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Zooplankton feeding ecology: contents of fecal pellets of the copepods *Eucalanus pileatus* and *Paracalanus quasimodo* from continental shelf waters of the Gulf of Mexico*

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ABSTRACT: Feeding patterns of adult female *Eucalanus pileatus* and *Paracalanus quasimodo* were examined by comparison of fecal pellet contents and available phytoplankton at 12 stations in northern Gulf of Mexico continental shelf waters. Pellets contained remains of a wide variety of various-sized solitary and chain-forming phytoplankters, tintinnids, crustaceans, amorphous detritus, and/or Mississippi River sediment. Dominant phytoplankters in fecal pellets largely corresponded to those dominant in the water at time of collection. There was, however, an apparent lack of ingestion of the most abundant phytoplankter *(Ditylum brightwellii)* by *P. quasimodo* at one station. This diatom may be too large for ingestion by *P. quasimodo*. At the same station, the larger *E. pileatus* did eat *D. brightwellii*. Phytoplankton species ingested changed markedly in accordance with changes in phytoplankton species available. Crustacean, tintinnid and detrital remains were present in pellets mainly when phytoplankton abundance was low. In the plume of the Mississippi River, riverine sediment was a major component of pellets. Comparison of the phytoplankters ingested by both copepods at the same stations revealed that *E. pileatus* and *P. quasimodo* have many food items, encompassing a broad array of particle sizes, in common. These results reveal that *E. pileatus* and *P. quasimodo* are omnivorous and primarily opportunistic herbivores.

INTRODUCTION

In order to identify potential pathways of pollutant and energy flow through pelagic marine food webs which support important fish species, it is necessary to describe the feeding habits of zooplankters that are prey of fish larvae. Although there have been many studies of the feeding responses of some zooplankters (reviews by Marshall, 1973; Conover, 1979; Frost, 1980; Turner, in press), most have focused on quantitative aspects of feeding (food size selection, feeding rate, total particulate volume, biomass or carbon ingestion) using either laboratory-cultured or natural particulate diets. There has been less emphasis on qualitative description of species-specific feeding patterns of zooplankters upon the total array of food items available in nature. In short, we know much more about *how much* many zooplankters eat, than about exactly *what* they eat. In view of recent suggestions that climatic- or anthropogenic-induced alteration of phytoplankton species assemblages may adversely modify selective feeding patterns of zooplankton and ichthyoplankton (Greve and Parsons, 1977), it appears important to specifically define trophic pathways through pelagic communities.

An effort is underway to identify food webs that support larvae of 3 important fish species (Atlantic croaker *Micropogonias undulatus*; spot *Leiostomus xanthurus*; and gulf menhaden *Brevoortia patronus*) in northern Gulf of Mexico continental shelf waters during the winter spawning period. Gut contents studies (Govoni et al., 1983) have revealed that adults and subadults of at least a dozen copepod genera, pteropods, juvenile pelecypods, and tintinnids are important prey items of larvae of the three fish species.

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In order to describe the food webs which support these larvae, the present paper and forthcoming ones examine *in situ* feeding habits of zooplankters that are larval fish prey items. The present study examined and compared the feeding habits of the calanoid copepods *Eucalanus pileatus* and *Paracalanus quasimodo*.

The primary method employed is scanning electron microscope (SEM) analysis of zooplankton fecal pellet contents. This method has been used by Turner (1978) to study copepod feeding habits, and subsequently to examine the diets of salps and pteropods (Silver and Bruland, 1981) and penaeid larvae (Youngbluth, 1982). SEM analyses of fecal pellet contents are not quantitative, but they do provide specific information on the types of food ingested *in situ*. In order to compare dominant food items ingested with dominant food items available, quantitative phytoplankton analyses were made on water samples taken coincidentally with zooplankton sampling. Thus, such comparisons provide 'qualitative electivity' information.

The distribution of *Eucalanus pileatus* is circumglobal in epiplanktonic tropical and subtropical coastal waters (Fleminger, 1973). This species is a common member of the copepod fauna of continental shelf waters off the southeastern United States (Bowman, 1971; Paffenhöfer, 1980) and in the northern Gulf of Mexico (Minello, 1980). Adults and subadults have been shown to feed upon several types of cultured diatoms and dinoflagellates (Paffenhöfer and Knowles, 1978; 1979) and adult females ingest fecal pellets of *E. pileatus* nauplii (Paffenhöfer and Knowles, 1979). Cinematographic studies of *E. pileatus* (Koehl and Strickler, 1981; Paffenhöfer et al., 1982) and *E. crassus* (Alcaraz et al., 1980; Paffenhöfer et al., 1982; Strickler, 1982) reveal that members of the genus *Eucalanus* do not 'filter feed' by straining food particles from the water using bristled appendages as open rakes. Rather, they are 'suspension feeders', using appendages as solid paddles to capture parcels of water containing food particles. Although there have been several recent studies of aspects of feeding by *E. pileatus* on laboratory-cultured diets, this is the first to examine *in situ* feeding patterns by this species.

Paracalanus quasimodo is often one of the most abundant copepods in continental shelf waters of the Gulf of Mexico (Minello, 1980) and the Atlantic off the southeastern United States (Bowman, 1971). It is likely that most of the '*Parcalanus* sp.' specimens found to comprise the dominant calanoid taxon in North Carolina and east Florida shelf waters (Atkinson et al., 1978; Hofmann et al., 1981; Paffenhöfer, 1980; 1983; Paffenhöfer et al., 1980) were *P. quasimodo*. *Paracalanus* sp. adults and copepodites also are one of the most frequently-ingested copepods of larval gulf menhaden (*Brevoortia patronus*), spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) in the northern Gulf of Mexico (Govoni et al., 1983).

The few studies of feeding by members of the genus *Paracalanus* (reviewed by Turner, in press), indicate that most species are primarily herbivorous. However, virtually all of these studies examined the feeding of the temperate species *P. parvus*. The feeding habits of subtropical and tropical *Paracalanus*, such as *P. quasimodo*, are not well known. This is unfortunate since the calculations of Paffenhöfer (1982) indicate that these copepods can exert a substantial grazing impact. The present study is the first to examine *in situ* feeding habits of *P. quasimodo*.

METHODS

Samples were collected from 12 stations at 5 locations over the northern Gulf of Mexico continental shelf (Fig. 1) in December 1981 and February 1982. Surface water samples (500 ml) for characterization of abundance and composition of available phytoplankton were taken immediately prior to collecting the zooplankton and were preserved in Utermöhl's solution (Guillard, 1973). Zooplankton were collected by 5 min surface tows at 0.5 to 1.0 knots with 363 µm mesh nets. *Eucalanus pileatus* and *Paracalanus quasimodo* adult females were sorted under a dissecting microscope and isolated in surface sea water in petri dishes within 15 min (usually 5 min) of collection. After

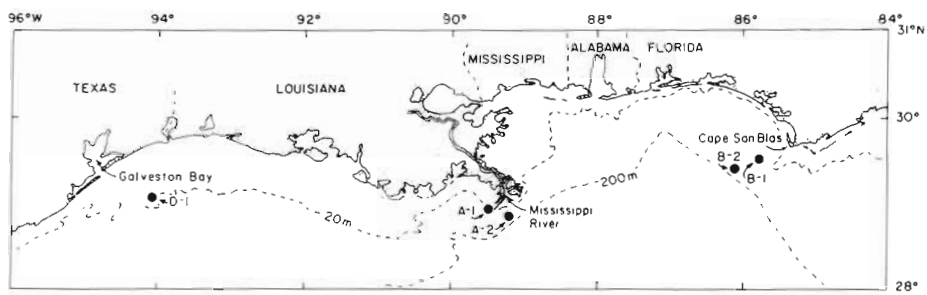

Fig. 1. Station locations

approximately 0.5 to 2.0 h of isolation, fecal pellets representing gut contents at time of collection were present in petri dishes. These were individually removed by pipette, and placed in petri dishes containing a mixture of filtered sea water and 20 µm screened surface sea water (containing natural microbes) and left for 24 to 36 h at approximately 20 °C for microbial stripping of pellet peritrophic membranes which initially mask pellet contents (Turner, 1977, 1978, 1979). Subsequently, pellets were individually removed by pipette and placed in scintillation vials containing approximately 5 % formalin:sea water solutions. Ashore, preserved pellets were again individually removed by pipette, placed in filtered sea water and drawn onto Whatman* GFC glass fiber filters. These filters, with attached pellets, were taken through SEM specimen preparation, including distilled water washing for salt elimination, dehydration in a graded ethanol series (50, 70, 95, 100 %), critical-point drying, and coated with gold : palladium (Turner, 1978). Pellets were examined with an ISI-30 SEM at 15 KV.

Two hundred forty micrographs were taken from 47 *Eucalanus pileatus* fecal pellets produced at 9 stations, and 254 micrographs were made from 69 *Paracalanus quasimodo* fecal pellets from 7 stations. Numerous additional pellets had largely intact peritrophic membranes that obscured pellet contents. These were not photographed and were not included in the counts of pellets examined.

SEM analyses were made prior to phytoplankton counts to reduce possible bias in characterization of pellet contents. Entire visible sides of pellets were examined with the SEM, and conspicuous food remains were photographed until all remains had been recorded or, in some cases, until so many micrographs of the same food item had been obtained that additional ones were considered redundant. The 67 micrographs presented here (14 % of those taken) are considered a representative sampling of food items ingested.

The abundance and composition of available phytoplankton food in surface waters where pellets were obtained were determined by the Utermöhl inverted microscope method (Lund et al., 1958). In all but 3 cases, the phytoplankton present in 100 ml of the 500 ml collected was concentrated by sedimentation. For 3 samples laden with silt, the phytoplankton in only 10 or 25 ml was concentrated. This produced aliquots of 205 to 1204 cells counted ($\overline{X} = 582$), in most cases giving a counting accuracy of better than ± 10 % (Guillard, 1973). Measurements of cell dimensions were made with an ocular micrometer. Where possible, phytoplankters were identified to species. In some cases, however, only generic classifications were made; when several congeners were present in the same sample, size categories were separately maintained.

*Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

RESULTS

Abundance and composition of available phytoplankton (Fig. 2) varied widely among the 12 stations. In all cases, however, diatoms overwhelmingly dominated the phytoplankton. A few dinoflagellates were present at most stations, but never comprised > 9 % of total cell number. Silicoflagellates were sporadically present but never comprised > 1 % of total cell number. Athecate flagellates were only sporadically recorded. This is not, however, considered an artifact of preservation since athecate dinoflagellates of the genus *Gyrodinium* were recorded in low numbers in most samples, and athecate estuarine nanoflagellates (*Chroomonas amphioxea*) preserved for several months in Utermöhl's solution still have both flagellae as well as cell membranes intact (see Fig. 5 of Turner and Anderson, in press).

