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Feeding habits of the midwater polychaete, *Poeobius meseres* (Heath, 1930) in Monterey Bay, California

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(Heath, 1930) in Monterey Bay, California**

Uttal-Cooke, Lisa, M.S.

San Jose State University, 1992

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FEEDING HABITS OF THE MIDWATER POLYCHAETE, *POEOBIUS MESERES*
(HEATH, 1930) IN MONTEREY BAY, CALIFORNIA

A Thesis
Presented to
The Faculty of Moss Landing Marine Laboratories
San Jose State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

By
Lisa Uttal-Cooke
August, 1992

APPROVED FOR MOSS LANDING MARINE LABORATORIES

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ABSTRACT

FEEDING HABITS OF THE MIDWATER POLYCHAETE, *POEOBIUS MESERES* (HEATH, 1930) IN MONTEREY BAY, CALIFORNIA

by Lisa Uttal Cooke

This study presents the first quantitative and temporal feeding study of a gelatinous midwater organism. With the Monterey Bay Aquarium Research Institute's remotely operated vehicle (ROV), VENTANA, regular collections of *Poeobius meseres* over a one year period have yielded both qualitative and quantitative results of feeding morphology and stomach contents. *In situ* observations suggest that *P. meseres* feeds in two possible ways: 1) it may produce mucus which collects particles from the water column for consumption; and 2) it may feed on detrital material in the water column with its ciliated tentacles. Results from stomach content analysis show conclusively that *P. meseres* is primarily coprophagic with a diet dominated by fecal pellets from euphausiids and copepods. Although fecal pellets were the most important food item volumetrically, *P. meseres* also consumed large numbers of diatoms and small numbers of dinoflagellates, radiolarians, foraminiferans, chrysophytes and eggs. The diet of *P. meseres* appears to reflect primary productivity in the surface waters with different food items abundant in the diet at different times of the year. Pennate diatoms were most abundant in the diet during the fall; centric diatoms were most abundant during the summer, and fecal pellets during the winter. The composition of *P. meseres* diet suggests that these and other midwater gelatinous organisms may have a significant role in the remineralization of particles as they sink from the surface to the deep.

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INTRODUCTION

Gelatinous zooplankton include a heterogeneous assemblage of soft-bodied organisms which are diverse in the world's pelagic marine ecosystems. These organisms are abundant in the epipelagic (Seki, 1973; Hirota, 1974; Hamner *et al.*, 1975; Harbison *et al.*, 1978; Deibel, 1980; Biggs *et al.*, 1981; Purcell, 1981a) and the mesopelagic zones of the ocean (Barham, 1957; Rogers *et al.*, 1978). Past studies suggest that gelatinous zooplankton are significant consumers and have a large impact on the trophic structure of marine ecosystems (Alldredge, 1984; Michaels and Silver, 1988). Quantitative analyses of diet composition have been made for several epipelagic groups such as scyphozoans (Larson, 1978), ctenophores (Hirota, 1974; Anderson, 1974), siphonophores (Biggs, 1976; Purcell, 1981a,b, 1982; Purcell and Kremer, 1984), heteropods (Seapy, 1980), appendicularians (Diebel, 1980; Alldredge, 1981; Alldredge and Madin, 1982) and salps (Madin, 1974). Comparatively little information is available regarding the types and quantities of food consumed by mesopelagic gelatinous organisms.

Study of these fragile organisms has been hampered due to difficulties associated with collecting and/or observing at depth. Whereas pelagic organisms studied at one place and time may yield important information, returning to that same habitat time after time to study populations is impossible because the water column is three-dimensional and continuously moving. Additionally, traditional sampling with midwater trawls has underestimated the actual importance of many gelatinous organisms and does not successfully sample what are known to be large populations. Gelatinous organisms collected with trawls usually come to the surface as indistinguishable pieces of jelly, and little is known about the exact depth or location from which they were collected. With the recent advent of remotely operated vehicles (ROVs) and manned submersibles, gelatinous organisms can now be sampled without many of the problems of trawling.

Collections from submersibles and ROVs *in situ* with appropriate sampling devices can yield intact organisms for which the depth, location and time of capture is known.

Among these ubiquitous groups of mesopelagic, gelatinous organisms is the unusual polychaete, *Poeobius meseres* Heath (1930). *Poeobius meseres* is distinguished from a typical polychaete in that it lacks external segments, setae and parapodia. Ranging up to 27 mm in length, the transparent body has a visible digestive tract, and the body is separated by septa into three coelomic spaces (Fig. 1). As a result of these and other unusual morphological and physiological characteristics, *P. meseres*' taxonomic position remains uncertain. It has been placed in the phyla Echiura (Grasse, 1959) and the Annelida (Pickford, 1947; Hartman, 1955; Berkeley and Berkeley, 1960; Dales, 1963), as well as somewhere between these two (Heath, 1930; Fisher, 1946). The most recent classification considers *P. meseres* to be most closely related to the Flabelligerid polychaetes because the tentacles are retractable and they have chlorocruorin as one of their blood pigments. Currently, *P. meseres* is placed in its own family, the Poeobiidae (Hartman, 1955).

Poeobius meseres has a discrete vertical distribution in the water column. Individuals are distributed throughout the continental borderlands of the North Pacific Ocean with greatest abundance occurring from 150-300 m in the western Pacific and from 300-1300 m in the eastern Pacific (Hartman, 1955; McGowan, 1960). In a brief reference, Barnes *et al.* (1976) estimated a density of 3 *P. meseres* per 100 m³ from submersible dives off southern California. In the Monterey submarine canyon in Monterey Bay, California, *P. meseres* has been observed frequently from dives with the remotely operated vehicle, VENTANA, year-round between depths of 260-950 m. Despite apparent high abundances, the ecological importance of *P. meseres* in the midwater is not yet known.

Recent studies suggest that midwater organisms are important in mediating the overall flux of particles from the surface waters to the deep (Alldredge and Silver, 1988; Michaels and Silver, 1988). Although physical processes such as turbulence and mixing contribute to the degradation of materials in the water column, it seems likely that grazers are important in the remineralization of materials (Alldredge, *et al.*, 1990). The estimated order of magnitude of reduction in the abundance of detrital material below the epipelagic zone (Martin, *et al.*, 1987) suggests that the role of consumption should be quantified. Organisms consuming detrital material may represent a significant mechanism by which material is broken down in the water column. However, no quantitative information exists regarding the importance of consumption by midwater gelatinous organisms.

This study examines feeding habits of *P. meseres* in an effort to understand its ecological role as a gelatinous consumer in Monterey Bay. The specific goals of this study were to: 1) describe the feeding apparatus to gain insight into how *P. meseres* feeds; 2) qualitatively and quantitatively determine the composition of food items in the stomachs of *P. meseres* throughout one year including three seasons; 3) examine the diet of *P. meseres* with regard to food availability; and 4) to evaluate the ecological implications of feeding by *P. meseres* in midwater.

