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## Natural diets of vertically migrating zooplankton in the Sargasso Sea

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**Abstract** The feeding preferences of three common diel vertically migrating zooplankton were investigated from December 1999 to October 2000 at the U.S. JGOFS Bermuda Atlantic Time-Series Study (BATS) station in the Sargasso Sea. Gut content analysis of the copepods *Pleuromamma xiphias* (Giesbrecht) and *Euchirella messinensis* (Claus) and of the euphausiid *Thysanopoda aequalis* (Hansen) indicated that all three species fed on a wide variety of phytoplankton, zooplankton, and detrital material. Diet changes generally reflected seasonal trends in phytoplankton community structure. However, species-specific feeding preferences and differences in feeding selectivity among the three species were evident, and in general agreement with feeding habits predicted from the analysis of mouthpart morphology. The euphausiid *T. aequalis* fed equally on more different food types compared to both copepod species. The copepod *P. xiphias* consumed a diverse assemblage of phytoplankton from late winter through the summer (78–93% of gut items, by number, were phytoplankton) and based its diet more strongly on carnivorous feeding in autumn and early winter (31% and 61% of gut items were phytoplankton, respec-

tively). *E. messinensis* showed the greatest feeding specialization, with a strong preference for pennate diatoms in winter and spring and for coccolithophorids during late summer and fall (constituting 67–93% of gut items by number). All three species consumed diatoms more than other phytoplankton taxa, even though diatoms form only a small fraction of the phytoplankton biomass in the Sargasso Sea. Although the majority of gut items identified were phytoplankton cells, the relative biomass contribution of these small cells may be lower than that of zooplankton and detritus. Zooplankton on which the three species primarily preyed were protozoans and crustaceans, but also included other metazoans such as chaetognaths and cnidarians. Marine snow was also an important component of the diet in all three species, with typically >50% and rarely <20% of the gut content being olive-green debris. Marine snow from larvacean houses was found in the guts of all three species, while *E. messinensis* appeared to selectively consume marine snow aggregates enriched with bicapitate *Nitzschia* spp. Large cyanobacteria (>4 µm in diameter) found in guts were also likely consumed with marine snow. The species-specific differences in the diets of these three migrating species suggest that an individual species approach is important in determining how feeding habits affect the structure of pelagic food webs and carbon cycling in the sea. Electronic supplementary material to this paper can be obtained by using the Springer LINK server located at <http://dx.doi.org/10.1007/s00227-002-0815-8>.

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### Introduction

Diet preferences of zooplankton impact resource partitioning and biogeochemical cycling in marine ecosystems (Fowler and Knauer 1986; Michaels and Silver 1988; Dagg 1997). Generally, how a zooplankton forages depends on its ability to feed selectively and its

nutritional requirements, which may change with developmental stage, season, and food availability (Kleppel 1993). While the feeding habits of epipelagic copepods have been extensively analyzed, fewer studies have focused on feeding in mesopelagic (Foxton and Roe 1974; Schoeneck et al. 1990; Flock and Hopkins 1992; Steinberg 1995) and bathypelagic species (Gowing and Wishner 1986, 1992). In the meso- and bathypelagic zones, where food resources are limited, zooplankton may consume detritus sinking from productive euphotic waters, prey on other zooplankton at depth, or undergo diel vertical migrations (Paffenhöfer and Knowles 1979; Gowing and Wishner 1992; Kinsey and Hopkins 1994; Steinberg 1995). The purpose of the present study was to examine the natural diets of vertically migrating zooplankton, which constitute a significant fraction of the mesopelagic biota (Longhurst and Harrison 1989).

Diel vertical migration is a common strategy for mesopelagic zooplankton to access food-rich surface layers and avoid being visible to predators (Longhurst and Harrison 1989). Migrators ascend at night to feed, and descend to residence depths of several hundred meters before dawn. Migrators pass through a considerably changing food environment within a 24-h period, and one might expect opportunistic feeding in response to these variations in food quality and quantity (Schoeneck et al. 1990; Kinsey and Hopkins 1994; Atkinson 1996). Despite these variations in food availability, feeding preferences can be found in migrating zooplankton, whereby some species primarily consume either zooplankton or phytoplankton prey, as shown for euphausiids from the southern tropical Pacific (Roger 1973). What migrators consume impacts the amount and composition of particulate organic carbon (POC) exported from the euphotic zone to depth and that becomes available for deep-sea organisms (Gowing and Wishner 1986, 1992; Michaels and Silver 1988).

As part of a larger study on active export of dissolved and particulate matter due to diel vertical migration at the Bermuda Atlantic Time-Series Study (BATS) site (Steinberg et al. 2000; Schnetzer and Steinberg 2002), we studied the natural diets of three common diel vertically migrating zooplankton species over nearly a year. Changes in gut content (determined by epifluorescence microscopy) were compared to seasonal succession in phytoplankton community structure in the Sargasso Sea (determined by HPLC analysis). The feeding appendages of all three species were examined using light microscopy, as mouthpart structure can generally indicate if species are suspension or raptorial feeders (Flock and Hopkins 1992; Bradford-Grieve et al. 1999). The goal was to determine whether modifications in diet of each migrating species over the seasons were the product of selective feeding behavior or solely reflected changes in food availability.