Eucalanus pileatus fecal pellets contained a wide variety of food remains (Table 1). Pellets from Station A-1 on 9 December 1981 (Fig. 3) were packed with crushed frustules of the diatoms *Skeletonema costatum*, and to a lesser extent, *Thalassionema nitzschoides*. Some *S. costatum* frustules were crushed at the valve end (Fig. 3b), but others, from cells that had been ingested in pairs, had the hypotheca of one cell still attached to the epitheca of the adjacent one (Fig. 3c, d). There was additional evidence for separation of hypothecae from epithecae during ingestion (Fig. 3e), as well as for crushing of individual cells into small fragments (Fig. 3a, f). The *T. nitzschoides* frustules present had mostly been bitten in half (Fig. 3d). The overwhelming dominance of *S. costatum*, followed by *T. nitzschoides*, in these pellets is not surprising since these diatoms constituted 80 and 12 %, respectively, of the high numbers (36,320 cells l^{-1}) of the phytoplankton cells present (Fig. 2).

At Station A-1 on 5 February 1982, when the silt-laden plume of the Mississippi River was pronounced, all pellets contained conspicuous amounts of riverine sediment (Fig. 4a, b, c, d), as well as *Chaetoceros* spines (Fig. 4a, c, e). There also were broken frustules of *Thalassiosira* sp. (Fig. 4b) and *Pleurosigma* sp. (Fig. 4e), and fragments of other diatoms. The most abundant phytoplankter was *Ditylum brightwellii* (68 % of total cells); largely intact cells (Fig. 4d) as well as fragments of ends (Fig. 4f) of cells were present in pellets.

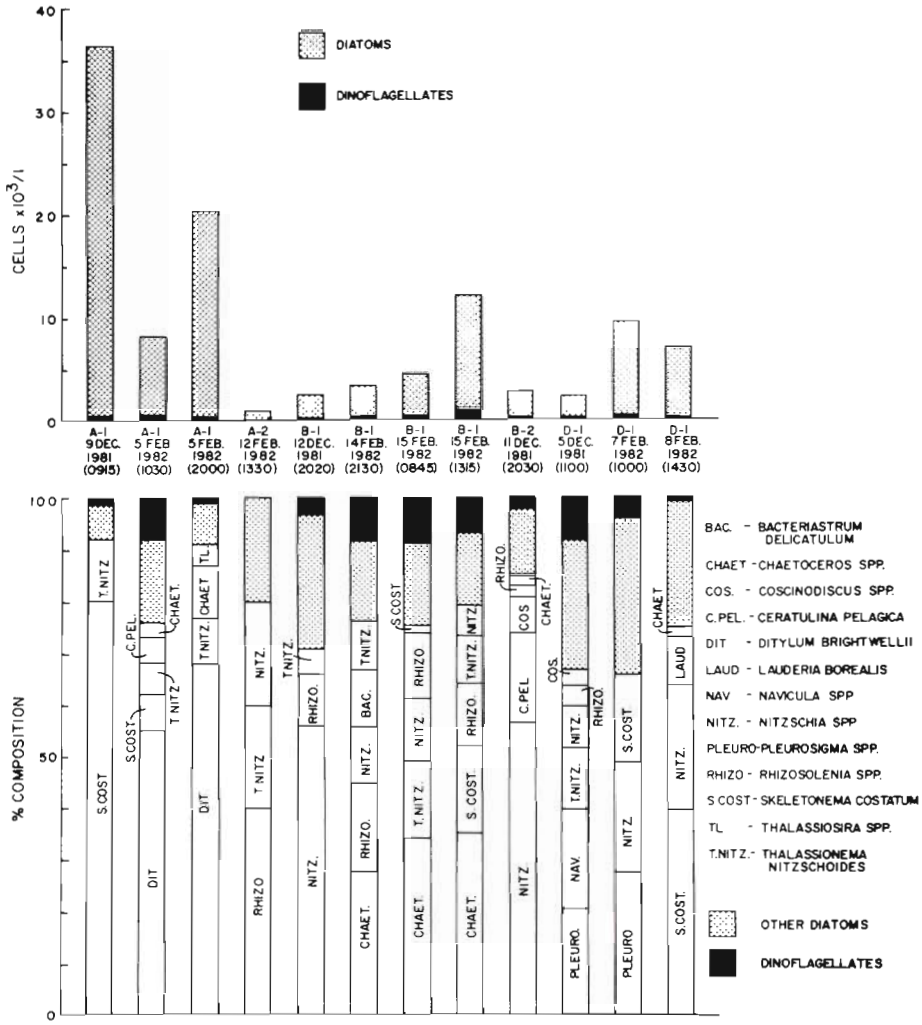

Fig. 2. Abundance (upper) and composition (lower) of the phytoplankton at stations where *Eucalanus pileatus* and *Paracalanus quasimodo* fecal pellets were collected

At Station B-1 on 12 December 1981, pellets contained spines of *Chaetoceros (decipiens, peruvianus)*, which together comprised 3.2 % of cells present, broken fragments of diatoms of the genus *Nitzschia*, the 7 varieties (species?) of which comprised 56 % of total cells, portions of broken *Rhizosolenia* spp. cells (9.8 % of available cells), and fragments of several other unidentified diatom species (Table 1).

At Station B-2 on 11 December 1981, pellets contained the widest variety of food remains. These included intact as well as fragmented cells of the two varieties of *Nitzschia* present (Fig. 5a, b, c, e, 6c), which together comprised 57 % of total cells, *Chaetoceros* sp. spines (Fig. 5a), broken *Rhizosolenia (alata, setigera)* cells (Fig. 5d, 6c, d, e) which comprised 2.3 % of available cells, and macerated frustules of an unidentified *Coscinodiscus* species (Fig. 6a, b, d) which comprised 6.7 % of total cells. Distributed throughout most pellets were finely-fragmented remains of numerous other unidentified diatoms (Fig. 5c, f, 6c, 7a). Some largely intact cells were cracked, suggesting mandibular maceration during ingestion (Fig. 7b), others were clearly bitten (Fig. 7c), and others appeared to have been swallowed intact (Fig. 5a, 7d). In some cases, bitten and swallowed cells were solitary centric diatoms or dinoflagellates of approximately the same size (compare Fig. 7c and d) or *Nitzschia* cells of apparently the same species (compare Fig. 5a and c). There was also evidence of carnivorous feeding by *Eucalanus pileatus* at Station B-2. The mandibular blade of another microcrustacean (Fig. 5b), crustacean appendages (Fig. 6f) and a tintinnid lorica (Fig. 8) were present in pellets. It appears that the force of filtration caused fragmentation of the fecal pellet shown in Fig. 8a, revealing an intact tintinnid lorica (Fig. 8a, b). High magnification of the oral end of the lorica (Fig. 8c)

Table 1. Food items comprising the dominant components of *Eucalanus pileatus* and *Paracalanus quasimodo* fecal pellets

Station	Date & (time of day)	Copepod	Dominant components	Longest dimension (μm)
A–1	9 Dec 1981 (09.15)	*E. pileatus*	*Skeletonema costatum*	7
			Thalassionema nitzschoides	66
A–1	5 Feb 1982 (10.30)	*P. quasimodo*	*Skeletonema costatum*	7
			Chaetoceros breve	16
			Chaetoceros lorenzianum	20
			Other diatoms	–
A–1	5 Feb 1982 (20.00)	*E. pileatus*	Sediment	–
			Ditylum brightwellii	66–149
			Chaetoceros breve	14
			Chaetoceros lorenzianum	20
			Thalassiosira sp.	40
			Pleurosigma spp.	50– 66
			Other diatoms	–
A–2	12 Feb 1982 (13.30)	*E. pileatus*	Crustaceans	–
			Amorphous detritus and/or sediment	–
B–1	12 Dec 1981 (20.20)	*E. pileatus*	*Chaetoceros decipiens*	26
			Chaetoceros peruvianum	20
			Nitzschia spp.	20–442
			Rhizosolenia alata f. *indica*	548
			Rhizosolenia setigera	403
			Rhizosolenia stolterfothii	396
			Rhizosolenia styliformis	594
			Other diatoms	–
B–1	14 Feb 1982 (21.30)	*E. pileatus*	Crustaceans	–
B–1	14 Feb 1982 (21.30) 15 Feb 1982 (08.45) 15 Feb 1982 (13.15)	*P. quasimodo*	*Chaetoceros affinis*	13– 17
			Chaetoceros atlanticus	4
			Chaetoceros dichaeta	3
			Chaetoceros didymus	26
			Chaetoceros lorenzianum	13– 26
			Chaetoceros messanensis	23
			Chaetoceros peruvianum	20
			Skeletonema costatum	7
			Nitzschia spp.	26– 46
			Thalassiothrix frauenfeldii	160–180
			Pleurosigma spp.	46– 66
			Other diatoms	–
			Crustaceans	–
B–2	11 Dec 1981 (20.30)	*E. pileatus*	*Nitzschia* sp.	66– 79
			Nitzschia sp.	165–528
			Chaetoceros sp.	40
			Rhizosolenia alata	198
			Rhizosolenia setigera	92
			Coscinodiscus sp.	33– 59
			Other diatoms	–
			Crustaceans	–
			Tintinnids	230
D–1	5 Dec 1981 (11.00)	*E. pileatus*	Crustaceans	–
D–1	5 Dec 1981 (11.00)	*P. quasimodo*	*Thalassiothrix frauenfeldii*	92
			Other diatoms	–
D–1	7 Feb 1982 (11.00) 8 Feb 1982 (14.30)	*E. pileatus*	Amorphous detritus	–
			Crustaceans	–
D–1	7 Feb 1982 (11.00) 8 Feb 1982 (14.30)	*P. quasimodo*	*Skeletonema costatum*	7
			Coscinodiscus spp.	59–122
			Lauderia borealis	46– 85
			Nitzschia closterium	109
			Nitzschia paradoxa	152
			Nitzschia pungens	165
			Nitzschia sp.	119–132
			Nitzschia sp.	20– 40
			Rhizosolenia alata	264
			Rhizosolenia setigera	100
			Rhizosolenia styliformis	500
			Thalassiosira spp.	33– 79
			Other diatoms	–
			Crustaceans	–