MATERIALS AND METHODS

Study Site and Collection of Samples

This study was conducted in the deep waters of the submarine canyon of Monterey Bay, California. This study was part of scientific cruises by Dr. Bruce Robison at the Monterey Bay Aquarium Research Institute (M.B.A.R.I.) and therefore, all dives were conducted at his study sites. The study area was situated approximately 7 miles northwest of Pt. Pinos (36° 42'N, 122° 02'W)(Figure 2), and lies over the canyon in 1640 m of water. One of two midwater stations within one mile of each other were visited over a one year period for a total of 27 ROV dives made from the R/V PT. LOBOS.

In situ observations and collections of *P. meseres* were conducted with the Monterey Bay Aquarium Research Institute's Hysub ROV, VENTANA, made by International Submarine Engineering. From October, 1990 to November, 1991, 70 *P. meseres* were collected into one of five 2-liter cannisters with a variable speed suction sampler mounted on the ROV. All collections were between depths of 260-480 m, which is the uppermost vertical distribution of *P. meseres*. Simultaneous real-time observations of *P. meseres* with a high resolution Sony DXC 3000 video camera mounted on the ROV, were conducted during all collections. Upon retrieval of the ROV, specimens were fixed in 5% formalin for gut content analysis and 2% glutaraldehyde for scanning electron microscopy.

To study the availability of potential food in the water column, samples of seawater and *P. meseres* were collected with the ROV at the same time and place. Seawater samples were collected in a 200 ml GO FLO water bottle mounted within the tool sled of the ROV. The tripping mechanism of the bottle was activated hydraulically after the collection of a *P. meseres* into the suction sampler. It was only possible to collect one water sample per dive due to the configuration of equipment on the ROV and

the type of tripping mechanism employed. Upon retrieval, all water samples were shaken in case of settling and preserved in 5% formalin .

Head Morphology

Observations of head morphology were made on preserved specimens with a scanning electron microscope (SEM) to gain insight into the way *P. meseres* feeds. The heads with palps and cirri were carefully excised with a scalpel at the beginning of the digestive tract, dehydrated in a graded ethanol series (70%-100%), soaked in 100% ethanol, postfixed in osmium tetroxide, critical-point-dried in carbon dioxide, coated with gold and photomicrographed with an ISI #WB-6 SEM. Entire visible surfaces of the cephalic region, including palps and cirri, were photographed.

Diet Composition

In filtered seawater, digestive tracts of preserved specimens of *P. meseres* were removed by teasing away the outer hypodermis and the inner epithelium. Stomach contents were placed into a settling chamber base, dispersed and stained with 0.2 ml nuclear fluorochrome diamidinophenylindole (DAPI)(Gowing and Coale, 1989). All food items in the entire stomach were examined at 320X magnification, identified to the lowest taxon possible, tallied, and their length, width and/or thickness were measured with an ocular micrometer on a Zeiss Axiovert 10 epifluorescence inverted phase contrast microscope. Since only two dimensions (length and width or length and thickness) of some of the diatoms and dinoflagellates were visible under the microscope, assumptions about the third dimension were made based on values from Kovala *et al.* (1965): 1) Centric diatoms, thickness of valve = $0.5 \times$ length (diameter); 2) Pennate diatoms: width of valve = thickness of valve; and 3) Dinoflagellates: $0.5 \times$ width = thickness. If only fragments of food items were present, the dimensions were still

measured so that estimates of those kinds of food present could be made. All food items were assigned a shape (sphere, ellipsoid, cylinder or pennate) and converted to volumes using the appropriate geometric formulae (Table 1).

Light microscope observations of diatoms with one valve intact were often difficult to differentiate from those with both valves intact; therefore, most cells were considered whole in the volume calculations. Although both length and diameter of the pellets were recorded, fecal pellet types were based on pellet diameters because the diameter is related to the size of the producer and because cylindrical pellets easily break into pieces. Minipellets were differentiated from fecal pellets by their elliptical shape and small size ($<50\ \mu\text{m}$) (Gowing and Silver, 1985). Only food items larger than $5\ \mu\text{m}$ were counted; therefore, bacteria were not considered in this study.

Individual food types were grouped into 12 major food categories for analysis (Table 2, in bold). The percent number and percent volume of each food group were averaged for all samples to determine overall percentages. Frequency of occurrence of each food group was calculated by taking the percentage of stomachs in which an item occurred. Diet was represented by the Pinkas *et al.* (1971) Index of Relative Importance (IRI), in which each food group's importance is a combination of the numerical importance (%N), volumetric importance (%V), and frequency of occurrence (%FO) according to the equation; $\text{IRI} = (\%V + \%N)(\%FO)$, which was represented as rectangles in three-way graphs with %N, % V on the y-axis and %FO on the x-axis. The IRI value is actually the area of the rectangle and is a measure of the relative importance of each food item compared to the others. The IRI can range from zero (food item not found in diet) to 20,000 (when all three variables are 100% or a monodiet) (Cailliet and Ebeling, 1990). Volume was the most meaningful measure of a food group's contribution to the diet. Percent number and percent frequency of occurrence overestimated the importance of small prey, especially pennate and centric diatoms.

Scanning electron microscopy of stomach contents was conducted to further characterize the food items ingested by *P. meseres*. Stomach contents of specimens fixed in 5% formalin were placed in filtered seawater and drawn onto 0.2 μ Nuclepore membrane filters, washed with distilled water and air dried. Filters were mounted onto stubs with double sided tape, were sputter coated with gold palladium and photomicrographed for identification.

Adequacy of sample size for food items was tested by plotting the cumulative number of all food items in Table 2 against the number of stomachs analyzed. The counts for individual stomachs were randomly accumulated one at a time, until the cumulative number of food items and species increased to the total food items observed in the stomachs (Hurturbia,1972). This was done 10 times and the mean trophic diversity, with its standard error, was calculated.

Nutrition

Phytoplankton and microzooplankton with intact protoplasmic and nuclear material stained bright blue with DAPI and were categorized as "nutritious," along with fecal pellets, minipellets and eggs. Empty frustules of phytoplankton, tests and shells of microzooplankton, crustacean exoskeletons and moults were categorized as "non-nutritious." Volumes for both nutritious and non-nutritious food items were calculated (as described for diet composition) and compared. Carbon content for nutritional food categories in foreguts and hindguts were estimated using appropriate volume to carbon relationships from the literature (Table 1).