## Materials and methods

### Zooplankton collection

Zooplankton were collected at the U.S. JGOFS BATS station in the Sargasso Sea (31°45'N; 64°10'W). Vertical tows within the surface 175 m were performed at night (between 10:30 p.m. and 2:00 a.m.) on six cruises between December 1999 and October 2000 (Table 1). We used a 2 m diameter net with a 500 µm mesh and a non-filtering, large-volume cod end, which maintains the zooplankton in good condition (Steinberg et al. 2000). Tows lasted <20 min, after which contents of the cod end were immediately poured into a tray, and within ~10 min of net recovery healthy, active zooplankton were individually pipetted onto a 333 µm mesh sieve, rinsed with 0.2 µm filtered seawater, and preserved in vials containing a 10% formaldehyde/seawater solution. Errors in our results due to cod-end feeding are likely minimal due to the large net mesh size (excludes most phytoplankton), relatively short towing time, and the long gut clearance times (41–191 min; Schnetzer and Steinberg 2002) of the species examined (i.e. most material consumed at depth would still be in their guts upon net retrieval). The vials were covered with foil to prevent pigment degradation and stored in the refrigerator until analysis in the laboratory. Common migrating species used for analyses were the adult copepods *Pleuromamma xiphias* (Giesbrecht) (Metridiidae) and *Euchirella messinensis* (Claus) (Aetedeidae), and the euphausiid *Thysanopoda aequalis* (Hansen) (Euphausiidae). No distinction was made between gender. These species are abundant in night tows at BATS throughout the year (Steinberg et al. 2000), and belong to the larger zooplankton size classes (>2 mm), which comprise 56% of the total migrant community at BATS (Madin et al. 2001).

**Table 1.** *Pleuromamma xiphias*, *Euchirella messinensis*, *Thysanopoda aequalis*. Food items of probable detrital origin in the guts of three species of migrating zooplankton (*olive-green debris*, estimate for percentage of gut content being olive-green debris, see "Results"; +, large cyanobacteria and/or remnants of larvacean houses were present in migrator guts; –, items not found in gut samples)

	Olive-green debris (%)	Large cyanobacteria	Remnants of larvacean houses
<i>P. xiphias</i>			
Dec 1999	> 50	+	–
Feb 2000	> 50	–	+
Mar 2000	> 50	–	+
May 2000	> 50	–	–
Aug 2000	> 50	+	–
Oct 2000	20–50	+	–
<i>E. messinensis</i>			
Dec 1999	20–50	–	–
Feb 2000	< 20	–	–
Mar 2000	< 20	–	–
May 2000	20–50	–	–
Aug 2000	> 50	–	+
Oct 2000	< 20	–	–
<i>T. aequalis</i>			
Dec 1999	20–50	–	–
Feb 2000	> 50	–	+
Mar 2000	> 50	–	+
May 2000	< 20	–	–
Aug 2000	20–50	+	–
Oct 2000	20–50	+	–

## Feeding appendages

Feeding appendages of all three species were examined as possible indicators of different feeding modes (i.e. herbivorous filter feeder, carnivorous raptorial feeder, or a combination) using light microscopy (Olympus SZH10 dissecting microscope). We examined and interpreted the structural features of the feeding appendages based on comparative morphological studies previously conducted for copepods (Arashkevich 1969; Schnack 1989; Bradford-Grieve et al. 1999) and euphausiids (Mauchline 1989; Gibbons et al. 1999).

## Gut content analysis

Relative measures of feeding preferences for the three species were obtained by identifying food items in their guts. Guts were dissected, and the contents spread onto a microscope slide. Stomach contents of three individuals per species for each sampling date (except for May and August 2000 for *E. messinensis* when  $n=2$ ) were analyzed by light and epifluorescence microscopy (Olympus Provis AX70) linked to a computer and equipped with image analysis software (Image Pro Plus version 4.0). Alternation between light and fluorescence microscopy facilitated identification of food items in the zooplankton guts. A blue (372 nm) excitation filter rendered chlorophyll *a* autofluorescence red and phycobiliprotein (cyanobacteria) autofluorescence yellow. Both types of pigment fluoresced bright red using green (552 nm) excitation. We selected specimens with at least one-third of their gut filled to guarantee a sufficient number of recognizable food items in the guts. All samples were analyzed within 3 months of collection. The May 2000 samples were picked from preserved night tows archived as part of the BATS zooplankton time series (Madin et al. 2001). These samples were taken and preserved using a similar procedure, but were not refrigerated. The lack of refrigeration did not affect the analysis, as phytoplankton in the guts of these previously collected organisms retained their natural fluorescence.

## Phytoplankton composition in ambient water

Seasonal and interannual variability in phytoplankton community structure is part of the ongoing BATS program and is determined using high performance liquid chromatography (HPLC). Sampling procedures and the HPLC method were described by Knap et al. (1997). Pigment concentrations were converted to chlorophyll *a* biomass and partitioned among the different phytoplankton groups using the pigment algorithms of Letelier et al. (1993) as described in Steinberg et al. (2001). Seasonal changes in the phytoplankton taxa found in the gut contents of the three zooplankton species were compared to seasonal trends in phytoplankton biomass and community structure reported for the Sargasso Sea (Steinberg et al. 2001).

## Results

### Feeding appendages

The structure of the mouthparts – especially the morphology of setae and mandibles – of the three species was investigated to provide additional insight into their feeding habits. *Pleuromamma xiphias* has numerous long setae with small intersetula spacing (Fig. 1a, b, c), and the cutting edge of the mandible bears pronounced teeth (Fig. 1d). In comparison to *P. xiphias*, both maxillae and the maxilliped of the copepod *Euchirella messinensis* are equipped with fewer, stouter setae (Fig. 1e, f, g), and the mandibles have hard dental plates and cutting edges with shorter teeth (Fig. 1h). The euphausiid *Thysanopoda aequalis* has a well-developed filtering basket