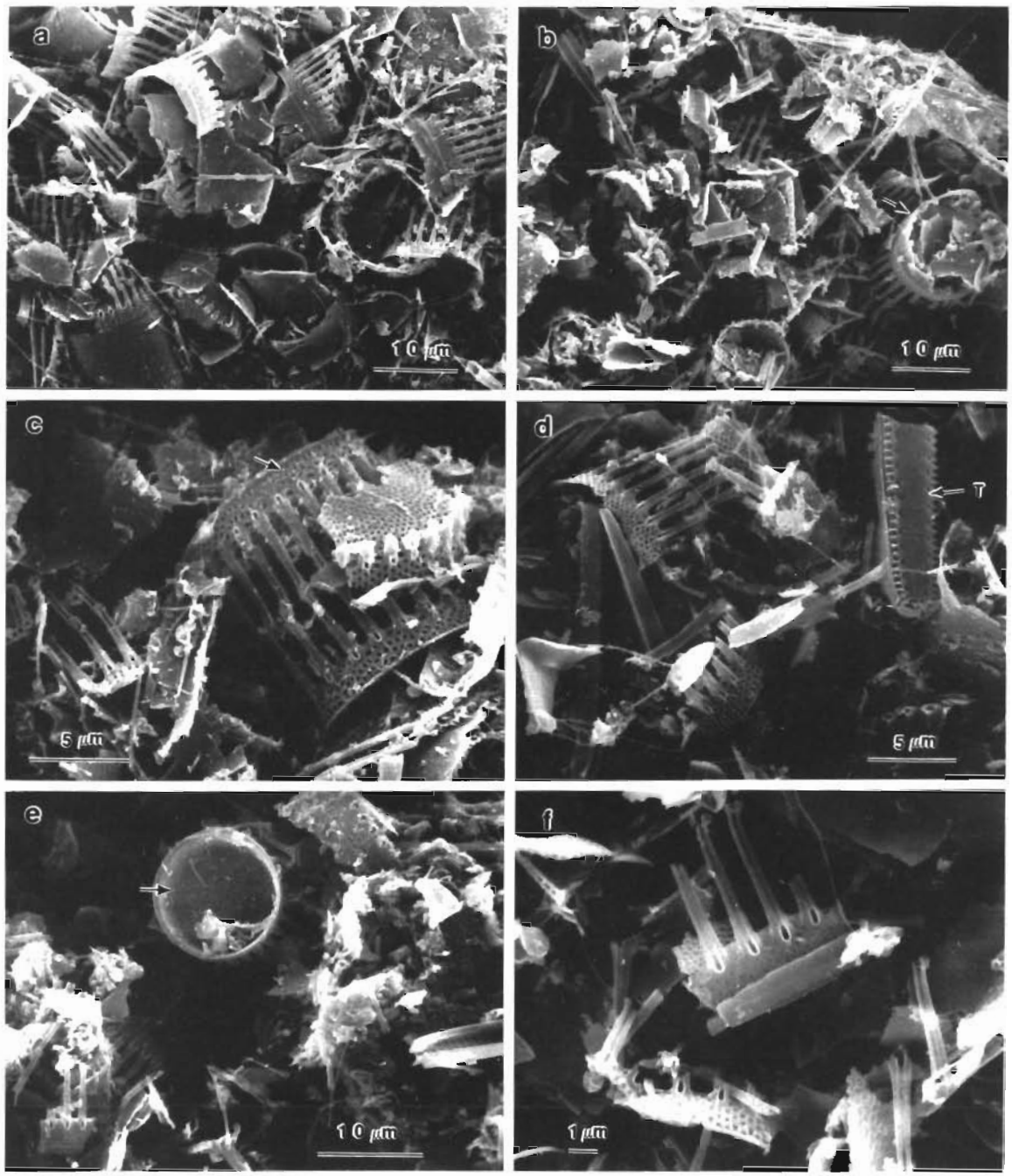

Fig. 3. Contents of *Eucalanus pileatus* fecal pellets from Station A-1 on 9 December 1981 (19.15 tow). (a) General appearance of pellets which were packed with broken *Skeletonema costatum* frustules; (b) *S. costatum* frustule crushed at valve end (arrow); (c) connected hypotheca and epitheca of attached adjacent *S. costatum* cells (arrow); (d) broken *S. costatum* and *Thalassionema nitzschoides* (T) frustules; (e) *S. costatum* cell separated at girdle (arrow); (f) small fragments of *S. costatum* thecae

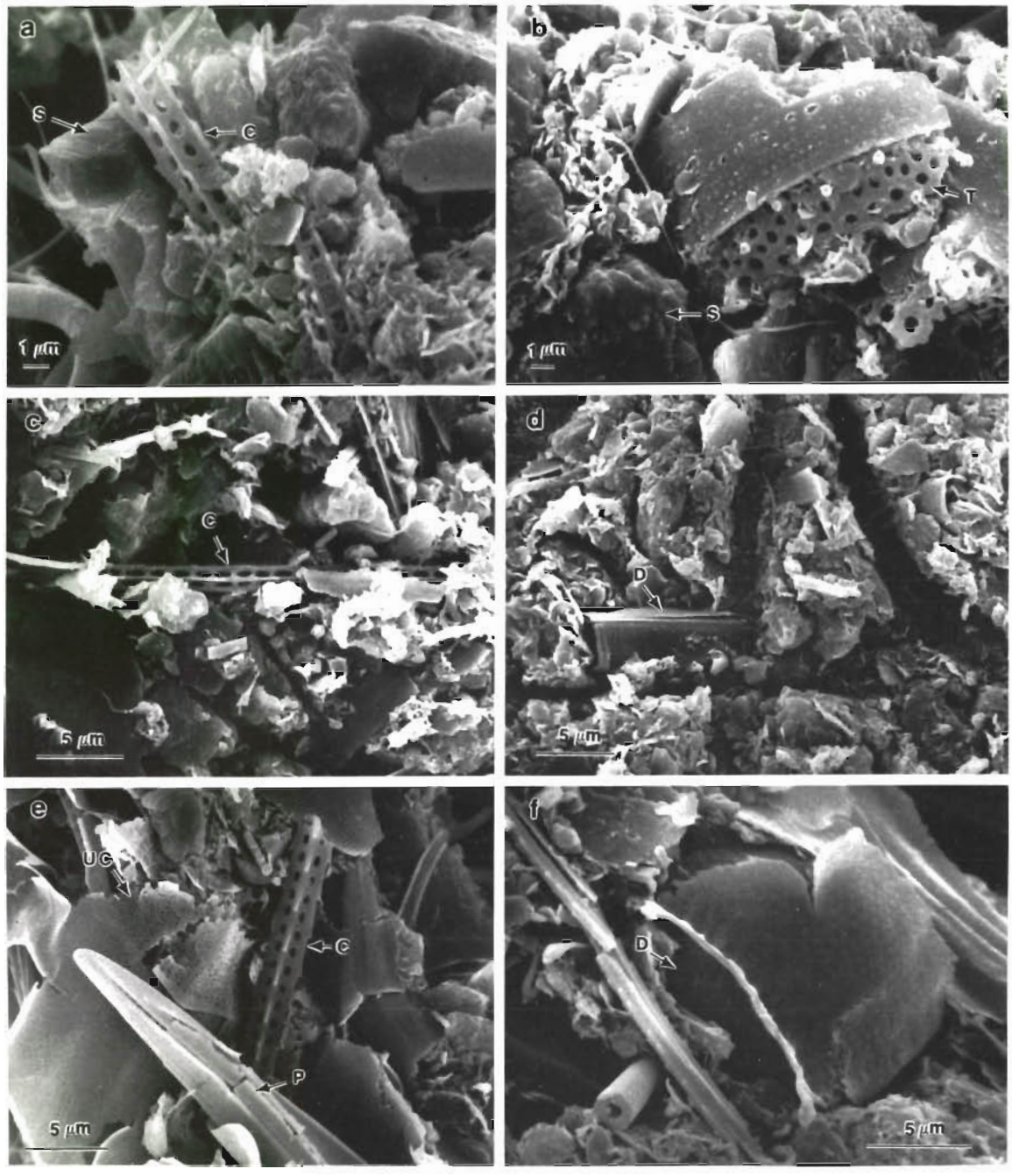

Fig. 4. Contents of *Eucalanus pileatus* fecal pellets from Station A-1 on 5 February 1982 (20.00 tow). (a) *Chaetoceros* spine (C) and sediment (S); (b) *Thalassiosira* (T) cell fragment and sediment (S); (c) *Chaetoceros* spine (C) embedded in sediment; (d) *Ditylum brightwellii* cell (D) embedded in sediment; (e) *Chaetoceros* spine (C), crushed *Pleurosigma* cell (P), and fragments of an unidentified centric (UC) diatom; (f) end portion of *D. brightwellii* (D) cell