Seasonal Variation of Diet

To investigate diet changes over the year, stomach contents of *P. meseres* were analyzed and processed in a manner similar to that described for total composition and

were compared among three oceanographic seasons. Identification of seasons was based on temperature data from bottle casts in Monterey Bay in 1991 (Rosenfeld, MBARI, unpubl. data) and compared with a 6-year study by Bolin and Abbott (1963) in Monterey Bay. Seasons were defined as: 1) The Davidson period (November-February), characterized by strong southerly winds and uniform temperatures; 2) the Upwelling period (March-August), characterized by northwesterly winds driving surface water offshore, with deep, cold, nutrient-rich water upwelling to replace it; and 3) the Oceanic period (September-October), characterized by calm weather and high thermal stratification. A total of 19 *P. meseres* stomachs was analyzed during the Davidson period; 33 stomachs were analyzed during the Upwelling period and 10 stomachs were analyzed during the Oceanic period.

Adequacy of sampling was calculated similar to total composition (see above) for the total number of stomachs sampled during three oceanographic seasons; however, because of the small sample size during the Oceanic and Davidson periods, food types were grouped into the 12 major food categories (Table 2, in bold).

The IRI for each season was determined and the Kendall-tau rank correlation test (Sokal and Rohlf, 1969) was used to test for similarity between % N and % V of food groups between three seasons. Rank correlation was used because of the very large sample size required for parametric tests and to avoid the assumptions of normality.

The differences in abundance of the three dominant food groups in the stomachs of *P. meseres* were estimated on a bimonthly basis because there was no significant difference among the food types between seasons. The mean number of individual food items was calculated for food items such as fecal material (including minipellets), pennate diatoms (*Nitzschia* spp., unidentified pennates) and centric diatoms (*Skeletonema* spp., *Chaetoceros* spp., *Rhizosolenia* spp., *Thallasiosira* spp., and unidentified centrics) and compared in area graphs.

Food Availability

Fifty milliliters of preserved seawater were subsampled from water collected at the same time as *P. meseres*, allowed to settle for a minimum of 24 hours and stained with DAPI for microscope identification and counts of available food particles. Six samples were collected: on July 17 and 22, September 30, October 4, 24 and November 22, 1991. As with stomach content analysis, all identifiable organisms and detrital material were counted in a settling chamber at 320X magnification. The concentrations of both “nutritious” and “non-nutritious” available food in the 50 ml subsamples were extrapolated to one liter. Comparisons among all six samples were made with Percent Similarity Indices (PSI)(Sanders, 1960).

RESULTS

Feeding Behavior and Morphology

Remotely operated vehicle observations indicate that *P. meseres* collected its food in two possible ways. *Poeobius meseres* was observed hanging neutrally buoyant in the water column, attached to what appeared to be mucus spread out above the body. The mucus was always connected to the head region of the worm as "strings" or a "net" and was densely aggregated with small particles. The composition of the particles attached to the mucus was difficult to determine because water turbulence from the ROV destroyed it when the vehicle came too close. Although it is not known if *P. meseres* produces mucus in the water column, 480 video observations of *P. meseres* showed 70 worms associated with mucus, 10 worms associated with detrital material and 400 not associated with any kind of mucus or detrital material. *Poeobius meseres* was also observed frequently with its tentacles attached to large aggregates of detrital material or marine snow.

In the cephalic region of *P. meseres*, there is a pair of thick, longitudinally grooved palpi, 5-6 pairs of cirri in a transverse row, and a lip complex surrounding the mouth. Each palp has two types of ciliary structures, short cilia running along the groove and tufted cilia located along the lateral edges of the palp (Figure 3 a,c). Each cirrus has dense bands of cilia along the tip with diagonal bands of cilia encircling the entire length (Figure 3 b,d). The surface area without ciliation was convoluted. SEM observations did not reveal any pores. Pores would be expected to constitute glandular areas from which mucus is secreted.

Diet Composition

The mean cumulative number of food items plotted against the pooled number of stomachs indicated the number of *P. meseres* sampled was adequate to sufficiently describe the total composition of the diet. The curve leveled off at approximately 25 of

the 62 stomachs sampled (Figure 4). Standard error approached zero in all ten randomizations of the 62 stomachs.

Examination of 62 stomachs revealed that *P. meseres* fed on fecal pellets, phytoplankton and microzooplankton (Table 2). The diet was dominated by fecal pellets, pennate diatoms, centric diatoms and crustacean exoskeletons using all three measures of importance. The IRI values, represented by the areas of the rectangles in Figure 4, for fecal pellets (8694), pennate (3960) and centric diatoms (3306) were significantly larger than for any of the other food items (Table 3). Numerically, *P. meseres* ingested mostly pennate diatoms, fecal pellets and centric diatoms, while volumetrically the bulk of the diet was comprised of fecal pellets, crustacean exoskeletons and centric diatoms (Table 3). Fecal pellets, and centric and pennate diatoms occurred in more than 90% of the stomachs sampled while minipellets, tintinnids and crustacean exoskeletons occurred in 72%, 79%, and 64% of the stomachs, respectively. Dinoflagellates occurred in 45% of the stomachs, with radiolarians, foraminiferans, moults, eggs, and chrysophytes occurring in less than 25% of the stomachs sampled.

Fecal material from zooplankton made the most important contribution to the diet of *P. meseres*. Fecal pellets from euphausiids, copepods and larvaceans occasionally contributed an average 58% of the total diet numerically and an average of 30% of the diet volumetrically. The majority of fecal pellets observed were cylindrical in shape and were characteristic of euphausiids and copepods (Martens, 1978). Euphausiid fecal pellets were large (up to 200 μm in diameter), with frayed ends. Frequently, antennae and appendages from crustaceans protruded out of the broken ends of pellets. Copepod fecal pellets were small (up to 50 μm diameter) with pinched off ends and were much less prevalent than large euphausiid fecal pellets (Figure 6b). Minipellets were also present in the diet, but did not contribute substantially in number (7%) or volume (2%) (Figure 6 c,d).

Fecal pellets in the hindgut of *P. meseres* appeared watery and remained intact when stomach contents were egested from animals observed in a petri dish.

Observations using scanning electron microscopy revealed that fecal pellets and minipellets contained numerous diatom fragments as well as complete frustules (Figure 6). Rare occurrences of radiolarian and foraminiferan fragments and shells were also observed in fecal pellets.

Intact diatom frustules and chains not associated with fecal pellets made the second most important contribution to the diet of *P. meseres*. Centric diatoms with cell diameters between 9-800 μm were conspicuous contributors to the diet, represented primarily by *Skeletonema* spp., *Coscinodiscus* spp., *Rhizosolenia* spp., *Thalassiosira* spp. and *Chaetoceros* spp. (Figure 7). They contributed an average 25% of the total diet numerically and an average 16% of the diet volumetrically. Centric diatom resting spores were also occasionally observed in the samples (Figure 7c). Pennate diatoms with valve lengths of 15-260 μm were predominantly a single species of *Nitzschia*, or possibly *Pseudonitzschia australis*, and various species of *Navicula*, *Pleurosigma*, *Surirella* and *Grammatophora* (Figure 8). Pennate diatoms were very important numerically, contributing 32% to the total diet. However, they were rather insignificant volumetrically (2.5%)(Figure 5).