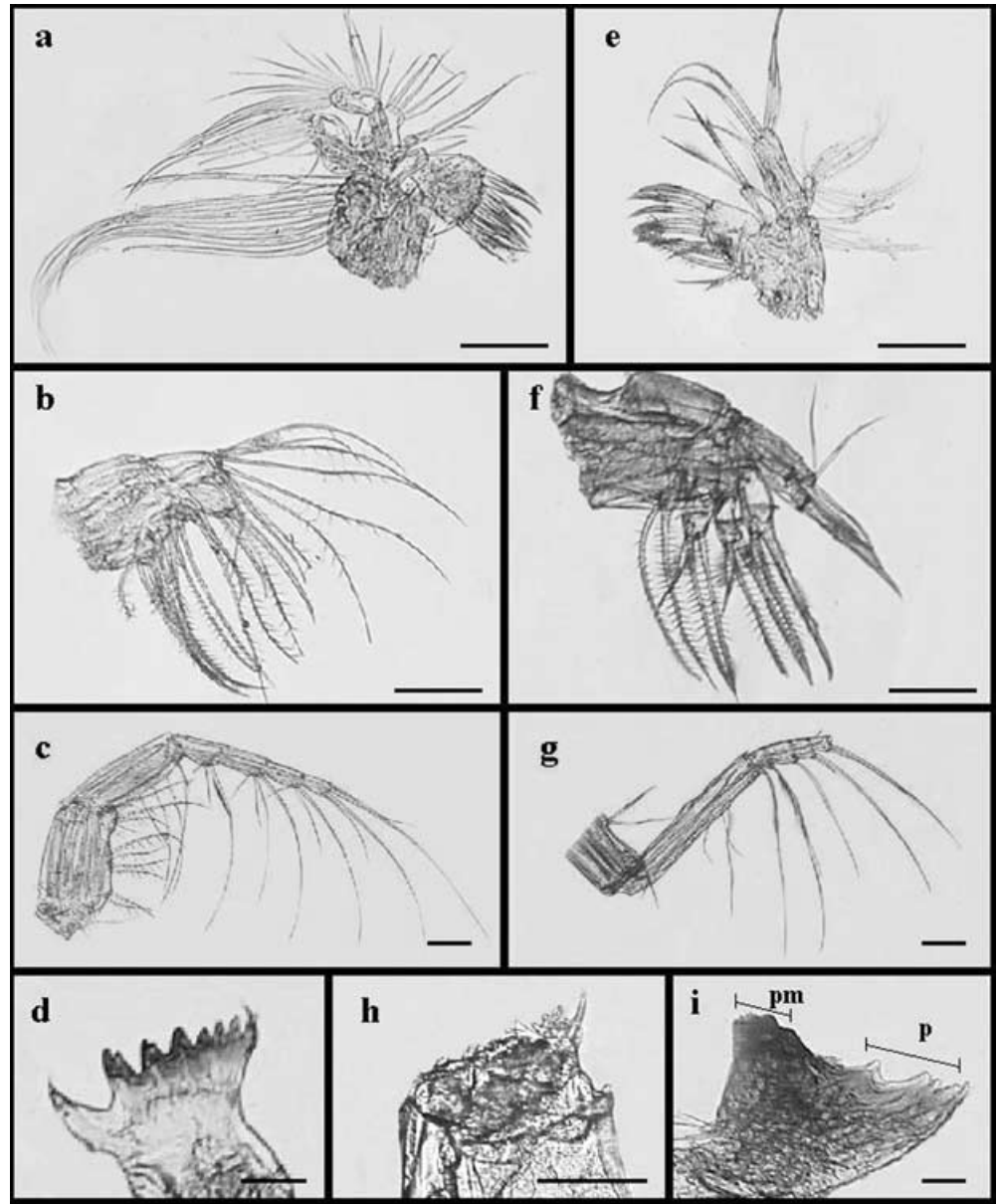
formed by the thoracic legs (not shown). In *T. aequalis* the pars mandibularis and the pars incisiva areas of the mandible, where food is ground and pierced, respectively (Fig. 1i), are both moderately developed. A large pars molaris is generally indicative of a predominantly herbivorous diet, whereas largely carnivorous species tend to have a larger pars incisiva (Mauchline 1989).

### Gut contents

A wide variety of food items including phytoplankton, zooplankton, and detritus was found in the guts of all three species examined, as shown by the percent of individuals containing each food type in their gut (Fig. 2). Diatoms were the most abundant phytoplankton found in guts and present in nearly all gut samples (Fig. 2). Coccolithophorids and dinoflagellates were the next most abundant, and silicoflagellates were rare (Fig. 2). Centric diatoms usually still contained chloroplasts as indicated by their bright autofluorescence, while the majority of pennate diatoms were empty frustules. The most common intact centric diatoms identified belonged to the genera *Thalassiosira*, *Coscinodiscus* and *Rhizosolenia*. *Planktoniella sol* was found in several guts in all three species (Fig. 3a). About half of all pennate diatoms encountered were bicapitate *Nitzschia* spp. (Fig. 3b). Two other types of pennate diatoms commonly found could not be further identified. Differences in the type of diatoms preferred by each migrator were apparent. While the copepod *P. xiphias* consumed both pennate and centric diatoms to a similar extent, nearly two-thirds of the diatoms ingested by *E. messinensis* were pennate. The euphausiid *T. aequalis* almost exclusively fed on centric diatoms with only every tenth diatom being a pennate form. When coccolithophorids were consumed, they often numerically dominated over other phytoplankton in the guts of all three species, with whole cells and numerous coccoliths present (Fig. 3c). The majority of the coccolithophorids (size range = 5–10  $\mu\text{m}$ ) brightly autofluoresced. Intact dinoflagellates were detected in gut contents of all three species, but in smaller numbers than diatoms or coccolithophorids (Fig. 2). The dinoflagellates most frequently found in the guts were members of the genera *Ornithoceros* (Fig. 3d), *Dinophysis*, and *Prorocentrum*. Occasionally *Protoperdinium* sp. and *Oxytoxum* sp. were present; only one gut contained *Ceratium* sp. A small unidentified dinoflagellate was commonly found in gut content samples (size:  $\sim 8 \times 12 \mu\text{m}$ , Fig. 3e). About 20% of dinoflagellates in guts were cysts (diameter ranging from  $\sim 25$  to  $60 \mu\text{m}$ , Fig. 3f). Only a small number of intact silicoflagellate skeletons were found. Using light microscopy, we were not able to determine whether numerous broken spines present in guts originated from silicoflagellates or protozoans.