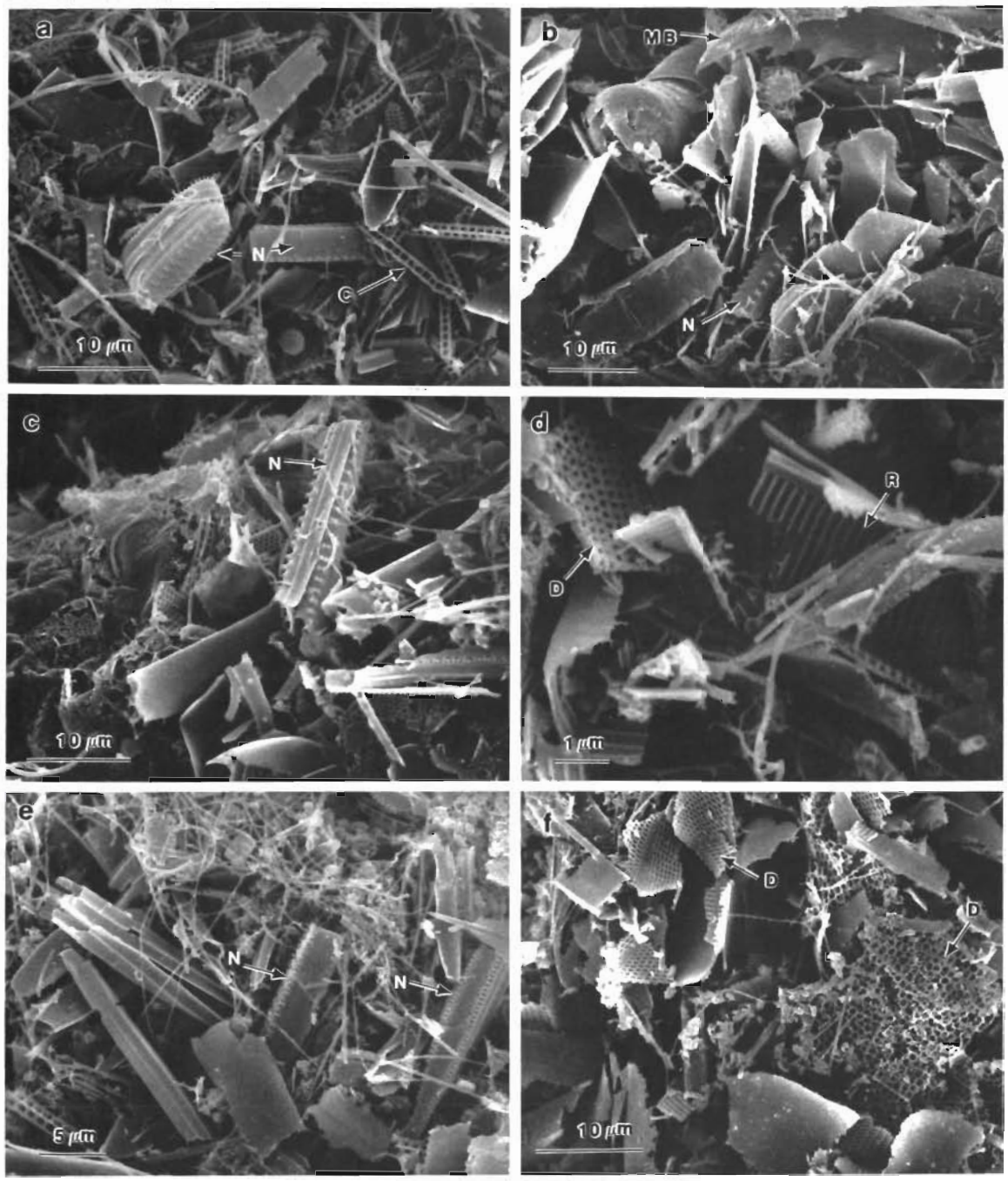

Fig. 5. Contents of *Eucalanus pileatus* fecal pellets from Station B-2 on 11 December 1981 (20.30 tow). (a) *Chaetoceros* (C) spines and *Nitzschia* (N) cells; (b) *Nitzschia* (N) fragments and a crustacean mandibular blade (MB); (c) *Nitzschia* (N) fragment; (d) *Rhizosolenia* (R) and unidentified diatom (D) fragments; (e) *Nitzschia* (N) fragments; (f) unidentified diatom (D) fragments

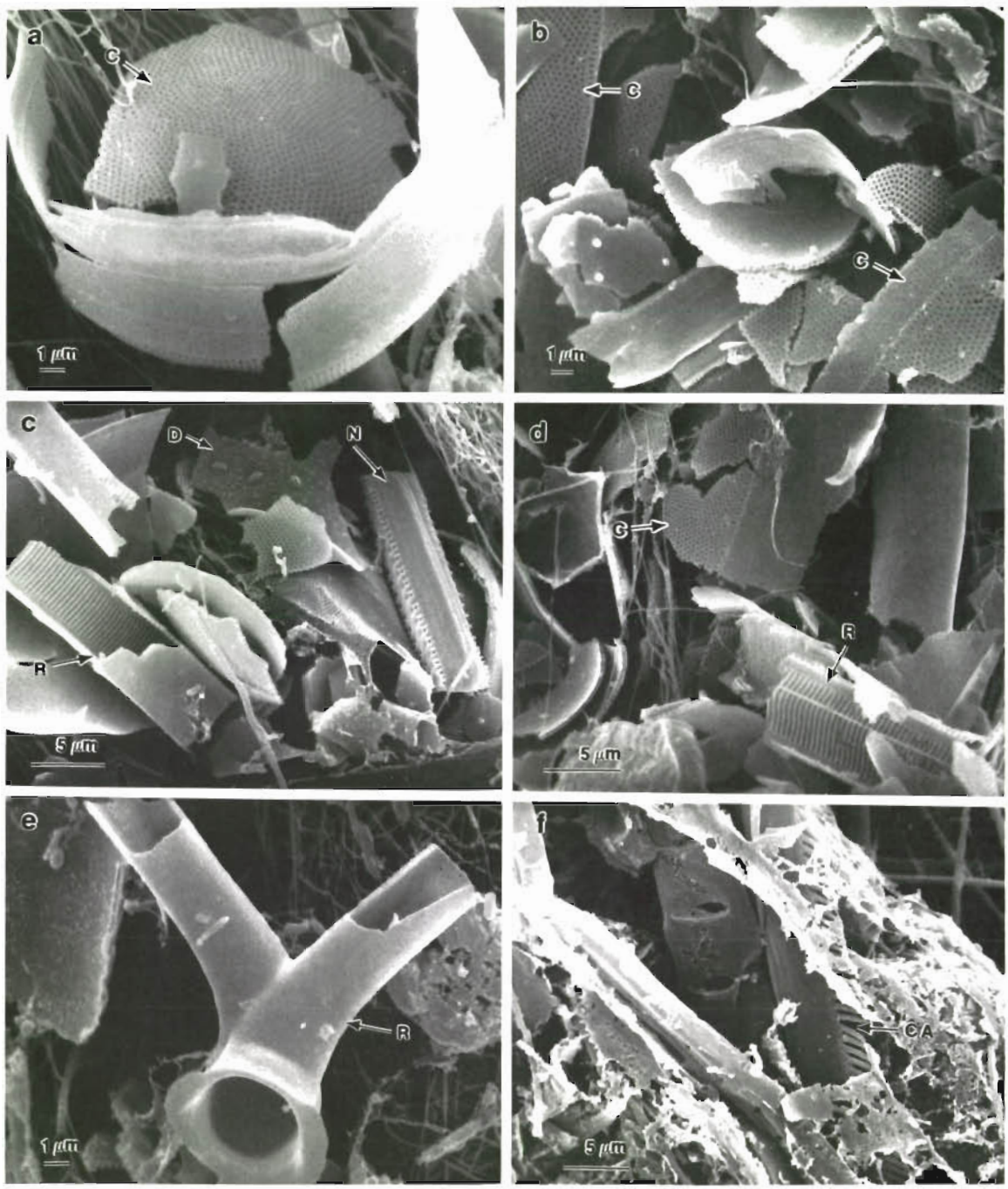

Fig. 6. Contents of *Eucalanus pileatus* fecal pellets from the same station as those shown in Fig. 5. (a) *Coscinodiscus* (C) cell; (b) *Coscinodiscus* (C) fragments; (c) *Nitzschia* (N) cell, *Rhizosolenia* (R) and unidentified diatom (D) fragments; (d) *Coscinodiscus* (C) and *Rhizosolenia* (R) fragments; (e) *Rhizosolenia* (?) fragment (R); (f) crustacean appendages (CA)

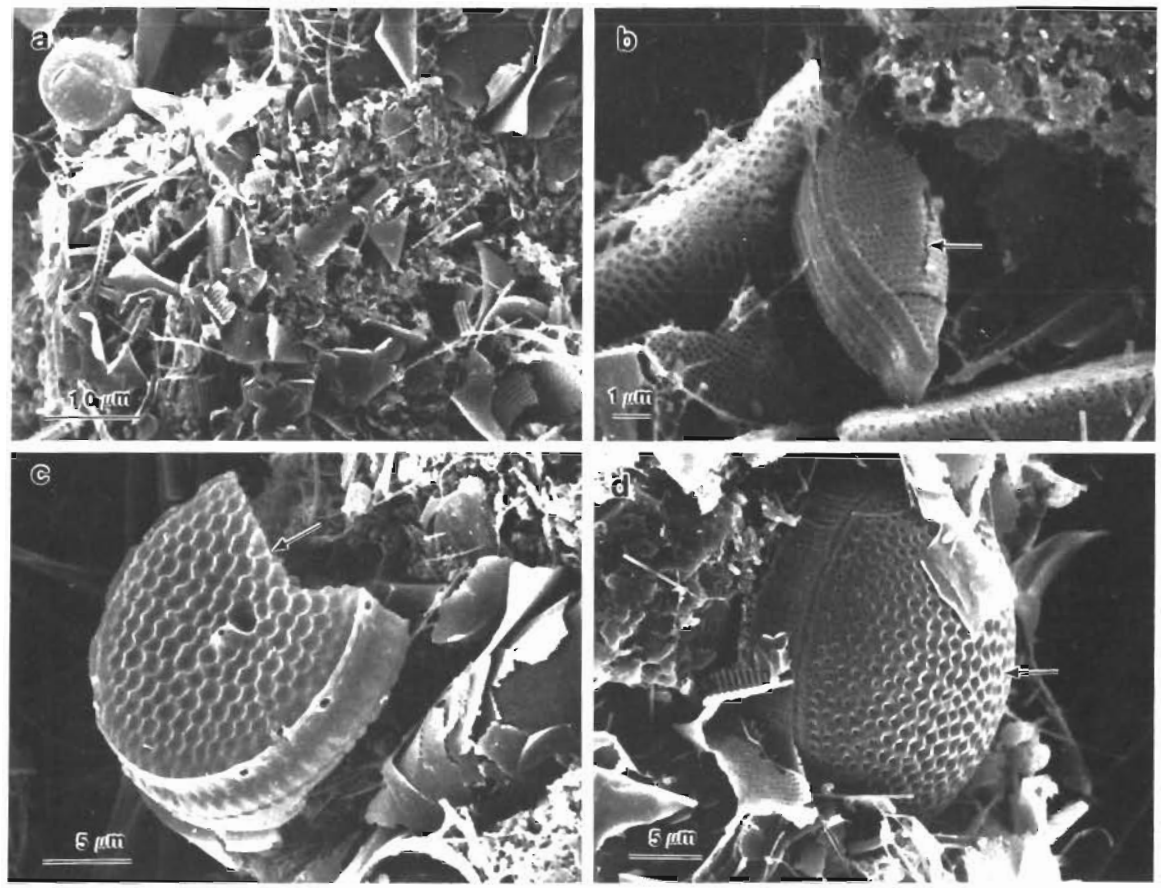

Fig. 7. Contents of *Eucalanus pileatus* fecal pellets from the same station as those shown in Fig. 5 and 6. (a) General appearance of pellets, showing mixture of fragments of numerous small and large diatoms; (b) largely intact pennate diatom frustule with crack (arrow); (c) bitten centric diatom frustule (arrow); (d) intact *Prorocentrum* sp. valve (arrow)

revealed that diatom fragments were stuffed into, and completely surrounding the oral end. Thus, the tintinnid lorica was an integral part of the pellet before fragmentation, not a contaminant introduced during filtration.