Tests of dinoflagellates and radiolarians, skeletons of chrysophytes, lorica of tintinnids and appendages and antennae exoskeletons from crustaceans contributed less than 10% of the total number and volume to the remaining part of the diet of *P. meseres* (Figure 9). Whole crustacean moults and eggs from crustacean zooplankton were rare, present in only 5 of the 62 stomachs sampled and contributing less than 1% of the total diet.

Additional very small size cells (<5 μm) were observed in the stomach contents with the light microscope. These may have been the grey bodies or "olive-green bodies"

described by Silver and Alldredge (1981). As they occurred much less frequently and were difficult to identify, they were not included in the counts of food types. Small amounts of unidentifiable detrital material also occurred, but were not considered in the diet analysis.

Carbon estimates

The degradation of the internal protoplast of DAPI-stained phytoplankton and microzooplankton was observed with the light microscope. In general, empty silicious valves remained whole and were easily distinguished from intact frustules, tests and shells of phytoplankton and microzooplankton with protoplasm. Nutritious food groups in the diet of *P. meseres* were primarily fecal pellets, minipellets and diatoms, contributing an average percent volume of 75%, 17%, and 7%, respectively (Figure 10a). Dinoflagellates, radiolarians and eggs contributed less than 1% of the total volume of nutritious food items in the diet. In contrast, non-nutritious pennate diatoms and centric diatoms accounted for an average 58% and 41% of the volume while crustacean exoskeletons, tintinnids, dinoflagellates, chrysophytes, radiolarians and foraminiferans contributed less than 10% of the total volume in the diet.

Fecal pellets contributed an average of 97% of the carbon to the diet of *P. meseres* (Figure 10c). Comparatively, minipellets and pennate diatoms contributed minute quantities (2% and 1%, respectively) to the overall nutrition of the diet.

Seasonal Variability

Adequacy of sampling was calculated for three oceanographic seasons for 12 major food groups. During the Davidson period ($n = 19$), the mean cumulative number of food categories leveled off at 9 stomachs (Figure 11a) and during the Upwelling period

(n = 33)(Figure 11b), the mean cumulative number of food categories leveled off at 11, indicating adequate sampling . During the Oceanic period (n = 10)(Figure 11c), the mean cumulative number of food types did not level off, due to the small sample size and four rare food groups (chrysophytes, moults, eggs and radiolarians) present in only a few stomachs. Because they were rare and the sample size was small, they did not occur often enough to allow the curve to level off.

Poeobius meseres ate the same general kinds of food over three seasons, with its diet dominated by fecal pellets, pennate diatoms, centric diatoms and crustacean exoskeletons. Ranks of food items for %N and %V were significantly correlated between all three seasons (Kendall-tau, $p < .01$); however, different types of foods dominated the diet during different seasons (Figure 12). Fecal pellets in the stomachs of *P. meseres* ranked first in dietary importance during the Davidson (IRI=9960) and the Upwelling periods (IRI=8987), but ranked second in dietary importance during the Oceanic period (IRI=5359)(Table 4). Pennate diatoms were consistently important in the diet throughout all three seasons ranking first in the diet during the Oceanic period (IRI=8276), and ranking second and fourth during the Davidson (IRI=4114) and the Upwelling periods (IRI=1612). Centric diatoms ranked second in the diet during the Upwelling period (IRI=5359), contributing substantially less to the diet during the two other seasons, ranking third during both the Davidson period (IRI=1575) and the Oceanic period (IRI=3638).

Crustacean exoskeletons were most important in the diet during the Upwelling period (IRI=2024), but were significantly less important during the other two seasons. Minipellets, tintinnids, dinoflagellates, radiolarians, moults, eggs and chrysophytes were not important and did not contribute much to the diet of *P. meseres*. The combined IRI values were less than 1000 in all three seasons.

Although the composition of food groups was not significantly different between the three seasons, the abundance of major food species and types varied from month to month (Figure 13). Throughout the year, *P. meseres* ingested high numbers of pennate diatoms. The major species which dominated the stomachs was *Pseudonitzschia australis*, contributing 88% numerically during September and October. Several other genera, including *Navicula*, *Pleurosigma*, *Pseudoenotia*, *Amphora*, *Sururiella*, *Grammatophora* and unidentified pennates were present in less than 9% of the stomachs.

A gradual decline of *P. australis* spp. from January to March was marked by an increased number of fecal pellets in the stomachs of *P. meseres* (Figure 13b). In March and April, fecal pellets made up 59% of total stomach contents, up from 21% in January and February. Entire stomachs were packed from mouth to anus with euphausiid fecal pellets (Figure 14 a,b). In May and June, fecal pellet abundance dropped to 37% of the total stomach contents, dropping even lower to 4% in September and October until November when there was an increase to 19%. Minipellets contributed a small percentage of the fecal pellet contribution to the diet throughout the year with a peak abundance of 13% during January and February.

Centric diatoms were a conspicuous component of *P. meseres*' diet throughout the year (Figure 13c). Peak abundances of *Rhizosolenia* spp. (22%), *Chaetoceros* spp. (11%) and unidentified centrics (16%) occurred in July and August, and abundances dropped off to less than 3% during September and August. *Skeletonema* spp. (14%) was most abundant during March and April. *Thalassiosira* spp. was consistently present in the diet in low numbers (<3% throughout the year).

Food Availability

With the exception of ciliates, radiolarians, chrysophytes and moults that occurred rarely, the stomach contents of individual *P. meseres* and the water column samples

contained the same types of organisms and detrital material. These included fecal pellets, minipellets, crustacean exoskeletons, tintinnids, centric and pennate diatoms and dinoflagellates.

Examination by light microscopy of the water column samples revealed high numbers of chain diatoms. In comparison, examinations of the stomach contents contained low numbers of chain diatoms. As noted in diet composition analyses, fecal pellets in the stomachs were often broken into pieces with frayed ends. In contrast, fecal pellets were generally intact in the water samples.

Comparison of the stomach contents to water column samples with Percent Similarity Indices (PSI) indicated that samples #1 and #2 collected in the summer were similar in composition among each other while samples #3, #4 and #6 collected in the fall were similar in composition among each other (Table 5). Stomach #5 and water sample #5 were not similar to each other or any of the other samples collected.