Remnants of protozoan and crustacean origin were found in the majority of guts of all three species (Fig. 2). Foraminifera with bright autofluorescent symbionts

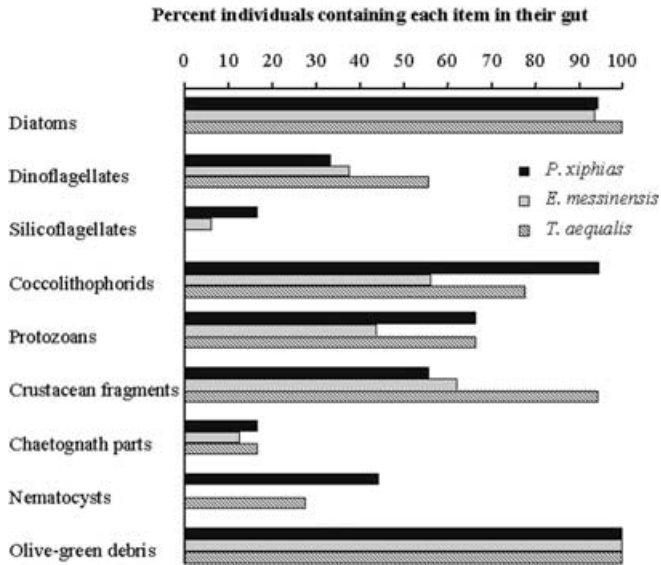
**Fig. 1a–i.** *Pleuromamma xiphias*, *Euchirella messinensis*, *Thysanopoda aequalis*. Mouthparts: **a, b** first and second maxilla of the copepod *P. xiphias*; **c** maxilliped of *P. xiphias*; **d** cutting edge of mandible of *P. xiphias*; **e, f** first and second maxilla of *E. messinensis*; **g** maxilliped of *E. messinensis*; **h** cutting edge of mandible of *E. messinensis*; **i** mandible of *T. aequalis* (*pm* posterior side showing pars mandibularis; *p* spines of pars incisiva). Scale bars: 200  $\mu\text{m}$  (a–c, e–g); 100  $\mu\text{m}$  (d, h, i)



were common, and tintinnid loricae of the genera *Cyrtarocyclus* (Fig. 4a), *Codonellopsis*, *Epiploocyclus*, *Favella*, *Dictyocyclus*, and *Xystonellopsis* were present. Acantharian (arrow-shaped spines, Fig. 4b) and radiolarian fragments were especially abundant in fall and winter gut samples, while aloricate ciliates were rare (Fig. 4c). Crustacean fragments such as mandibles (Fig. 4d), antennulae, and parts of crustacean cuticle were found in nearly all euphausiid guts and in the majority of the copepod guts (Fig. 2). Evidence of consumption of gelatinous zooplankton included nematocysts (Fig. 4e) and chaetognath mouthparts (Fig. 4f). While chaetognaths were part of the diet of all three species, cnidarian nematocysts were common in the guts of *P. xiphias* and *T. aequalis*, but absent in *E. messinensis* (Fig. 2).

All zooplankton guts contained olive-green debris (Fig. 2), characteristic of marine snow (Aldredge and

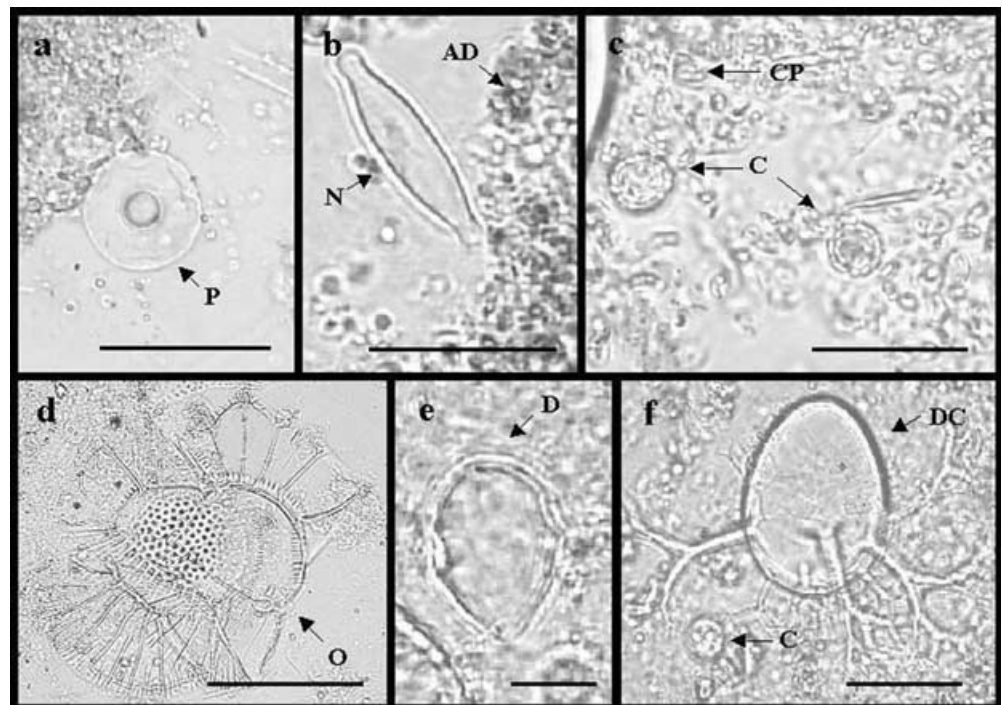
Silver 1988; Lampitt et al. 1993). The amorphous detritus contained large numbers of coccoid cyanobacteria (*Synechococcus* sp.,  $\sim 1 \mu\text{m}$ ) as indicated by epifluorescence microscopy (Appendix 1, electronic supplementary material). Other small phytoplankton cells, such as coccolithophorids, and occasionally small fecal pellets ( $< 50 \mu\text{m}$ ), presumably of protozoan origin, were also present. We roughly estimated how much of the gut content displayed this marine snow signature (Aldredge and Silver 1988; Lampitt et al. 1993) and grouped the samples into three categories:  $> 50\%$ ,  $20\text{--}50\%$ , and  $< 20\%$  of gut content as olive-green debris (Table 1). On several dates larger ( $\sim 4 \mu\text{m}$ ), yellow-fluorescing (372 nm), ovoid cyanobacteria were found in the guts of *P. xiphias* and *T. aequalis* (see Appendix 1, electronic supplementary material; Table 1). These cyanobacteria were almost exclusively found grouped in patches. In the



**Fig. 2.** *Pleuromamma xiphias* (copepod;  $n=18$ ), *Euchirella messinensis* (copepod;  $n=16$ ), *Thysanopoda aequalis* (euphausiid;  $n=18$ ). Summary of gut contents found in three species of migrating zooplankton. Data from all months sampled are pooled for each species

months of February and March stringy mucous material, most likely the remains of feeding structures or “houses” of larvaceans, occurred in the guts of the copepod *P. xiphias* and the euphausiid *T. aequalis* (Fig. 4g; Table 1). Remnants of larvacean houses were also found in the guts of the copepod *E. messinensis* in August. When present, this material was densely packed and comprised most of the gut content.

