Vol. 147: 167–179, 1997 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published February 27

Role of mesopelagic zooplankton in the community metabolism of giant larvacean house detritus in Monterey Bay, California, USA

Deborah K. Steinberg[1,*], Mary W. Silver[2,3], Cynthia H. Pilskaln[4]

[1]Bermuda Biological Station for Research, Inc., Ferry Reach GE 01, Bermuda
[2]Institute of Marine Sciences, University of California, Santa Cruz, California 95064, USA
[3]Monterey Bay Aquarium Research Institute, Moss Landing, California 95039, USA
[4]School of Marine Sciences, University of Maine, Orono, Maine 04469, USA

ABSTRACT: The mucous feeding structures or 'houses' of the giant larvacean *Bathochordaeus* spp. provide a useful detrital system to study biological processes that mediate remineralization of particulate organic carbon in the mesopelagic zone: degradation by bacteria and grazing by zooplankton. The role of particle-associated zooplankton in remineralization in the mesopelagic zone has not previously been studied, mostly due to sampling difficulties. We collected houses between 100 and 500 m in Monterey Bay, California, USA, using a submersible ROV (remotely operated vehicle) and measured community metabolism on houses using oxygen electrodes. Houses were sites of elevated metabolic activity compared to surrounding waters. The average daily oxygen utilization indicates that approximately 1% of house C is used daily to sustain community respiration, although the rate is higher (8%) when large numbers of zooplankton are present. Estimated rates of zooplankton remineralization of houses are similar to bacterial remineralization rates reported for other types of detritus. Respiration rates provide minimal estimates of carbon transformations by communities on detritus, especially when metazoans are present. Based on published estimates of the relationship between zooplankton carbon consumption and respiration rates, and our measurement of zooplankton abundance on houses, we calculate that a mean of 6% and up to 43% of house C is ingested by zooplankton each day. Thus, a substantial part of the house could be consumed by detritus-feeding zooplankton before sinking out of the mesopelagic zone. Particle-associated zooplankton are important in recycling carbon on these houses and potentially on other aggregates at depth, not only by consuming and remineralizing detritus, but also by altering detritus through repackaging it in fecal pellets, releasing it as DOC, and fragmenting its fragile structure into smaller particulate matter

KEY WORDS: Mesopelagic zooplankton · Respiration · Larvacean · Detritus · Monterey Bay

INTRODUCTION

Particle remineralization below the euphotic zone is a crucial component of elemental cycling. However, there are few studies of the metabolic activities of mesopelagic communities on detritus other than bulk measurements from sediment trap material (e.g. Gardner et al. 1983, Ducklow et al. 1985, Karl et al. 1988) and measurement of heterotrophic activity on small, individual marine snow particles (Alldredge & Youngbluth 1985, Davoll & Youngbluth 1990).

Biological processes that mediate remineralization of particulate organic carbon (POC) into a dissolved form include degradation by microbes and grazing by zooplankton. The microbial community associated with particles is usually assumed to remineralize much of the sinking detritus, but the relative importance of the microbial versus zooplankton communities in the remineralization of particles at depth is not well known. Microbial activity on sinking particles appears insufficient to account for the observed attrition of particulate

*E-mail: debbie@bbsr.edu

carbon with depth, as measured by sediment traps (Karl et al. 1988, Taylor & Karl 1991). Alternatively, carbon may be lost via fragmentation of sinking matter into small, slower-settling particles, or via consumption by zooplankton, or both. Elevated hydrolytic enzyme activity in surface aggregates suggests that particles may be more rapidly solubilized than previously thought, in spite of the relatively low growth rate of the attached bacteria (Smith et al. 1992). Other studies hypothesize that remineralization in the midwater zone occurs mostly on small, suspended particles and that free-living bacteria decompose most particles (Cho & Azam 1988).

Less is known about the role of detritus-feeding zooplankton in remineralization of particulate organic matter at depth. Many investigators have proposed that zooplankton in this zone may break up particles or graze them (e.g. Sasaki et al. 1988, Angel 1989, Lampitt 1992, Dagg 1993, Uttal & Buck 1996). Jackson (1993) suggests that 'flux feeders' should be (but are usually not) included in studies of carbon recycling below the euphotic zone. Recent work has revealed that a variety of zooplankton inhabit and consume large particles (giant larvacean houses) in mid-water. (Steinberg et al. 1994, Steinberg 1995).