DISCUSSION

Feeding Behavior and Morphology

ROV observations suggest *P. meseres* is a suspension feeder, passively collecting detrital material in the water column. *Poeobius meseres* appears to feed with a fine, delicate structure of mucus that originates from the anterior end of its body. The small particles of marine snow collected on the surface of the "net" made it appear more dense than the surrounding waters. In the benthic and pelagic environments, mucous webs are an optimal foraging strategy for maximizing food collection (Hamner *et al.* 1975; Jorgensen, 1981). Many benthic polychaetes and the pelagic larval polychaete, *Poecilochaetus* sp. are known to feed with mucous nets. *Poecilochaetus* sp. secretes a three-dimensional network of fine strands to collect particles for ingestion. Secretion of a mucous web for food collection is also known in many pelagic organisms such as pteropods (Gilmer, 1972), appendicularians (Aldredge, 1977, Deibel, 1986) and salps (Madin, 1974). These studies suggest that feeding with an external mucous web is a fundamental adaptation enabling gelatinous organisms to exploit an abundant organic resource.

Although the production of the mucous by *P. meseres* was not observed, Robbins (1965) suggested that *P. meseres* traps particles with mucus secreted from glandular cells on the palps. It is possible that *P. meseres* could produce a net from these same cells. Deposit feeding polychaetes are known to secrete mucus from their tentacles to collect detrital material (Barnes, 1980). *Chaetopterus* sp. and *Nereis* sp. possess head structures analogous to tentacles which extend out over the substrate, adhering to particles with mucous secretions (Jorgensen, 1966).

In addition to the hypothesis that *P. meseres* collects food with mucus, it may also collect food from the water column by grasping sinking detrital material with its tentacles. *Poeobius meseres* was often associated with detrital material that appeared to

be large aggregates of marine snow. Marine snow is a likely source of food because particles are known to be three times more concentrated on it than in the surrounding waters, providing a concentrated food source (Alldredge and Silver, 1988). Small larvacean houses and the carcasses of dead animals sinking through the water column while aggregating material, may also provide a source of food to *P. meseres*.

The scanning electron micrographs of the tentacles of *P. meseres* suggest that the cilia have an important role in handling food. The five pairs of heavily ciliated cirri probably transport particles of food to the palps as well as carrying food directly to the mouth. Particles of food on the palps may be transported to the mouth via the ciliary groove. Benthic deposit feeding polychaetes with grooved palps are known to handle small food particles differently from large particles (Dales, 1955). Small food particles are transported along the groove primarily by ciliary action. Large particles are transported along the groove by both ciliary action and muscular squeezing. Dales (1955) proposed that the groove of a tentacle can be partly opened or closed to form a tube, facilitating the transport of large food items. Food items too large for transporting along the groove are attached to the densely ciliated cirri and moved directly to the mouth.

The role of the cilia arranged in tufts on the palps of *P. meseres* is unknown; they may have a chemosensory or mechanosensory function (Figure 3 a,c). The tufts do not appear large enough to actually pick up and handle food. Morphologically similar structures have been described on the tentacles of the polychaete, *Eupolymnia nebulosa* (Gremare, 1988) and *Owenia* sp. (J. Nuremburg, Smithsonian, pers. comm.) and are thought to sense particle densities.

In contrast to most pelagic polychaetes which are active carnivores, seeking fast swimming zooplankton prey (Dales and Peter, 1972), *P. meseres* is a passive detritivore. This mode of feeding is typical of benthic terebellids and spionids (Barnes, 1980). These

findings support the hypothesis that *P. meseres* evolved from a benthic polychaete Robbins (1965). *Poeobius meseres* is thought to be most related to benthic flabelligerid polychaetes which have chlorocruorin blood and retractable tentacles (Hartman, 1955).

Diet Composition

The diet composition data are consistent with the hypothesis that *P. meseres* ingests aggregates of marine snow. Fecal pellets, diatom frustules, crustacean exoskeletons, bacteria and microzooplankton were the dominant kinds of organisms and detrital material found on epipelagic and bathypelagic aggregates of marine snow (Silver *et al.*, 1978; Silver and Alldredge, 1981). These studies suggested that marine snow makes food items such as fecal pellets and diatoms more readily available for consumption by large zooplankton.

The most important food items volumetrically in the stomachs of *P. meseres* were fecal pellets that originated from euphausiids, copepods and other metazoans. *Poeobius meseres* consumed primarily large cylindrical fecal pellets ranging up to 200 μm in diameter. Small fecal pellets from zooplankton copepods (<30 μm in diameter) were less abundant than large fecal pellets. *Poeobius meseres* may have ingested large fecal pellets more frequently because they were more available in deep waters. Very small fecal pellets are thought to be most abundant in surface waters, becoming degraded or consumed before they can sink to deep depths (Paffenhofer and Knowles, 1979; Turner and Ferrante, 1979). In contrast, large, robust fecal pellets are thought to sink quickly before becoming deteriorated and therefore make it to deeper depths (Fowler and Small, 1972; Honjo and Roman, 1978; Paffenhofer and Knowles, 1979; Small *et al.*, 1979).

Scanning electron microscope and light microscope observations indicate there are two types of fecal pellets ingested by *P. meseres*: one originating from herbivorous zooplankton and another originating from omnivorous zooplankton. Fecal pellets

ingested by *P. meseres* contained well digested, triterated fragments of phytoplankton (Figure 4 a,b,c) as well as whole, intact cells of phytoplankton. The presence of diatom fragments and frustules is characteristic of fecal pellets from herbivores, including copepods (Turner, 1986; Turner, 1991) and euphausiids (Ikeda, 1984). Large fecal pellets ingested by *P. meseres* also contained crustacean antennae and appendages. The presence of crustacean pieces is characteristic of fecal pellets from omnivores, including euphausiids which are able to feed on a wide variety of food, including copepods, crustacean larvae and other euphausiids (Ikeda, 1984). Martens (1978) described similar signs of carnivory in the Atlantic ocean euphausiid, *Meganyctiphanes norvegica*.

Many crustacean species are thought to be coprophagic and to have an important role as consumers in the water column (Frankenberg and Smith, 1967; Paffenhofer and Strickland, 1970; Paffenhofer and Knowles, 1979; Bishop *et al.*, 1986; Lampitt *et al.* 1990). However, the importance of coprophagy in the diet of gelatinous deep-sea organisms has not been quantified. Fecal pellets have been found in the stomachs of lobate ctenophores (G. Matsumoto, MBARI, pers. comm.) and of the giant larvacean, *Bathochordaeus charon* (Robison, MBARI, unpubl. data). Fecal pellets are a predominant component of flux in the upper layers of the water column dropping off significantly below 500 m (Pilskaln and Honjo, 1987). The results of the present study indicate that coprophagy by *P. meseres* may be important to understanding pelagic food web interactions.