**Fig. 3a–f.** *Pleuromamma xiphias*, *Euchirella messinensis*, *Thysanopoda aequalis*. Plant material in migrator guts. **a** Centric diatom *Planktoniella sol* (*P*); **b** pennate diatom bicapitate *Nitzschia* sp. (*N*) next to amorphous detritus (*AD*); **c** coccolithophorids (*C*) and coccolith plates (*CP*); **d** dinoflagellate *Ornithoceros* sp. (*O*); **e** small common unidentified dinoflagellate (*D*); **f** dinoflagellate cyst (*DC*) and coccolithophorid (*C*). Scale bars: 10  $\mu\text{m}$  (e); 20  $\mu\text{m}$  (a–d, f)

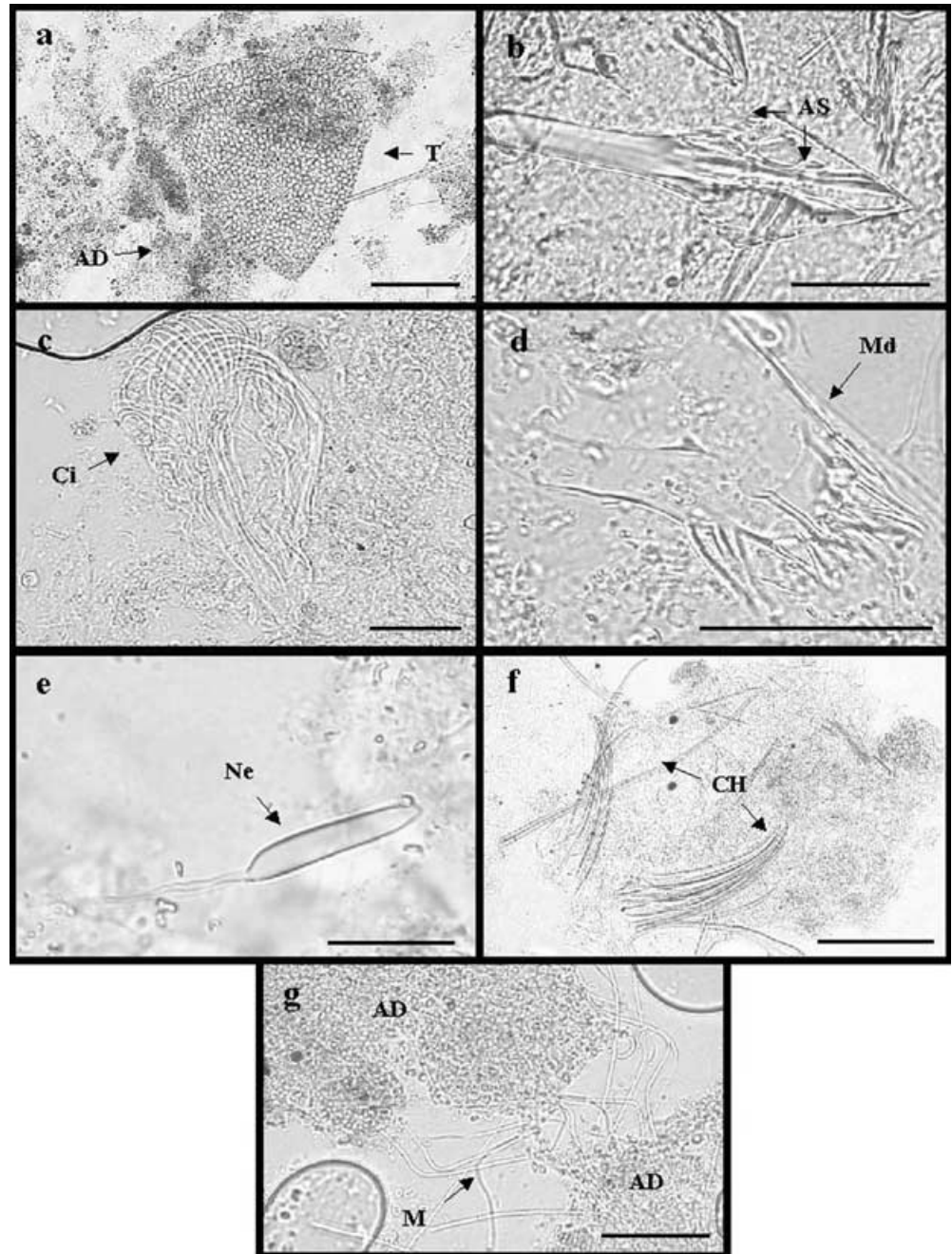


Seasonal changes in species-specific diet were compared among samples collected over six dates from December 1999 to October 2000 (Fig. 5). By plotting food items as percent of total gut items identified, we investigated changes in the relative importance of different food groups (Fig. 5). Intact diatoms and coccolithophorids, unbroken dinoflagellate frustules and skeletons of silicoflagellates, protozoans (intact foraminifera and whole tintinnid loricae), and crustacean and other metazoan parts (chaetognath mouthparts and nematocysts) were included. The comparison indicates that the copepod *P. xiphias* fed more intensively on phytoplankton from late winter until summer, while heterotrophic prey became more important in autumn and early winter (Fig. 5a). *E. messinensis* guts mainly contained phytoplankton remnants, predominantly diatoms in winter and spring and coccolithophorids in summer and autumn (Fig. 5b). The euphausiid *T. aequalis* consumed a wide variety of food types, which were more equally represented than in the diet of both copepods (Fig. 5c).