In this study, we use houses of the giant larvacean *Bathochordaeus* spp. to measure community metabolism on large particles. We concentrate on the role of metazoans, as less is known of their use of mesopelagic detritus than is known for the microbial community.

Larvaceans, or appendicularians, secrete a mucous 'house' to filter particulate food from the water (Deibel 1986). Houses are frequently discarded due to clogged filters or disturbance to the animal and, thus, are a common source of marine snow in near-surface waters (Alldredge 1979, Taguchi 1982). Deeper living, giant larvaceans (*Bathochordaeus* spp.) can be an important source of marine snow in Monterey Bay, California, USA, secreting meter-sized houses that occur year round, typically concentrated between 200 and 300 m depth (Pilskaln et al. 1991, Hamner & Robison 1992). Giant larvacean houses are also found in other midwater environments (Barham 1979, Galt 1979, Youngbluth 1984).

Giant larvacean houses provide a useful system to measure organism-related remineralization on aggregates. The houses are large enough to support sizable communities of microorganisms, as well as larger zooplankton. Similarity of house-microorganism communities to those on sinking detritus collected by sediment traps at our site (both in species composition and in ind. mg^{-1} C) indicate houses, aside from their unusual size, are typical of mesopelagic detritus at this site (M. Silver, S. Coale, C. Pilskaln & D. Steinberg unpubl.). Sinking detritus collected in sediment traps is often treated as the model for understanding remineralization at depth. Because of their size, it is possible to detect changes in community metabolic activity on houses over relatively short time periods. In addition, the numerous zooplankton that frequently accompany the houses (Steinberg et al. 1994), and the use of a remotely operated vehicle (ROV) to allow direct viewing and sampling of the large aggregates with their associated organisms, provide a novel opportunity to study the contribution of metazoans to remineralization of large particles at depth.

MATERIALS AND METHODS

Field collections. We collected houses of the giant larvacean *Bathochordaeus* spp. at 100 to 500 m depth at the seaward edge of Monterey Bay, California (36° 42' 00" N , 122° 02' 00" W). The collection site lies over deep water (~1000 m) in the Monterey Bay submarine canyon. Collections were made during the day between June 1992 and January 1993 with the submersible ROV 'Ventana', operated by the Monterey Bay Aquarium Research Institute (MBARI) (Table 1). The ROV contains a high-resolution, broadcast-quality Sony camera, a CTD and oxygen sensor for continuous hydrographic depth profiles, and samplers for capturing houses.

Table 1 Giant larvacean house samples collected between June 1992 and January 1993. Dates shown as month/day; a, b distinguish between 2 different house samples collected on the same day. d: detritus sampler; s: suction sampler. (Note: paired control samples were taken at same depth and temperature as each house sample)

Date	Sampler	Depth (m)	Temperature (°C)
6/12 a	d	385	6.6
6/12 b	d	492	5.9
7/2 a	d	397	6.4
7/2 b	d	406	6.4
7/28 a	d	419	7.0
7/28 b	d	450	6.7
8/13 a	d	225	9.2
8/13 b	d	240	8.9
10/16 a	d	293	8.2
10/16 b	d	293	8.2
10/22 a	s	256	8.5
10/22 b	d	266	8.3
11/10 a	s	254	8.3
11/10 b	d	292	7.7
1/19 a	d	253	8.2
1/19 b	d	282	7.9
1/29 a	d	283	7.4

Houses were collected in 2 types of samplers. The detritus samplers were 7.5 l Plexiglas cylinders with hydraulically activated lids; the suction sampler consisted of a variable-flow vacuum system that siphoned houses through a vacuum nozzle and deposited them into sample canisters containing a 165 µm mesh net and cod end. The detritus samplers were used for most collections as they were less destructive to the house structure than the suction sampler. The suction sampler was occasionally used (Table 1) to collect houses too large to fit in the detritus sampler and because it may collect larger, faster-swimming zooplankton on houses before they can escape (Steinberg et al. 1994). In some cases (using either sampler) aggregates could be collected intact, whereas in others, sizable fractions of the house were used for measurements.