In addition to fecal pellets, the abundance of individual, autotrophic, ultrastructurally intact phytoplankton was an important food source in the diet of *P. meseres*. *Nitzschia* spp., a chain-forming pennate diatom, was the dominant form. When centric diatoms were present in significant amounts in the diet, the main contributors were the genera *Rhizosolenia*, *Thallasiosira*, *Chaetoceros*, and *Skeletonema*. There are two potential sources of these phytoplankton. First, diatoms in the surface waters may

aggregate with other detrital material and sink through the water column as marine snow, and then are ingested by *P. meseres*. Silver and Alldredge (1981) have shown that ultrastructurally intact phytoplankton is present on marine snow in the bathypelagic. Second, phytoplankton ingested by herbivores and egested as fecal pellets may be transported to the deep sea where *P. meseres* feeds on them. SEM observations suggest that diatoms and microzooplankton ingested by *P. meseres* originated from marine snow rather than fecal pellets because they were ultrastructurally intact and not well-digested.

Carbon Estimates

Poeobius meseres satisfied its nutritional requirements largely by feeding on fecal pellets. Fecal pellets provided a large and useful energy source, contributing 98% of the carbon by weight to the diet. In contrast, many of the other food items ingested were non-nutritious and consisted of siliceous frustules, tests, shells and chitinous material. These contributed very little carbon to the diet due to their small volume and low seasonal abundance. Siliceous food items present in the diet of *P. meseres* showed little external degradation due to their resilient nature.

Consumption of detrital material by *P. meseres* may result in the recycling or remineralization of materials sinking from the surface to the deep. It is generally believed that the flux of particles from the surface is a source of food for deep sea organisms (Vinogradov, 1962; Harding, 1974); however, the fate of detrital material in the ocean is poorly understood. Below the euphotic zone, the flux of materials is reduced with increasing depth (Martin *et al.*, 1987) with the greatest losses of organic carbon occurring in the upper mesopelagic zone (Suess, 1980). These losses have been attributed to biological degradation through consumption, decomposition by microorganisms or physical processes such as turbulence and mixing (Alldredge and Silver, 1988). Alldredge *et al.* (1990) postulated that biological disaggregation due to

grazing is more important than physical processes to the reduction of material in the water column, and that consumption by gelatinous organisms has been ignored as an important factor in overall carbon flux quantification.

Although data for carbon content calculations (Table 1) of food items were based on fresh fecal pellets, many of the fecal pellets ingested by *P. meseres* contained material which was probably reingested and digested several times. Digestive state was very difficult to measure quantitatively. Fecal pellets remained intact in both the foregut and hindgut; however, those in the hindgut appeared laden with water. Therefore, actual volume to carbon relationships used in this study are probably an overestimate of the carbon amount ingested.

Poeobius meseres may not break down all of its food completely, but might derive some of its nutrition by digesting bacteria on the outer peritrophic membrane of fecal pellets. Copepods have been observed ingesting the peritrophic membrane and attached bacterial flora of their own fecal pellets (Lampitt *et al.* 1990). Pilska and Honjo (1987) have found several structurally intact fecal pellets lacking a pellicle in sediment traps at 500 m and suggested that this may be a result of grazing by zooplankton.

Seasonal Variation in Diet

The general patterns of nutrient coupling between the shallow layers and the deeper benthic habitats has been outlined (Theil, *et al.*, 1989; Sancetta and Calvert, 1988), but a complete understanding of the link between the surface waters and midwater has not been accomplished. It is not known if deep sea gelatinous organisms experience dietary seasonal pulses. This study shows that the diet of *P. meseres* may be dependent on seasonal fluctuations in primary productivity in the surface waters and on activity by zooplankton that create fecal pellets. This indicates that *P. meseres* may be opportunistic

and consume whatever is available in the water column. The pattern of large numbers of pennate diatoms in the fall followed by large numbers of euphausiid fecal pellets in the stomachs of *P. meseres* during March and April corresponds well with camera observations of bathyl sediments by Lampitt (1985) and Billett *et al.* (1983). Their research suggested that transport of algal flocs early in the growth season alternated with zooplankton fecal pellet transport later in the year.

Similarly, research has shown that the abundance of euphausiids and copepods and the production of fecal pellets is strongly dependent on the seasonal cycle of primary productivity (Small *et al.*, 1983; Knauer and Martin, 1981; Honjo, 1980). During high phytoplankton production periods, food is consumed by crustaceans at fast rates for storage to allow survival during overwintering, and for reproduction. High numbers of phytoplankton in the surface water coupled with intense feeding by zooplankton result in large exports of fecal pellets to the midwater.

In general, the stomach contents of *P. meseres* appear to record the seasonal succession of dominant phytoplankton in the surface waters. Peak abundances of the autotrophic pennate diatom, *Pseudonitzschia australis* in the stomachs of *P. meseres* during September and October coincided with unusually high numbers of *P. australis* in the surface waters of Monterey Bay (Buck *et al.*, in prep.). The abundance of the diatom ranged from a high of 2.4 to 27×10^4 cells/ liter during October to a low of 0 at certain times of the year. During the fall 1991, the toxin, domoic acid in *P. australis* was responsible for over a hundred brown pelican and cormorant deaths in Monterey Bay (Garrison *et al.*, in press). Bolin and Abbott (1963) showed similar peaks of *Nitzschia* spp. during the Oceanic period (September and October) over a six-year period.

High numbers of autotrophic centric diatoms, *Chaetoceros* spp. and *Skeletonema* spp. in the stomachs of *P. meseres* during the Upwelling period corresponded with high peaks during June and July in Monterey Bay from 1954-1960 (Bolin and Abbott, 1963).

By contrast, diatom peaks in March and April during the present study were not observed in the stomachs of *P. meseres*. The lack of diatoms in the stomachs at this time may be due to heavy grazing by zooplankton in the surface waters.

High numbers of euphausiid fecal pellets in the diet of *P. meseres* during the Upwelling period may be due not only to heavy grazing but also to physical processes in the water column. Euphausiid fecal pellets can sink through the water column at rates up to 1000 m day⁻¹, but Alldredge *et al.* (1987) observed high numbers of fecal pellets remaining in the water column during autumn and winter. It was hypothesized that they do not sink immediately, but accumulate in the mixed layer due to turbulent mixing. The Upwelling period is characterized by mixing of different temperature gradients in the water column. Winter mixing may act as a mechanism to sustain fecal pellets and other detrital material in the water column. In comparison, the temperature regime of the Oceanic period is characterized by little mixing and high thermal stratification. During this time, fecal pellets may sink rapidly through the water column, perhaps being less available for consumption.

Food Availability

The types of food items in the stomachs of *P. meseres* generally reflected what was found in the synoptic water samples. When pennate diatoms were the dominant item in the water samples, high numbers were also found in the stomach contents. Examination by light microscopy indicated that diatom cells in the water column samples tended to be in chains more frequently than those found in the stomachs. Similarly, fecal pellets tended to be intact more frequently than those in the stomachs. This suggests that *P. meseres* breaks up food items during ingestion.