## Discussion

The ability of zooplankton to feed opportunistically on a variety of foods enhances the probability of obtaining a nutritionally complete ration in variable, dilute food environments (Kleppel 1993). Many mesopelagic zooplankton species may avoid resource limitation by undergoing diel vertical migration, since ascending into surface waters at night allows zooplankton to consume a larger variety of food types, particularly phytoplankton (Longhurst and Harrison 1989).

**Fig. 4a–g.** *Pleuromamma xiphias*, *Euchirella messinensis*, *Thysanopoda aequalis*. Zooplankton material and detritus in migrator guts. Zooplankton: **a** tintinnid (*T*) *Cyrtarocyclus* sp. and amorphous detritus (*AD*); **b** arrow-shaped acantharian spines (*AS*); **c** ciliate (*Ci*); **d** crustacean mandible (*Md*); **e** nematocyst (*Ne*); **f** chaetognath mouthparts (hooks) (*CH*). Detritus: **g** amorphous detritus (*AD*) with numerous coccolith plates and stringy mucus (*M*) from larvacean houses. Scale bars: 10  $\mu\text{m}$  (d); 20  $\mu\text{m}$  (b, e); 50  $\mu\text{m}$  (a, c, g); 100  $\mu\text{m}$  (f)

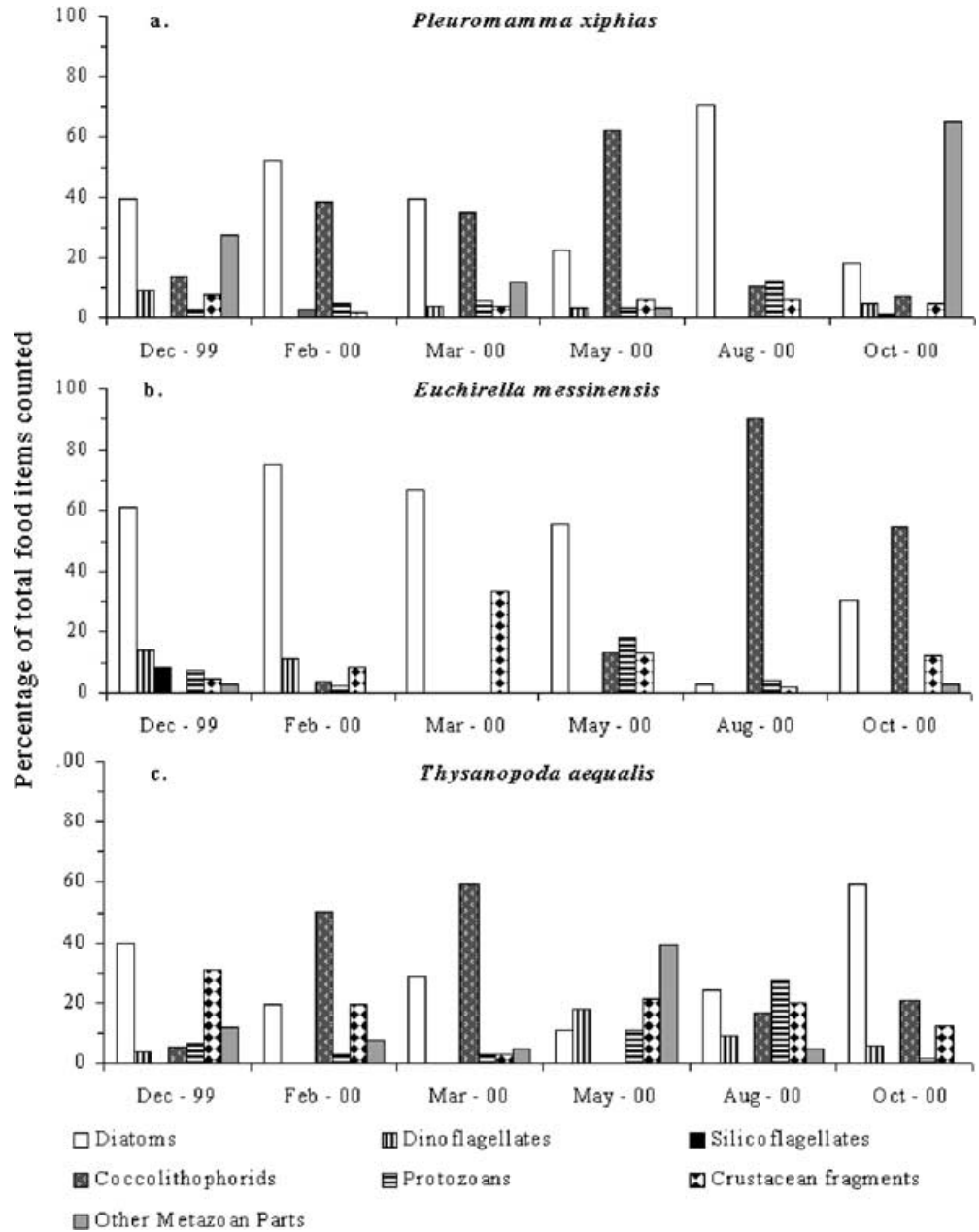


#### Mouthpart structure as an indicator of diet preference

The morphology of the mouthparts of the copepod *Pleuromamma xiphias* was a good indicator of feeding behavior. The large number of long setae characterizes *P. xiphias* as a typical particle feeder. *P. xiphias* maxillae and maxillipeds have small intersetulla spacing, and its mandibles carry relatively large pronounced teeth. This combination allows copepods to handle a wide range of particle sizes with a lesser degree of feeding specialization (Schnack 1989). The mouthparts of the copepod *Euchirella messinensis* did not reflect feeding habits as closely. The copepod has hard mandible cutting edges

adapted to grinding food, and gut content analysis showed a strong preference for pennate diatoms and coccolithophorids over other phytoplankton. However, although the stout setae of *E. messinensis* maxillae and maxillipeds are indicative of raptorial feeding, the only perceivable difference between animal remnants in the guts of the two copepod species was the absence of nematocysts in *E. messinensis*. Shape and structure of the feeding appendages of the euphausiid *Thysanopoda aequalis* are typical for a generalist feeder, as previously reported for members of the genus *Thysanopoda* (Flock and Hopkins 1992). *T. aequalis* seemingly switched from a predominantly carnivorous feeding mode to filter