Further evidence for carnivory by *Eucalanus pileatus* came from pellets collected at Station B-1 on 14 February 1982 (Fig. 9a, b, c) and Station D-1 on 5 December 1981 (Fig. 9d, e, f). At the right end of the pellet shown in Fig. 9a are elongate remains that are clearly those of crustacean appendages (Fig. 9b). High magnification revealed that they were tubular, with sequential notches (Fig. 9c). The notches are probably sockets in setae where setules had been attached. In the pellet shown in Fig. 9d, the only recognizable remains are crustacean fragments (Fig. 9e, f).

At Station A-2 on 12 February 1982, phytoplankton were present at the lowest levels recorded (10^3 cells l^{-1}). This station was in the plume of the Mississippi River, and salinities were 9 and 22 ‰, at the surface and 1 m, respectively. The only recognizable remains in pellets were those of other crustaceans. These were all tubular notched appendages similar to those shown in Fig. 9c. Otherwise, contents of pellets were amorphous, probably reflecting ingestion of detritus and/or sediment.

There was a similar situation at Station D-1 on 7 and 8 February 1982. There were substantial amounts of amorphous detritus present in phytoplankton samples, and contents of most *Eucalanus pileatus* fecal pellets were largely amorphous. A few crustacean remains were present, as well as a smattering of diatom and dinoflagellate fragments. Nonetheless, the overall appearance of *E. pileatus* pellet contents was amorphous.

Paracalanus quasimodo fecal pellets also contained a wide variety of food remains (Table 1). Pellets from Station A-1 on 5 February 1982 contained primarily crushed frustules of *Skeletonema costatum* (Fig. 10a) and spines from *Chaetoceros breve* and *C. lorenzianum* (Fig. 10b, c). There was, however, no evidence for ingestion of the large diatom *Ditylum brightwellii* (at least 66 µm long, 13 µm diameter), which accounted for 55 % of total phytoplankton cells at this station.

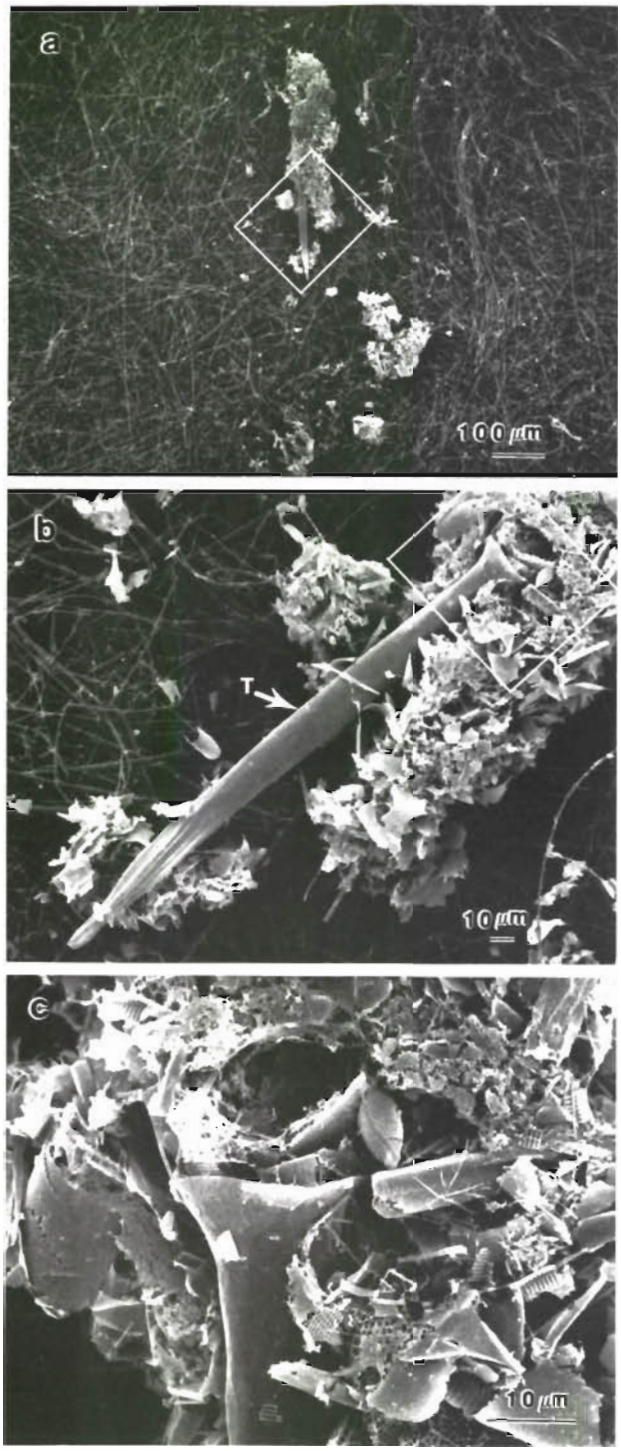

Fig. 8. Contents of *Eucalanus pileatus* fecal pellet from the same station as those shown in Fig. 5, 6, and 7. (a) Entire fragmented pellet (background is glass fiber filter); (b) high magnification of area in box in Fig. 8a, note intact tintinnid (T) lorica; (c) high magnification of area in box in Fig. 8b, note diatom fragments stuffed into, and surrounding the oral opening of the tintinnid lorica

Paracalanus quasimodo fecal pellets from Station D-1 contained a wide variety of diatom fragments (Table 1), and contents generally mirrored available phytoplankton taxa. Contents included fragments of *Skeletonema costatum* (Fig. 11c, d), *Coscinodiscus* spp. (Fig. 11a), *Rhizosolenia* spp. (Fig. 11d), *Lauderia borealis*, and numerous other unidentifiable diatoms (Fig. 11e, f). Also present were crustacean appendages (Table 1).

The contents of *Paracalanus quasimodo* fecal pellets from Station B-1 on 14 and 15 February 1982 (Fig. 12, 13, 14) were dominated by fragments of the 7 species of *Chaetoceros* present (Fig. 13d, e, f), which together constituted 34 to 35 % of available cells, *Skeletonema costatum* (Fig. 13a, c, d, e), which constituted up to 17 % of total cells, *Nitzschia* spp. (Fig. 12a, 14e, f), which constituted 6 to 12 % of available cells, and numerous unidentified diatoms. Also, numerous and varied remains of crustaceans were present (Fig. 15). These remains included a mandibular palp (Fig. 15a), an antenna (Fig. 15b) and other unidentified crustacean appendages (Fig. 15a, c, d, e). Some of these were tubular and notched (Fig. 15f), similar to those found in pellets of *Eucalanus pileatus* from the same station.

DISCUSSION

It is clear that both *Eucalanus pileatus* and *Paracalanus quasimodo* are omnivorous, ingesting not only a wide variety of various-sized solitary and chain-forming phytoplankters, but also other crustaceans, tintinnids, riverine sediment, and apparently, amorphous detritus. Further, food items ingested varied considerably from station to station, and dominant phytoplankton remains in pellets largely corresponded to dominant phytoplankters available in the water. The major exception was at Station A-1 on 5 February 1982 (10.30 tow), when remains of *Ditylum brightwellii*, the most abundant phytoplankter, were not observed in *P. quasimodo* fecal pellets. Perhaps this was because *D. brightwellii* is too large (66 µm long) for a copepod as small as a *P. quasimodo* female (0.8 to 1.0 mm total length) to effectively manipulate and ingest. Support for this suggestion comes from observations of Paffenhöfer et al. (1980) that *Paracalanus* sp. copepodites (< 0.5 mm total length) appeared unable to ingest other large elongate diatoms (*Rhizosolenia alata*). However, Checkley (1980) found that *P. parvus* females, which are of similar size to those of *P. quasimodo*, did ingest *D. brightwellii* when feeding in high-density unialgal cultures. Thus, although *P. quasimodo* probably *can* ingest *D. brightwellii*, it may not do so easily, and apparently did not at Station A-1 when presented with abundant alternative food items such as *Chaetoceros*