Mobile ciliates found in the water samples were never observed in the stomach samples of *P. meseres*. Since many ciliates do not have hard tests, they probably would

not show up in the stomach contents. Motile organisms such as dinoflagellates and ciliates may be attracted to substrates of detrital material after encountering them through random swimming movements (Silver *et al.*, 1978). Ciliates may escape from the substrate of food items ingested by *P. meseres*. With the exception of dinoflagellates, most of the food items in the stomachs of *P. meseres* were non-motile.

Percent similarity index comparisons of stomach contents to water samples support the hypothesis that *P. meseres* is opportunistic and consumes the organisms and detrital material that is available in the water column. High similarities to water samples collected during July and low similarity values of these same stomach samples to water samples collected during September, October and November indicate that *P. meseres* eats a wide variety of food depending on its availability.

There were several potential problems that may have biased the results in comparing the stomach contents to the water column samples. One water sample per dive may have been inadequate to characterize the water column sufficiently; large fast sinking fecal pellets and other material could not have been adequately sampled by the water bottle. This was evident in the lack of fecal pellets in some water samples.

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Table 1. Relationships used to calculate the volume and carbon content of food groups in the stomachs of *Poebius meseres*.

Prey items	Shape	Volume (μm^3)	Carbon Conversions	Peterson, (pers. comm.)
Chrysophytes Radiolarians Foraminiferans Eggs	Sphere 1	$\text{Volume} = \pi/6.0 \cdot (d \cdot d \cdot d)$	Eggs = .140 picograms C/ μm^3	Peterson, (pers. comm.)
Minipellets Dinoflagellates	Ellipsoid 2	$\text{Volume} = \pi/6.0 \cdot l \cdot w \cdot l$	Minipellets = .135 picograms C/ μm^3 Dinoflagellates = 0.94 (log 10(V) - 0.6)	Small, (1983) Mullin <i>et al.</i> , (1966) Strathmann, <i>et al.</i> , (1967)
Fecal pellets Crustacean parts Molts Tintinnids Centrics	Cylinder	Volume = $\pi/8.0 (l \cdot l \cdot l)$ Centrics Volume = $\pi/4.0 \cdot (w \cdot w \cdot l)$ fecal pellets	Fecal pellets = .135 picograms C/ μm^3 Centric = 0.76 = (log 10(V) - 0.29)	Small, (1983) Eppley, <i>et al.</i> (1970)
<i>Chaetoceros</i> <i>Pennates</i> <i>Biddulphia</i> <i>Eucampia</i>	Nitzschia Pennate	Volume = $w \cdot l (l - w + ((\pi/4.0) \cdot w))$	All diatoms = $0.76 \cdot (\log 10(V) - 0.29)$	Eppley <i>et al.</i> (1970)

Table 2. Food items found in the stomach contents of *P. meseres*. Food items (in bold) are the major food groups with more specific taxa listed below.

Fecal pellets
Minipellets
Crustacean parts
Whole moults
Tintinnids
Centric diatoms
Thalassiosira spp.
Coscinodiscus spp.
Rhizosolenia spp.
Chaetocerus spp.
Ditylum spp.
Skeletonema spp.
Dactylosolen spp.
Pennate Diatoms
Nitzschia spp.
Navicula spp.
Pleurosigma spp.
Pseudoenotia spp.
Amphora spp.
Sururiella spp.
Grammatophora spp.
Dinoflagellates
Thecate dinoflagellates
Atheate dinoflagellates
Protoperidinium spp.
Dinophysis spp.
Chrysophytes
Dictyocha spp.
Distephanus spp.
Radiolarians
Acantharians
Phaeodarians
Spumellarians
Nasellarians
Foraminiferans
Globigerina spp.
Eggs

TABLE 3. Values for total composition of major food groups in the 62 stomachs of *P. meseres*. (Mean %number +mean %volume) x (%frequency of occurrence) = Index of Relative Importance (IRI).

PREY ITEMS	Mean %N ($\pm$ SE)	Mean %V ($\pm$ SE)	%FO	IRI
Fecal pellets	30 (3.0)	58 (4.5)	98	8694
Centric diatoms	25 (2.8)	16 (3.7)	97	3960
Pennate diatoms	33 (3.3)	2 (.77)	94	3306
Crustacean parts	2.0 (.4)	17 (3.1)	79	1400
Minipellets	7.1 (1.4)	1.7 (1.3)	79	689
Tintinnids	1.3 (.33)	2.4 (.94)	65	241
Dinoflagellates	.74 (.23)	.10 (.03)	45	37
Radiolarians	.11 (.04)	.75 (.62)	16	14
Foraminiferans	.18 (.05)	.23 (.12)	24	10
Whole crustaceans	.01 (.005)	1.1(1.0)	3.2	4
Eggs	.14 (.12)	.27 (.2)	4.8	2
Chrysophytes	.03 (.01)	.001 (.0005)	10	.3

TABLE 4. Values for the composition of major food groups in the stomachs of *P. meseres* for the three oceanographic seasons. Calculations for IRI are the same as for TABLE 3.

DAVIDSON PERIOD

PREY ITEMS	Mean %N ($\pm$ SE)	Mean %V ($\pm$ SE)	%FO	IRI
Fecal pellets	27 (4.9)	73 (6.9)	100	9960
Pennates diatoms	41 (5.4)	2.1 (.44)	95	4114
Centrics diatoms	15 (3.4)	1.7 (.48)	95	1575
Minipellets	13 (3.8)	<1 (.2)	84	1120
Crustacean parts	2.0 (.90)	17 (6.0)	58	1095
Tintinnids	2.0 (.80)	3.9 (2.4)	58	317
Foraminiferans	.27 (.13)	.43 (.30)	26	18
Radiolarians	.21 (.13)	.35 (.29)	21	12
Dinoflagellates	.34 (.19)	.03 (.02)	26	10
Eggs	.07 (.07)	.52 (.52)	5.3	3
Chrysophytes	.01 (.03)	.05 (.05)	5.3	.3
Whole crustaceans	0 (0)	0 (0)	0	0

UPWELLING PERIOD

PREY ITEMS	Mean %N ($\pm$ SE)	Mean %V ($\pm$ SE)	%FO	IRI
Fecal pellets	40 (3.9)	53 (5.9)	97	8997
Centrics diatoms	33 (3.9)	20 (5.4)	100	5359
Crustacean parts	2.4 (0.5)	21 (4.7)	85	2024
Pennate diatoms	16 (1.6)	.24 (.05)	97	1612
Minipellets	5.1 (1.2)	2.6 (2.36)	85	649
Tintinnids	1.5 (.42)	1.1 (.43)	76	191
Dinoflagellates	1.1 (.41)	.13 (.05)	36	46
Radiolarians	.08 (.04)	1.2 (1.2)	15	19
Foraminiferans	.18 (.06)	.18 (.15)	30	11
Whole Crustaceans	.01 (.01)	.06 (.03)	3	.21
Eggs	.01 (.01)	.01 (.01)	3	.003
Chrysophytes	.001 (.01)	.02 (.02)	.001	0