**Fig. 5.** *Pleuromamma xiphias*, *Euchirella messinensis*, *Thysanopoda aequalis*. Gut content of three different species of migrators over 1-year sampling period. Food items for each food group are given as percent of total food items identified for each species in each month sampled. Protozoans: intact foraminifera and tintinnid loricae; other metazoan parts: chaetognath hooks and nematocysts (for further details see "Results"). Note: *E. messinensis* guts in March 2000 were almost empty and therefore only a mean of 6 food items ind.<sup>-1</sup> was counted



feeding, depending on the quantity and quality of phytoplankton available, a feeding behavior previously reported for euphausiids (Stuart and Pillar 1990; Stuart and Huggett 1992; Gibbons et al. 1999).

#### Phytoplankton community structure and migrator diet

The contribution of different phytoplankton taxa to the diet of all three species reflected seasonal changes in the food environment and indicated selective feeding on less-abundant phytoplankton groups. Diatom blooms are rare and only occur periodically during late or non-spring bloom periods at the BATS site, with taxa such as *Nitzschia* spp., *Rhizosolenia* spp., and *Chaetoceros* spp.

dominating (Steinberg et al. 2001). However, diatoms substantially contributed to diet throughout the entire sampling period for all three species, especially the copepods. Such a strong preference for diatoms in migrating species could result in an immediate grazing response and partly explain why, when diatom blooms do occur in the Sargasso Sea, they tend to be short-lived events. Although feeding on diatoms exclusively can be nutritionally insufficient, especially during times of growth and egg production in copepods, our results provide further evidence that diatoms are a major food source for calanoid copepods (Støttrup and Jensen 1990; Jónasdóttir et al. 1998).

The most abundant eukaryotic phytoplankton at BATS are prymnesiophytes (largely coccolithophorids)

and pelagophytes, with a peak abundance during the spring bloom (dominated by the coccolithophorid *Emiliania huxleyi*) around May, and a smaller prymnesiophyte bloom (predominantly *Umbellosphaera* spp. and *Florisphaera profunda*) in early fall (Haidar and Thierstein 2001; Steinberg et al. 2001). *P. xiphias* and *T. aequalis* extensively grazed on coccolithophorids during the spring bloom, while *E. messinensis* almost exclusively fed on coccolithophorids during late summer and fall. Although pelagophytes, such as silicoflagellates, are important contributors to the phytoplankton biomass at BATS (Steinberg et al. 2001), we rarely encountered intact skeletons of silicoflagellates in the guts of the three species, although fragments that might have derived from silicoflagellates were present.

Dinoflagellates were rarely consumed by any of the species examined, which is likely explained by their smaller contribution to the phytoplankton biomass at BATS (Steinberg et al. 2001). The role that dinoflagellates play as a potentially important food source for zooplankton is still unclear (Kleppel 1993). Culture studies indicate that the nutritional value of a dinoflagellate can exceed that of a diatom cell of the same size by several fold (Kleppel 1993). However, some dinoflagellates have the potential to produce chemical substances that induce avoidance behavior and can even kill certain copepod species (Huntley et al. 1986; Kleppel 1993).

Prokaryotic picoplankton (mainly prochlorophytes and cyanobacteria) regularly dominate the phytoplankton biomass at BATS (Steinberg et al. 2001), and cyanobacteria were often found in high concentrations in the guts of all three migrators. As these cells are too small to be ingested singularly by the species examined, they were likely ingested with microzooplankton, which had consumed the cyanobacteria, or with detritus (see "Discussion – Importance of detritus in the diet").

### Zooplankton prey

Gut content analysis demonstrated that vertically migrating zooplankton species prey foremost on protozoans and crustaceans, but also on other metazoans such as chaetognaths and cnidarians. The importance of each item in the diet of zooplankton is different depending on the biomass of the organism ingested. Although a large percentage of the three species fed on phytoplankton such as diatoms, the relative individual biomass contribution of these small cells is low compared to large crustaceans or other zooplankton. A previous study at BATS showed that the amount of carbon derived from non-plant material (detritus and other zooplankton), as calculated from comparisons of carbon ingestion based on gut fluorescence and fecal pellet production, is high for all three species: 85% for *T. aequalis*, and 83% and 71% for *E. messinensis* and *P. xiphias*, respectively (Schnetzer and Steinberg 2002).

Several studies show the importance of protozoans in zooplankton diet (e.g. Stoecker and Capuzzo 1990; At-

kinson 1996; Levinson et al. 2000). Increases in *Acartia tonsa* egg production after the addition of ciliates in feeding experiments have been reported (Stoecker and Egloff 1987), as well as higher clearance rates and assimilation efficiencies from feeding on ciliates than on diatoms of similar size (Stoecker and Capuzzo 1990; Atkinson 1996). In our study, skeletal remnants of radiolarians and acantharians were numerous in copepod guts in fall and winter, but were so highly fragmented that they were difficult to include in the analysis. Aloricate protozoans were rarely encountered, most likely because they are easily disrupted and leave no recognizable remains once digested. In the present study, overall, the present study likely underestimates the importance of protozoans as contributors to the diet of the three species.

The copepods and the euphausiid commonly consumed other crustaceans and occasionally chaetognaths. Cnidarians were consumed by the copepod *P. xiphias* in October and the euphausiid *T. aequalis* in May, as indicated by the large numbers of nematocysts in their guts. The presence of nematocysts has also been reported in the gut contents of predominantly carnivorous deep-sea copepods from the eastern tropical Pacific (Gowing and Wishner 1986, 1992).