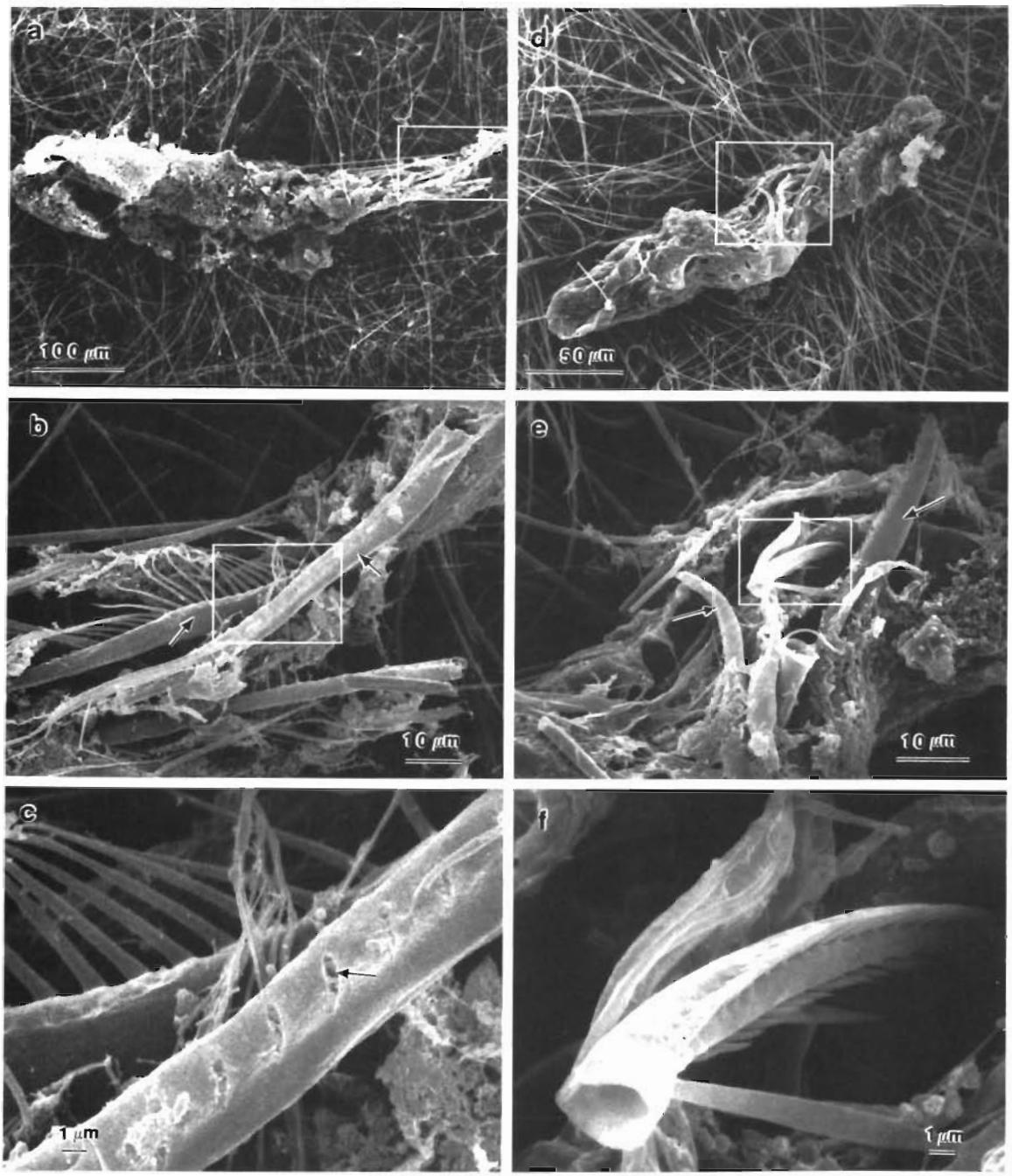

Fig. 9. (a–c). Contents of a *Eucalanus pileatus* fecal pellet from Station B-1 on 14 February 1982 (21.30 tow). (a) Entire pellet; (b) high magnification of area in box in Fig. 9a, note crustacean appendages (arrows); (c) high magnification of area in box in Fig. 9b, note notches (arrow) in tubular appendage. (d–f) Contents of a *Eucalanus pileatus* fecal pellet from Station D-1 on 5 December 1981 (11.00 tow): (d) entire pellet; (e) high magnification of area in box in Fig. 9d, note crustacean appendages (arrows); (f) high magnification of area in box in Fig. 9e, note crustacean appendage

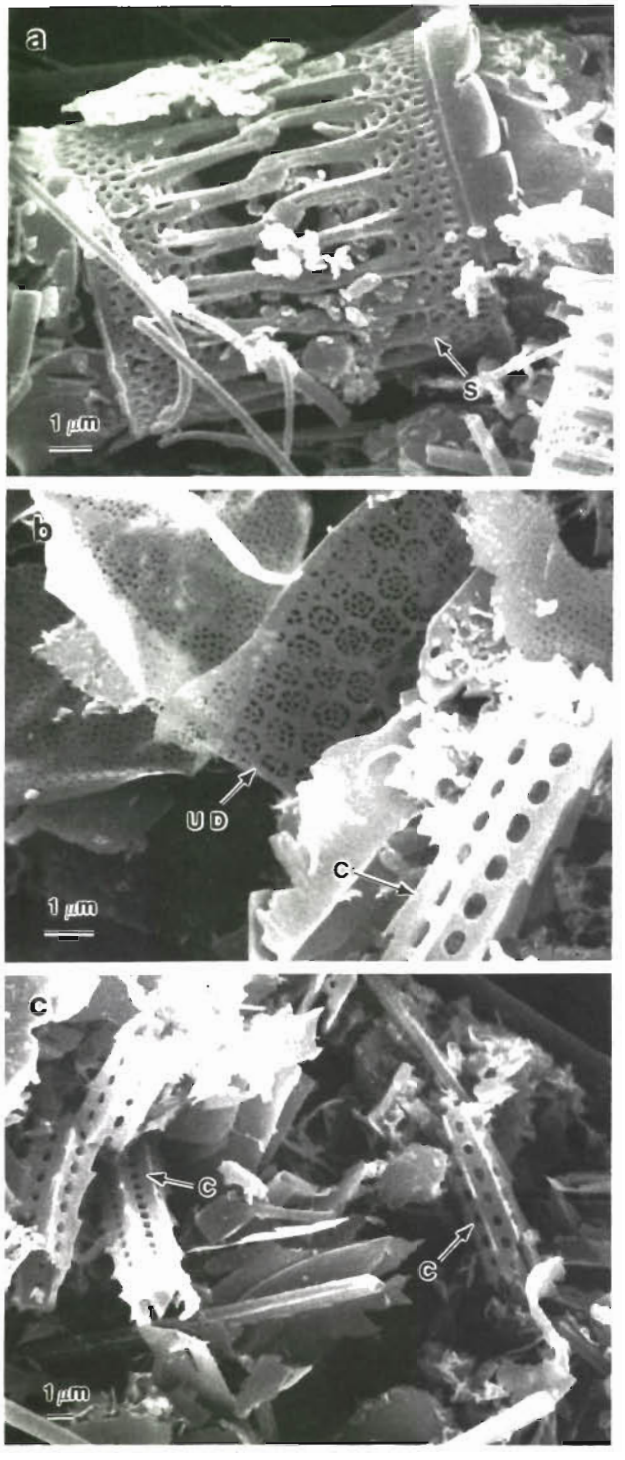

Fig. 10. Contents of *Paracalanus quasimodo* fecal pellets from Station A-1 on 5 February 1982 (10.30 tow). (a) *Skeletonema costatum* (S); (b) *Chaetoceros* spine (C) and fragments of an unidentified diatom (UD); (c) *Chaetoceros* spines (C)

spp. and *Skeletonema costatum*. In contrast, females of the larger copepod *E. pileatus* (total length approximately 2.5 mm) did ingest *D. brightwellii* on the same date at the same station but at a different time of day (20.00).

Although both copepods are capable of carnivory, the occurrence of crustacean remains in *Paracalanus quasimodo* fecal pellets was relatively uncommon, and evidence for carnivorous feeding by *Eucalanus pileatus* came only from stations where phytoplankton abundance was low (1,000 to 3,500 cells l^{-1}). At stations where phytoplankton abundance was high, such as A-1 on 9 December 1981 (36,320 cells l^{-1}), which was adjacent to, but not directly in the Mississippi River plume (surface salinity = 32 ‰), diatom frustules were the dominant component of *E. pileatus* fecal pellet contents. At stations in the plume water where phytoplankton abundance was moderately high, such as A-1 on 5 February 1982 (20,500 cells l^{-1}, surface salinity = 21 ‰), diatom frustules and sediment were dominant components of *E. pileatus* pellet contents. Even at stations where phytoplankton abundance was low, such as B-1 on 12 December 1981 (2,500 cells l^{-1}), but where the water was relatively free of detritus, diatom fragments were the dominant component of *E. pileatus* pellet contents. Conversely, at stations where phytoplankton abundance was relatively low, but amorphous detritus was abundant (D-1, 7 and 8 February 1982), *E. pileatus* pellet contents were primarily amorphous. All of this suggests that *E. pileatus* is primarily a herbivore-detritivore, resorting to carnivory only infrequently. The infrequent and sporadic occurrence of crustacean remains in the fecal pellets of *P. quasimodo* suggests the same for that species.

Diatoms ingested by both copepods included both large and small cells of both solitary and chain-forming taxa. For instance, the *Skeletonema costatum* cells (approximately 7 µm in longest dimension) ingested by *Eucalanus pileatus* at Station A-1 on 9 December 1981 (Fig. 3) were present in phytoplankton samples as chains of 2 to 20 cells $chain^{-1}$ ($\bar{x}$ = 7 cells $chain^{-1}$). Since the distances between adjacent cells were approximately the same as the dimensions of the cells, *S. costatum* chains might be perceived by copepods as single large particles of up to 280 µm in longest dimension. A similar argument might be made for *Chaetoceros* spp. chains ingested by *E. pileatus* at Station B-1 on 12 December 1981 (Fig. 5a), but not for the solitary *Nitzschia* spp. cells of approximately 10 µm in length (Fig. 5a, 6c) or solitary centric diatom or dinoflagellate cells of less than 15 µm diameter (Fig. 7c, d) ingested at the same station. In fact, throughout most pellets of both *E. pileatus* and *Paracalanus quasimodo* remains of small and large diatom cells, of both chain-forming and small and large solitary varieties, were found together (Fig. 4e, 5a, e, 6c, 7a, 8c, 10b, 11, 13). These results are similar to those obtained by Marshall (1924)

