest peak at a depth of ca. 40 m at the same station in February, 1981. The restricted vertical distibution of appendicularians in the upper 150 m (see Table 4) was probably related to this concentration gradient of chlorophyll *a*. Smaller and non-migrating mesopelagic species of *Oncaea* such as *O. tregoubovi* may be associated with mesopelagic appendicularians such as *Bathochordaeus* (Steinberg et al. 1994, Steinberg 1995) or sinking appendicularian houses from the upper zones. Since the sinking rate of the discarded appendicularian houses of *Oikopleura longicauda* was reported as 189 ± 31 m d^{-1} in the laboratory (Taguchi 1982), the discarded houses of epipelagic oikopleurids presumably reach the mesopelagic zones, becoming potential food for mesopelagic copepods.

The quality of the packed mucus and fibers in oncaeid guts in this study was quite similar to that found in the guts of *Scolecithrix danae* and *Oncaea* spp. which were observed to feed on appendicularian houses (Ohtsuka & Kubo 1991). Based on visual observations Alldredge (1972) and Ohtsuka et al. (1993) reported that *Oncaea* preferred food-concentrating filters to incurrent filters as a feeding site. The results from the present study give no clear evidence whether *Oncaea* fed directly and preferentially on the food-concentrating filters. Flood (1991) found rod-shaped clusters of globular granules (ca. 5 × 20 μm in size) on the external walls of the house membrane of *Oikopleura labradoriensis*, but no trace of such structures was found in the packed mucus from the guts of *Oncaea* in the present study. Appendicularian houses detected in the guts of the leptocephalus larvae of eels were entirely stained in reddish purple with a metachromatic dye (Mochioka personal communication), while those of *Oncaea* spp. were only partly stained. This difference may have been caused by long-term preservation of the specimens of *Oncaea* and/or by the occurrence of some kind of digestive chemical reaction in the guts of *Oncaea*. Fibers in the copepod guts were identified as those of the incurrent filter of oikopleurids based mainly on their diameters of ca. 0.5–1.0 μm. Fibers of the food-concentrating and pharyngeal filters are much finer than those of incurrent · fibers, ranging from 5 to 50 nm and from 97 to 330 nm in diameter, respectively (Deibel et al. 1985, Deibel & Powell 1987, Flood 1991). Although the net-like structures of incurrent filters (see Flood 1991, Fig. 4h) were not clearly found in the copepod guts in this study, our previous scanning electron microscopic observations revealed that parts of these entangled fibers with similar diameters do indeed exhibit mesh-like structures (Ohtsuka & Kubo 1991). Since the mandibular blade of *Oncaea* appears to be suited to the cutting and licking up of food rather than to grinding (cf. Giesbrecht 1892, Boxshall 1977), the rectangular structures of the incurrent filters of the houses might be torn during the feeding of *Oncaea* on

food attached to the filters.

Species of *Oncaea* are reported to be consumed by *Noctiluca* (Enomoto 1956), copepods (Fleminger & Hulsemann 1974, Ohtsuka & Onbé 1991, Steinberg 1995), decapods (Foxton & Roe 1974), chaetognaths (Sullivan 1980), and fishes (Odate 1977, Clark 1980). Foxton & Roe (1974) speculated that mesopelagic decapods indirectly ingest *Oncaea* through its larger "hosts" (conceivably appendicularians). Such indirect predation on *Oncaea* is also suggested in appendicularian house-eating calanoids such as *Scolecithrix danae* (Ohtsuka & Kubo 1991) and *Scopalatum vorax* (Steinberg 1995). The oceanic calanoid copepod *Pontellina* (family Pontellidae) exhibits a strong selectivity for *Oncaea* (Fleminger & Hulsemann 1974, Ohtsuka unpublished data). There was, however, no evidence of the indirect predation of *Pontellina* on *Oncaea* via appendicularian houses. Selective carnivory (e. g., Ohtsuka & Onbé 1989), opportunistic gorging (e. g., Boxshall 1989) and detritivory (e. g., Ohtsuka et al. 1993, Steinberg et al. 1994, Steinberg 1995) are more conspicuous in copepods occurring in oligotrophic regions or the deep seas.

The role of the genus *Oncaea* in marine ecosystems is considerably different from that of suspension-feeding calanoid copepods through: (1) effective utilization of nanoplankters through appendicularian houses (Alldredge 1972, Turner 1986, present study); (2) the excretion of fecal pellets, possibly containing mucopoly-saccharides (Alldredge 1976) or their derivatives originating from house membranes, which may differ in chemical compostion from those of particle-feeding calanoids; (3) the likely ability to feed on small cells due to the extremely small size of the adults of some species of ca. 0.2–0.3 mm in body length (Böttger-Schnack 1988, Böttger-Schnack et al. 1989). These characteristics presumably influence grazing on phytoplankters, the downward flux of particulate organic matter, and prey-predator relationships between zooplankters and fishes. Steinberg (1995) proposed that copepods associated with appendicularian houses are decomposers or remineralizers. Since mesopelagic zones are dominated by *Oncaea* species, amounting numerically to 60–80 % of all copepods present (Böttger-Schnack 1994), the distribution and feeding ecology of *Oncaea* are of paramount importance in order to understand trophodynamics and energy transfer in the sea.

Acknowledgments

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