Using plant and animal carotenoids as tracers, Kleppel et al. (1988) demonstrated that periods of intense carnivory are typical for copepods – including species known to vertically migrate. Overall, during fall and winter, carnivorous feeding was apparently more important for *P. xiphias*, and to a lesser degree for *E. messinensis*, while for *T. aequalis* zooplankton substantially contributed to the diet throughout most of the year.

### Importance of detritus in the diet

Detritivory has been reported for several surface-living (Kleppel et al. 1988; Bochdansky and Herndl 1992) as well as mesopelagic non-migrating (Steinberg 1995; Green and Dagg 1997) and migrating zooplankton species (Suh et al. 1991; Flock and Hopkins 1992; Lampitt et al. 1993; Dilling et al. 1998). Feeding on detritus enables mesozooplankton to utilize food of a smaller size class that cannot normally be directly ingested (Allredge 1972). For all three species, commonly > 50% and rarely < 20% of the gut content was olive-green debris. Quantities found in *P. xiphias* exceeded those in the guts of the other two species examined throughout the sampling period. Kleppel (1993) reported that marine snow provides zooplankton with specific nutritional components like C<sub>18</sub> saturated and unsaturated fatty acids and several amino acids that are scarce or lacking in diatoms. In addition, assimilation efficiencies on fresh diatom/larvacean snow as high as 75% have been reported (Dilling et al. 1998).

Marine snow aggregates are centers of elevated primary production and metabolism, which often creates

high concentrations of dissolved inorganic nutrients (Silver et al. 1986; Alldredge and Silver 1988; Gotschalk and Alldredge 1989; Kaltenböck and Herndl 1992). This might allow cyanobacteria trapped in aggregates to grow larger than those in the ambient water (Kaltenböck and Herndl 1992), and may explain the large cyanobacteria ( $\sim 4 \mu\text{m}$ ) in *P. xiphias* and *T. aequalis* guts between late summer and winter. Alternatively, these species may have fed on protozoans or phytoplankton that “host” cyanobacteria. For example, Buck and Bentham (1998) described cyanobacteria of generally larger size embedded in the extracellular matrix of an aplastidic protist (*Solenicola setigera*), which itself is found in association with a centric, chain-forming diatom found in North Atlantic waters.

Embedded in the mucous matrix were phytoplankton frustules and fragments, metazoan parts, and skeletal remnants of silicoflagellates, acantharians, radiolarians, and tintinnid loricae. In the present study it is not clear to what extent food items were ingested as detritus or as individual entities before being mixed inside the gut. In addition, amorphous detritus in zooplankton guts in part simply represents food digested beyond recognition (Gowing and Wishner 1986). Further evidence that the three migratory species did consume marine snow were the remnants of larvacean houses (a source of marine snow; Alldredge and Silver 1988; Steinberg 1995), and the presence of pennate diatoms, bicapitate *Nitzschia* spp., in the guts. Lee and Fryxell (1996) report that these raphid diatoms are not only trapped in aggregates but also actively adhere to and move on substrates. The diatoms grow and reproduce on marine snow, and the cells belong to one or two main size classes, indicating that they are clones (Lee and Fryxell 1996). The vast majority of *Nitzschia* spp. cells in the gut contents in the present study also belonged to two main size classes ( $\sim 13$  and  $25 \mu\text{m}$  long, all  $\sim 5 \mu\text{m}$  wide). It is notable that *E. messinensis* may have selectively consumed *Nitzschia* clones still attached to the aggregates or cells after their release into the ambient water, as two-thirds of all diatoms found in *E. messinensis* guts were bicapitate *Nitzschia* spp. Apparent selective grazing by this copepod could have ecological implications for this diatom group.

### Migrator diet and expected effects on POC export

The abundance of marine snow aggregates and fecal pellets in pelagic sediment traps identify these particles as the major agents in the vertical redistribution of carbon, nitrogen, and other biogenic elements (Honjo and Roman 1978; Fowler and Knauer 1986; Silver and Gowing 1991; Silver et al. 1998). Zooplankton can increase POC flux by packaging fine suspended particles into large, rapidly sinking fecal pellets (Fowler and Knauer 1986; Dagg 1997; Roman et al. 2002). Diel vertically migrating zooplankton release fecal pellets in the surface waters during nocturnal feeding (passive

POC flux), but also defecate surface-ingested carbon after their descent to daytime residence depths (active POC flux) (Flint et al. 1991; Atkinson et al. 1996; Morales 1999; Schnetzer and Steinberg 2002). Schnetzer and Steinberg (2002) show that active POC flux by vertically migrating zooplankton can contribute on average 3%, and a maximum of 18%, of the mean gravitational POC flux measured by sediment traps at 150 m in the Sargasso Sea. Zooplankton fecal pellets contain viable phytoplankton, high concentrations of digestion-resistant cyanobacteria, and a rich associated bacterial community (Silver et al. 1986; Schnetzer, unpublished data). When released at depth, these feces could be of high nutritive value for deep-sea organisms, in contrast to passively sinking pellets which are decomposed while sinking through the water column (Paffenhöfer and Knowles 1979; Alldredge et al. 1987; Silver and Gowing 1991; Urban-Rich 1999). Further, feeding and swimming activities of migrant macro- and mesozooplankton cause fragmentation of large sinking marine snow into smaller non-sinking aggregates (Green and Dagg 1997; Dilling and Alldredge 2000; Graham et al. 2000). This process diminishes aggregate flux to depth and alters the contribution of fecal pellets and sinking detritus to overall POC flux, which changes the chemical nature and therefore the availability of sinking particles for deep-sea organisms (Steinberg 1995; Dilling and Alldredge 2000).

In summary, all three diel vertically migrating species fed on a wide variety of phytoplankton, zooplankton, and detrital material, which is advantageous in a resource-limited pelagic environment. Although changes in the food environment partly explain diet modifications in all three species, differences in feeding preferences and in the degree of feeding selectivity among the species were evident. Thus, using an individual species approach is helpful in understanding how feeding habits of zooplankton affect planktonic community structure and carbon cycling in the sea.

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