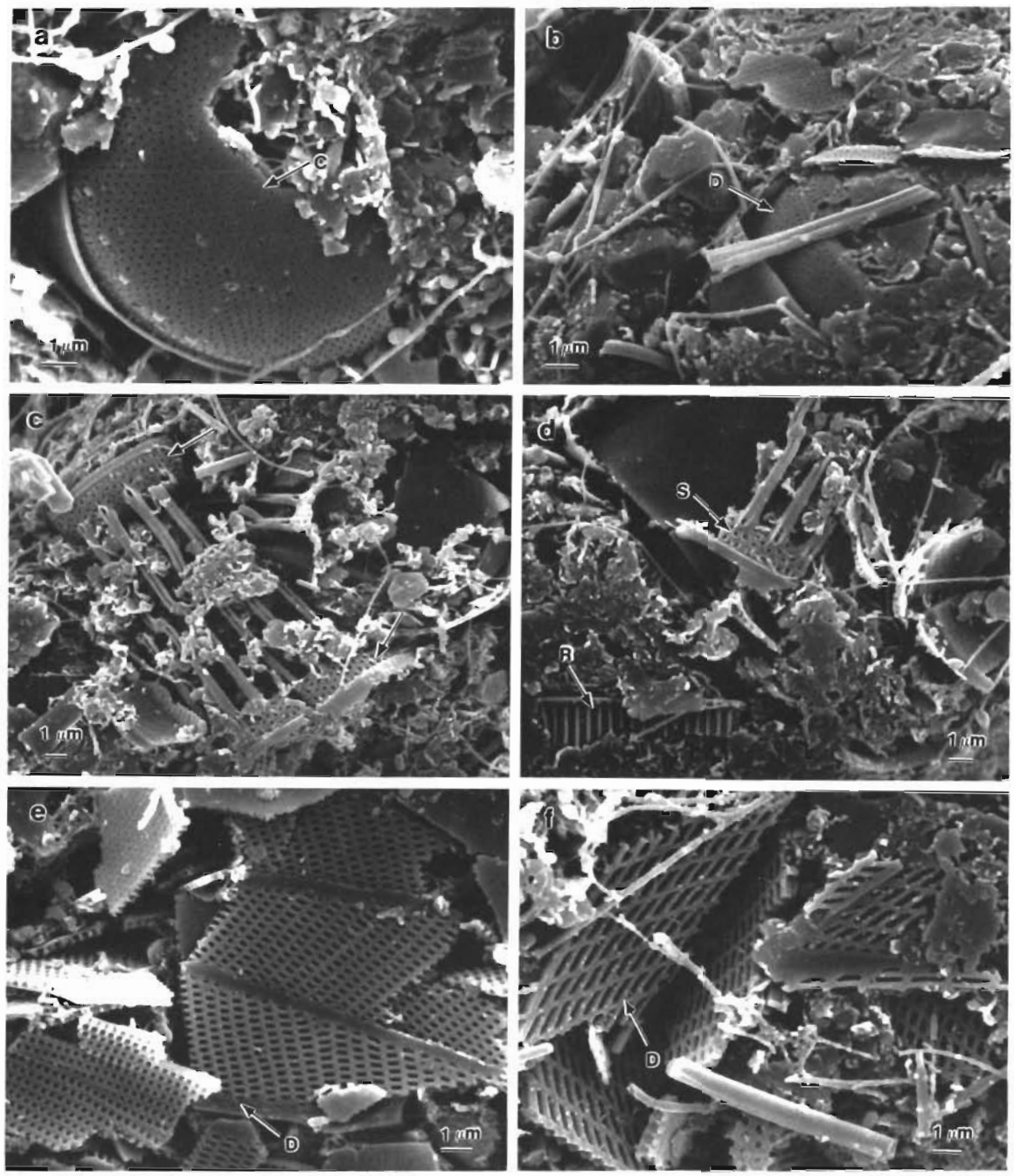

Fig. 11. Contents of *Paracalanus quasimodo* fecal pellets from Station D-1 on 7 February 1982 (10.00 tow). (a) Bitten *Coscinodiscus* (C) cell; (b) unidentified diatom (D) fragments; (c) hypotheca and epitheca of adjacent attached *Skeletonema costatum* cells (arrows); (d) fragments of *Skeletonema costatum* (S) and *Rhizosolenia* (R) cells; (e) and (f) unidentified diatom (D) fragments

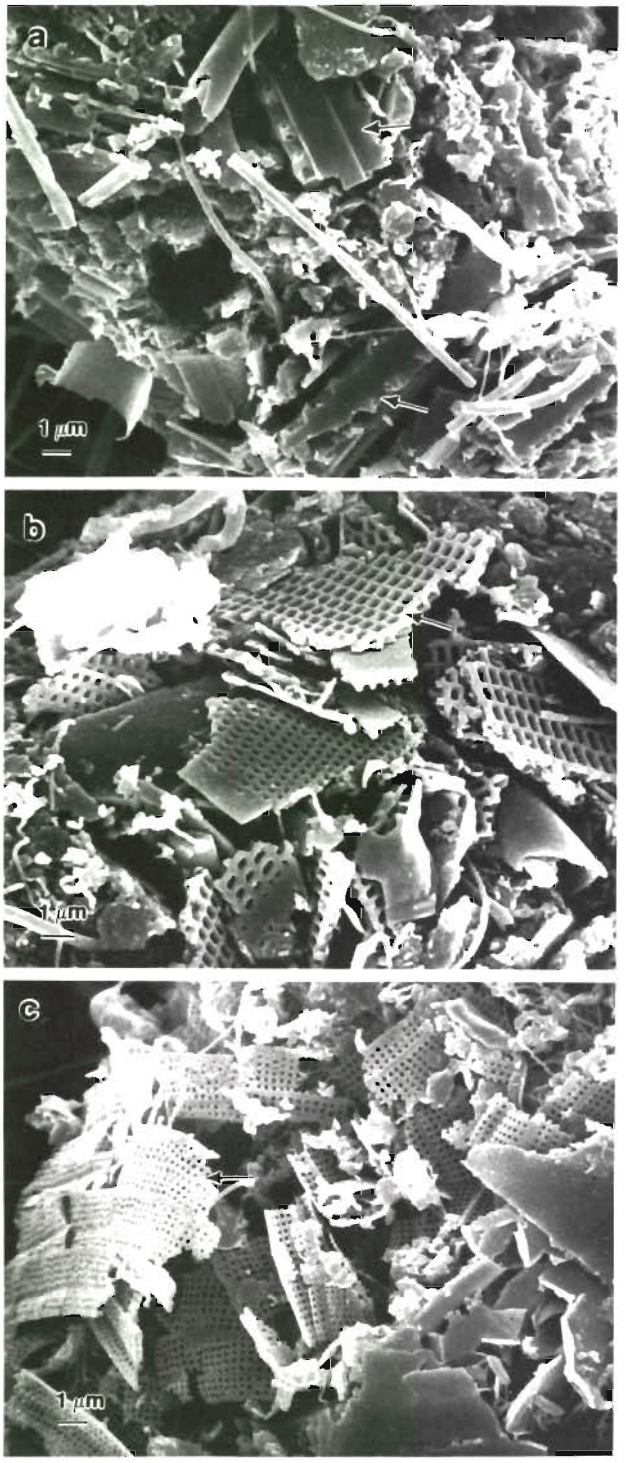

Fig. 12. Contents of *Paracalanus quasimodo* fecal pellets from Station B-1 on 14 February 1982 (21.30 tow). (a) *Nitzschia* fragments (arrows); (b) fragments of an unidentified diatom (arrow); (c) fragments of an unidentified diatom (arrow) different from that shown in Fig. 12b

in a study of gut contents of *Calanus finmarchicus*. Marshall found that the food remains in any single gut were mixed, that gut contents reflected the composition of the microplankton upon which the copepods fed, and that no marked preference for any particular type of phytoplankton was evident. Present results point more to opportunistic rather than selective feeding, in that both *E. pileatus* and *P. quasimodo* ingested numerous types and sizes of food particles, and fecal pellet contents largely mirrored those of available food. These results are also compatible with those of recent cinematographic studies (Koehl and Strickler, 1981; Paffenhöfer et al., 1982; Price et al., 1983) which reveal that *Eucalanus* and *Paracalanus* capture whole parcels of water containing food particles, rather than filtering individual particles on the basis of size. Such a feeding mechanism would explain the capture and ingestion of riverine sediment along with diatoms in the Mississippi River plume.

Since fecal pellets of both *Eucalanus pileatus* and *Paracalanus quasimodo* were obtained at four of the stations discussed here (B-1, 14 February 1982 – 21.30 tow; D-1, 5 December 1981 – 11.00 tow; D-1, 7 February 1982 – 10.00 tow; D-1, 8 February 1982 – 14.30 tow), it is instructive to further compare and contrast the feeding habits of these small (*P. quasimodo*) and larger (*E. pileatus*) copepods at the same stations. At Station B-1, *E. pileatus* pellets contained primarily crustacean remains. Although those of *P. quasimodo* also contained crustacean remains (Fig. 15), they also contained phytoplankton fragments (Fig. 12). Similarly, at Station D-1, *E. pileatus* pellets contained primarily crustacean remains and/or amorphous detritus, but *P. quasimodo* pellets contained fragments of a variety of diatoms (Fig. 11). The absence of diatom remains in *E. pileatus* pellets is puzzling, since many of the phytoplankton taxa ingested by *P. quasimodo* at D-1 were ingested by *E. pileatus* at other stations. These taxa include *Nitzschia* spp., *Skeletonema costatum, Chaetoceros* spp. and solitary centrics such as *Coscinodiscus* spp. and *Thalassiosira* spp. At stations where *E. pileatus* ingested representatives of these taxa, however, total phytoplankton abundance was usually higher than at D-1, or if not, diatoms rather than detritus were the dominant particles in the water. Possible explanations for this anomaly may be that abundance levels of phytoplankton taxa suitable for *E. pileatus* were too low at D-1 for effective grazing, that the abundance of amorphous detritus was so high at D-1, that it interfered with diatom grazing by *E. pileatus*, or that there was 'switching' (Landry, 1981) from herbivory to carnivory, with feeding on the plant or animal food that was in greatest relative abundance. Nonetheless, considering all stations sampled, the ingestion of many identical phytoplankters, of varying sizes suggests that both the small and the comparatively large copepod are rela-

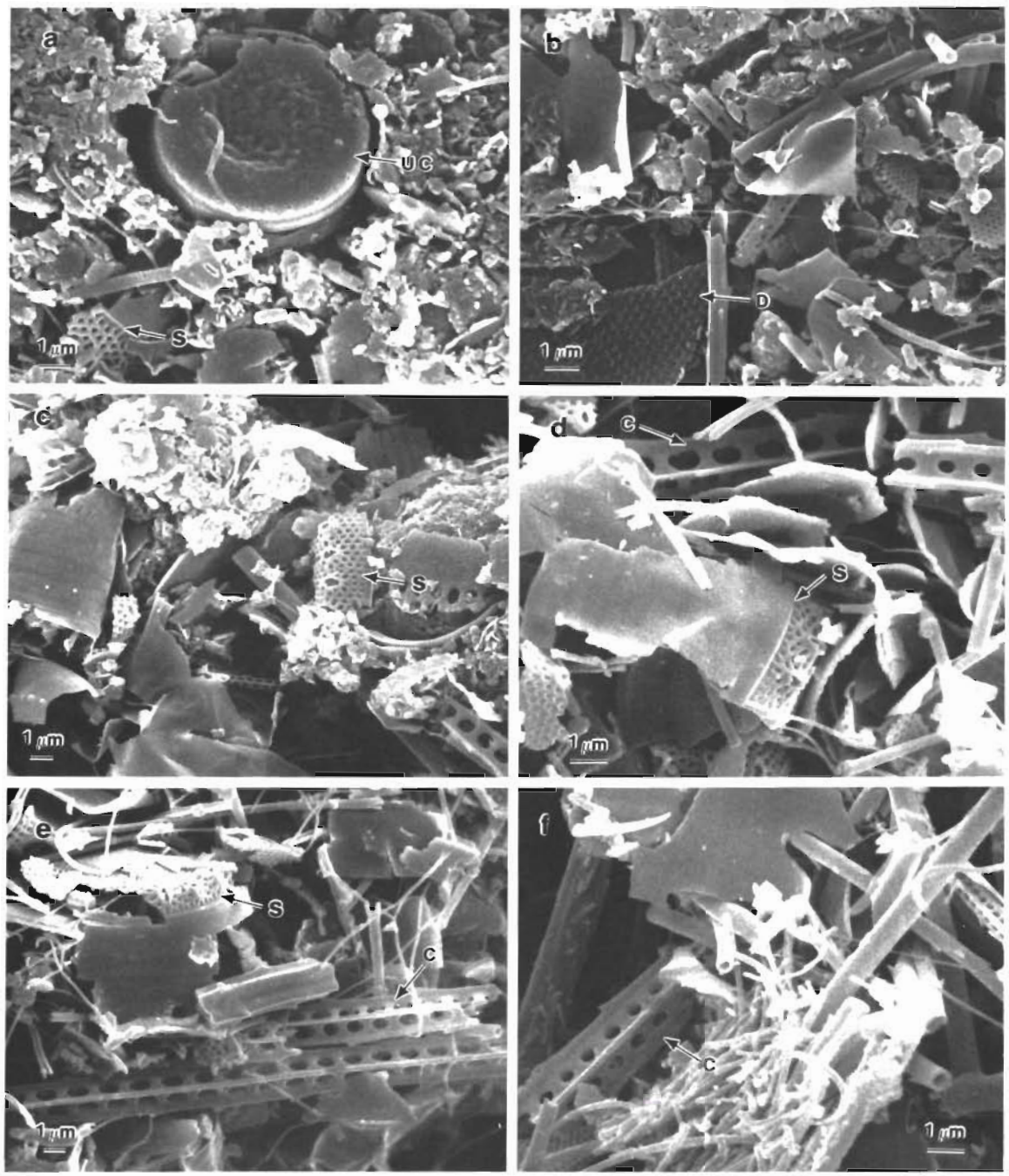

Fig. 13. Contents of *Paracalanus quasimodo* fecal pellets from Station B-1 on 15 February 1982 (08.45 tow). (a) Cracked cell of an unidentified centric (UC) diatom and fragment of *Skeletonema costatum* (S); (b) fragments of various diatoms, including that of a relatively large cell (D); (c) fragments of a variety of diatoms, including *Skeletonema costatum* (S); (d) and (e) *Chaetoceros* (C) spines and *Skeletonema costatum* (S) fragments; (f) *Chaetoceros* (C) spine