OCEANIC PERIOD

PREY ITEMS	Mean %N ($\pm$ SE)	Mean %V ($\pm$ SE)	%FO	IRI
Pennate diatoms	72 (6.7)	10 (3.9)	100	8276
Fecal pellets	7.7 (2.7)	45 (13)	100	5227
Centric diatoms	17 (7.5)	29 (13)	80	3638
Tintinnids	.37 (.17)	4.1 (3.5)	60	267
Crustacean parts	.40 (.3)	4.6 (1.7)	50	251
Minipellets	1.4 (.8)	.40 (.22)	50	88
Whole crustaceans	.02 (.02)	6.5 (6.5)	10	65
Eggs	.71 (.71)	.71 (.71)	10	14
Dinoflagellates	.21 (.12)	.08 (.05)	30	9
Radiolarians	.03 (.03)	.01 (.01)	10	0.4
Chrysophytes	.001 (.01)	.001 (.001)	10	0
Chrysophytes	.001 (0)	.001 (.001)	10	0

Table 5. Percent similarity index comparisons of stomach contents of *Poebius meseres* and water column samples.

PSI	Gut 1 (7/17/91)	Gut 2 (7/22/91)	Gut 3 (9/30/91)	Gut 4 (10/4/91)	Gut 5 (10/24/91)	Gut 6 (11/22/91)
Water 1	.80	.73	.56	.32	.50	.56
Water 2		.72	.64	.34	.34	.43
Water 3			.78	.86	.82	.84
Water 4				.98	.81	.76
Water 5					.40	.44
Water 6						.69

Figure 1. *Poeobius meseres*. Entire animal with internal organs visible through transparent body wall (Photo copyright Sea Studios, Inc.)

Figure 2. Site for observations and collections of *Poebius meseres* in Monterey Bay, California.

Figure 3. Scanning Electron Microscopy of feeding apparatus in *P. meseres*. The cephalic region is composed of a pair of thick, longitudinally grooved palpi and 5-6 pairs of cirri in a transverse row. a) Section of ciliated grooved palp; scale = 20 μm . b) Tip of cirri with dense bands of cilia; scale = 15 μm . c) Ciliary tuft on the lateral edge of the grooved palp; scale = 2 μm . d) Section of cirri with diagonal bands of cilia; scale = 20 μm .

Figure 4. Cumulative food items versus sample size curve to determine adequacy of sampling of stomachs in *P. meseres* over a one year period. Sixty-two stomachs were randomized ten times and the cumulative number of food items measured. The symbols are the mean of these ten randomizations with their associated standard error. The "*" shows the pooled number of stomachs necessary to reach stabilization of the curve. An adequate number of stomachs were sampled to describe the diet of *P. meseres*.

Figure 5. Percent composition of major food groups in *P. meseres* stomachs, and frequency of occurrence (%F.O.) and ranked by the index of relative importance (IRI) from left to right for *P. meseres* in Monterey Bay n = the number of stomachs analyzed. Code of abbreviations: FE= fecal pellets; CEN = centric diatoms; PEN = pennate diatoms; Crust = crustacean parts; MP = minipellets; Tin = tintinnids; Dino = Dinoflagellates; Rad = radiolarians; For = foraminiferans; Molt = crustacean molt; Eggs = eggs; Chry = chrysophytes.

Figure 6. Scanning electron microscopy of fecal pellets in the stomach contents of *P. meseres*. a) Fecal pellet with macerated *Thalassiosira* sp.; scale = 20 μm . b) Copepod fecal pellet; scale = 30 μm . c) Fecal pellet of unknown origin; scale = 5 μm . d) Minipellet with digested *Nitzschia* sp.; scale = 5 μm .

Figure 7. Scanning Electron Microscopy of centric diatoms in the stomachs of *P. meseres*. a) *Hemidiscus* sp.; scale = 5 μm . b) *Skeletonema* sp.; scale = 10 μm . c) Resting spore of *Chaetoceros* sp.; scale = 2 μm . d) Unknown centric diatom; scale = 2 μm . e) *Thalassiosira* sp.; scale = 5 μm . f) *Chaetoceros* sp.; scale = 10 μm .

Figure 8. Scanning Electron Microscopy of pennate diatoms in the stomach contents of *P. meseres*. a) Unknown pennate diatom; scale = 5 μm . b) *Pseudoenotia* sp. scale = 10 μm . c) *Pseudonitzschia australis*; scale = 15 μm . d) *P. mesere* gut contents containing a high abundance of intact diatom frustules; scale = 20 μm .

Figure 9. Scanning Electron Microscopy of less abundant prey items in the stomachs of *P. meseres*. a) *Borgetella* sp.; scale = 20 μm . b) *Protoperidinium* sp.; scale = 10 μm . c) Tintinnid; scale = 15 μm . d) *Dinophysis* sp.; scale = 10 μm . e) Crustacean part; scale = 50 μm . f) *Protocystis* sp. (Phaeodarian); scale = 10 μm .

a

b

c

Figure 10. a) & b) Relative % volume of nutritious and non-nutritious food groups in the stomachs of *P. meseres* averaged over a one year period. c) The % volume of nutritious food were converted into %carbon (picograms) to show which food items *P. meseres* derived most of its nutrition.

Figure 11. Adequacy of sampling over three oceanographic seasons in Monterey Bay; a) Davidson period (November-February), b) Upwelling period (March-August) and, c) Oceanic period (September-October). The "*" shows the pooled number of stomachs necessary to reach the stabilization of the curves.

Figure 12. Composition of the major food groups in the stomachs of *P. meseres* for three oceanographic periods: 1) Davidson period (November-February), 2) Upwelling period (March-August) and, 3) Oceanic period (September-October). Abbreviations as for Figure 4.

Figure 13. Relative abundance of the three most common food groups in the stomachs of *P. meseres*. Counts of each food type were averaged on a bimonthly basis and expressed as a percentage of the total stomach contents; a) Pennate diatoms were most abundant during September; b) Fecal pellets were most abundant during March and, c) Centric diatoms were most abundant during July and August.

Figure 14. a) In March, the stomach contents of *Poeobius meseres* were packed with euphausiid fecal pellets from mouth to anus. b) Compound microscope of euphausiid fecal pellets (320X magnification). Pellets were cylindrical in shape with frayed ends and often had crustacean spines protruding out of the broken ends.