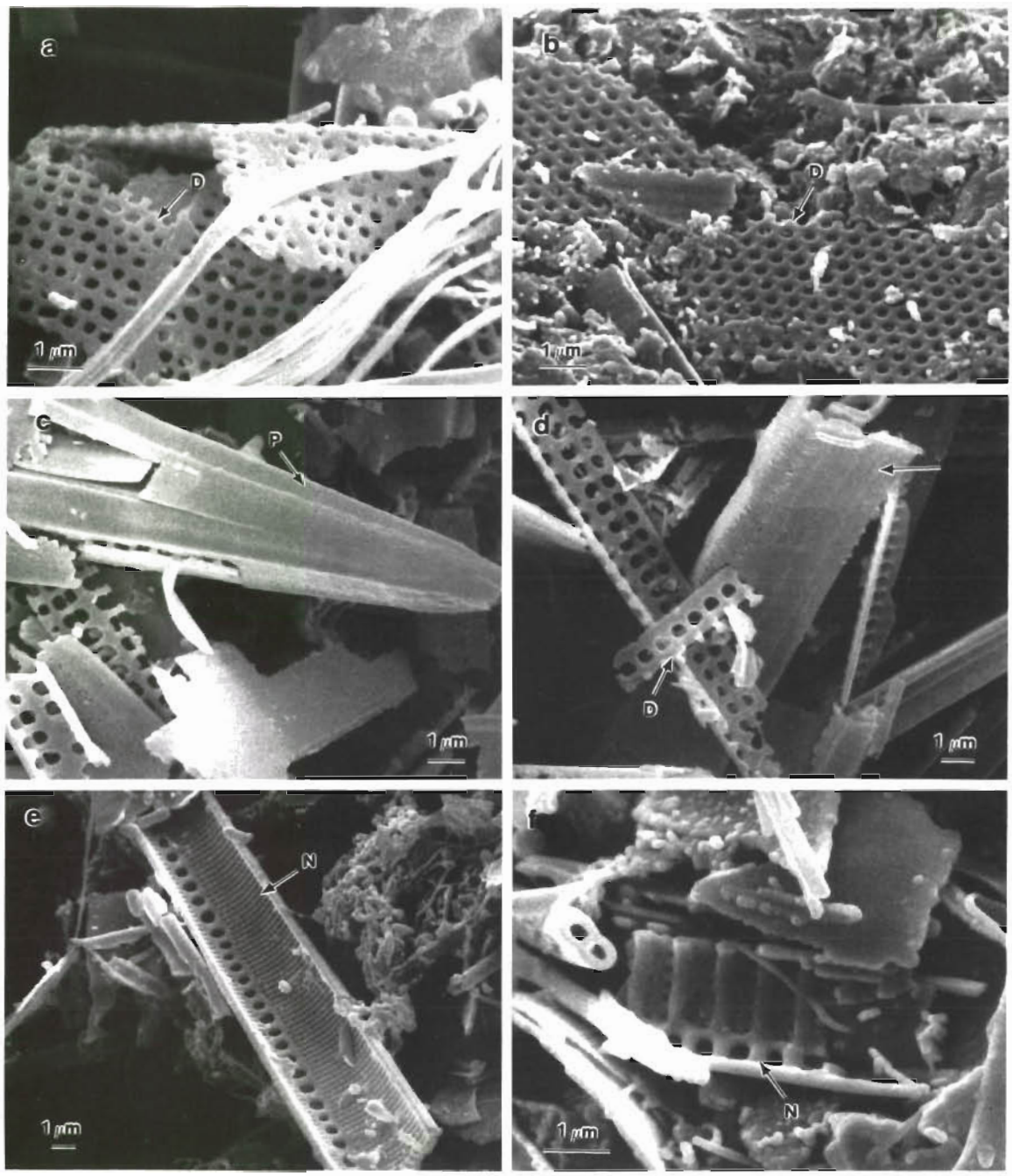

Fig. 14. Contents of *Paracalanus quasimodo* fecal pellets from the same station as those shown in Fig. 13. (a) and (b) Fragments of unidentified diatoms (D); (c) fragments of a *Pleurosigma* cell (P); (d) fragments of an unidentified diatom (D) and *Thalassiothrix frauenfeldii* (arrow); (e) and (f) *Nitzschia* (N) fragments

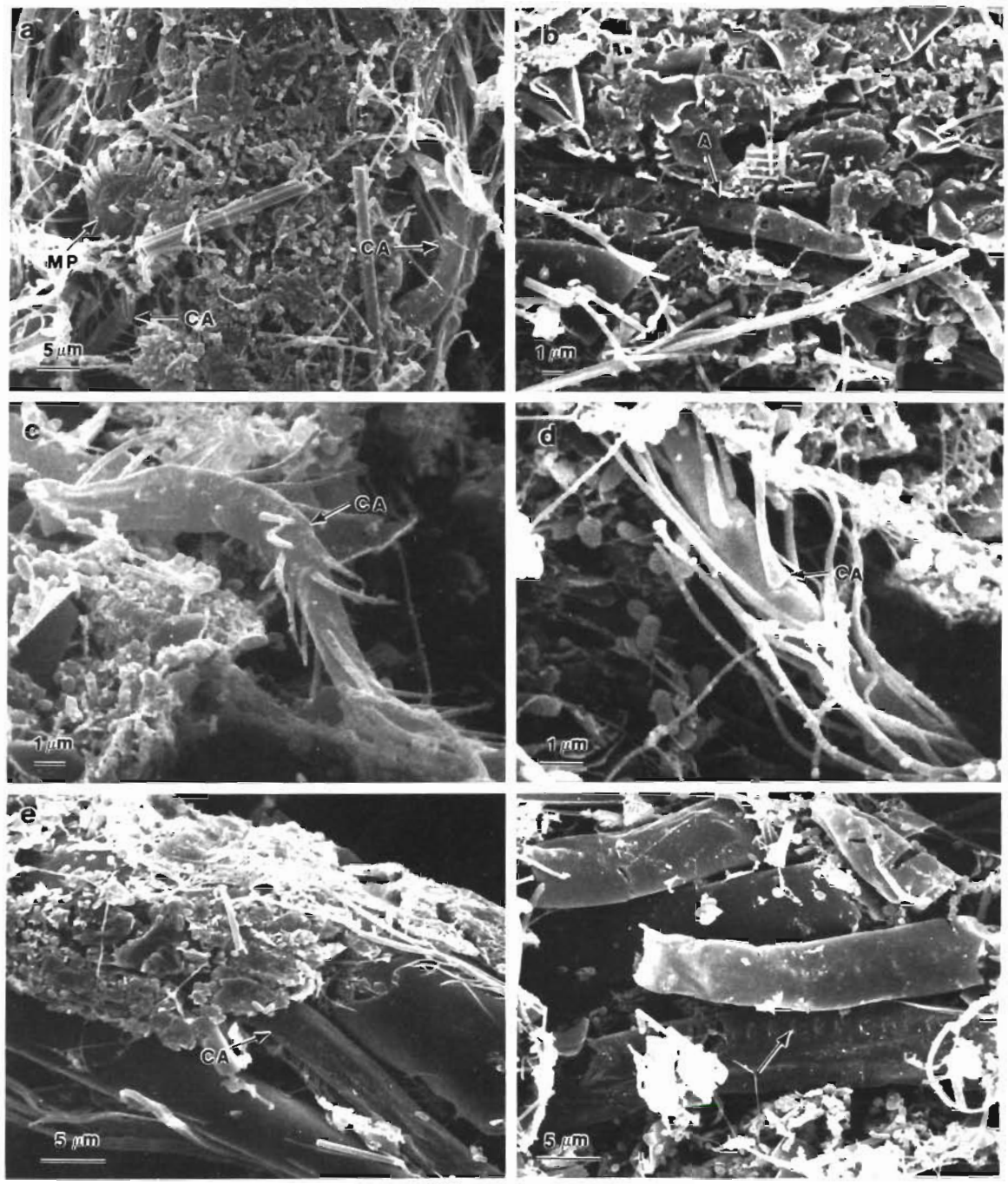

Fig. 15. Evidence of carnivory by *Parcalanus quasimodo* in fecal pellets from Station B-1 on 15 February 1982 (13.15 tow) (a–d, f) and 14 February 1982 (21.30 tow) (e). (a) Mandibular palp (MP) and crustacean appendages (CA); (b) antenna (A); (c, d, e) crustacean appendages (CA); (f) tubular notched (arrow) crustacean appendages

tively unselective as to the size of particles ingested. Further, it appears that both copepods eat many of the same food items over a broad array of particle sizes. Such a pattern was noted by Harris (1982) in a comparison of the sizes of particles ingested by other comparatively small (*Pseudocalanus* sp.) and large (*Calanus pacificus*) copepods.

In summary, results indicate that *Eucalanus pileatus* and *Paracalanus quasimodo* are omnivorous, but both are primarily opportunistic herbivores. Their utilization of a broad variety and size array of food sources likely contributes to their persistence in dynamic and fluctuating continental shelf habitats.

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