Control samples of surrounding water that lacked house material were obtained after a house had been collected. Controls were sampled in the same manner as houses. Thus, detritus sampler controls were simply collected from water near houses, and suction sampler controls were drawn through the vacuum system for the same time and flow rate as the paired house sample (Steinberg et al. 1994).

Metabolic measurements. Houses and control samples were prepared for incubation in 130 ml glass reagent bottles on board ship immediately after ROV recovery. In all cases, houses had collapsed to a small volume by the time of ROV recovery, allowing them to fit easily into incubation bottles. This collapse is a potential error source as it changes the internal environment of the house, possibly affecting the behavior (and thus respiration) of some associated organisms. This collapsed state is not unnatural, however, and because houses occur both collapsed (discarded) and inflated (larvacean present) in the field, some were already collapsed when collected. In addition, there were no detectable differences between the assemblages of zooplankton or microrganisms occurring on collapsed versus inflated houses in the field (Steinberg et al. 1994, Silver et al. unpubl.). The bottles were filled with water from depth (collected with the detritus sampler) and then house material was gently pipetted from samplers with a wide-bore pipette. The transfer was completed quickly to avoid gas exchange and retain oxygen concentrations as near to ambient as possible. Ambient oxygen concentrations at depth of house collection were undersaturated and ranged from 1.1 to 2.4 ml l^{-1}, and initial O_2 concentrations in bottles at the start of an incubation were never more than twice the ambient concentration. The remaining water was siphoned from the detritus sampler through 53 µm mesh set in a finger bowl to gently concentrate any zooplankton (mostly copepods) that may have become separated from the house material, or concentrated into the cod end for suction samples, and then added to the house portion. Water for controls was concentrated in the same manner. Incubation bottles containing houses and paired controls were immediately stoppered and stored in a cooler for the hour-long trip to shore.

Oxygen uptake and temperature were measured continuously with an ENDECO/YSI® Type 1125 Pulsed Dissolved Oxygen System (Marion, MA, USA). The pulse rate was set to sample every 15 min to attain a high resolution profile, but was infrequent enough to avoid complications from electrode oxygen consumption. Electrodes were calibrated as per manufacturer's instructions (ENDECO® manual) against 5% O_2 certified, bottled gas and air-saturated water (by bubbling in room air with an aquarium pump). Oxygen electrodes were equilibrated to the appropriate temperature of incubation before use.

Incubations were conducted in MBARI's dock-side support laboratory, and were initiated within 1.5 h of ROV recovery (experiments typically began 5 h after the houses were sampled at depth). In the laboratory, bottles were fitted with oxygen electrodes and then immersed in a water bath set at the ambient temperature of house collection. The bath was set to gently swirl the samples in order to keep oxygen partial pressure uniform. Although houses were not kept suspended by this very low level of mixing, this gentle flow of water inside bottles avoided further disruption of the house matrix and community: excessive agitation can lead to erroneous measurements of metabolism in many organisms (Childress 1977, Saiz & Alcarez 1992). Bottles were incubated in the dark for 24 h. Oxygen levels were never close to being depleted at the end of incubations, assuring that oxygen concentrations stayed above the critical partial pressure required for most species. Incubation at surface hydrostatic pressure was considered an unlikely source of error, as pressure has little, if any, effect on the metabolism of most zooplankton from similar depths (Torres & Childress 1983, Childress & Thuesen 1993). Bacteria were also not likely affected, as pressure does not seem to affect optimal growth of bacteria above depths of ~2000 m (Yayanos 1986), and all our samples were from above 500 m. We do acknowledge the possiblity of pressure affects on bacteria, however, as the metabolic rate of bacteria from 1100 m depth in the Mediterranean Sea (in stratified water conditions) decreases with decompression (Bianchi & Garcin 1993).

Oxygen concentration and temperature in each incubation bottle were automatically logged into a computer, and respiration rates were determined by linear regression of O_2 concentration versus time (Fig. 1). For the regression, we excluded the initial high O_2 consumption rates that may have been due to handling;

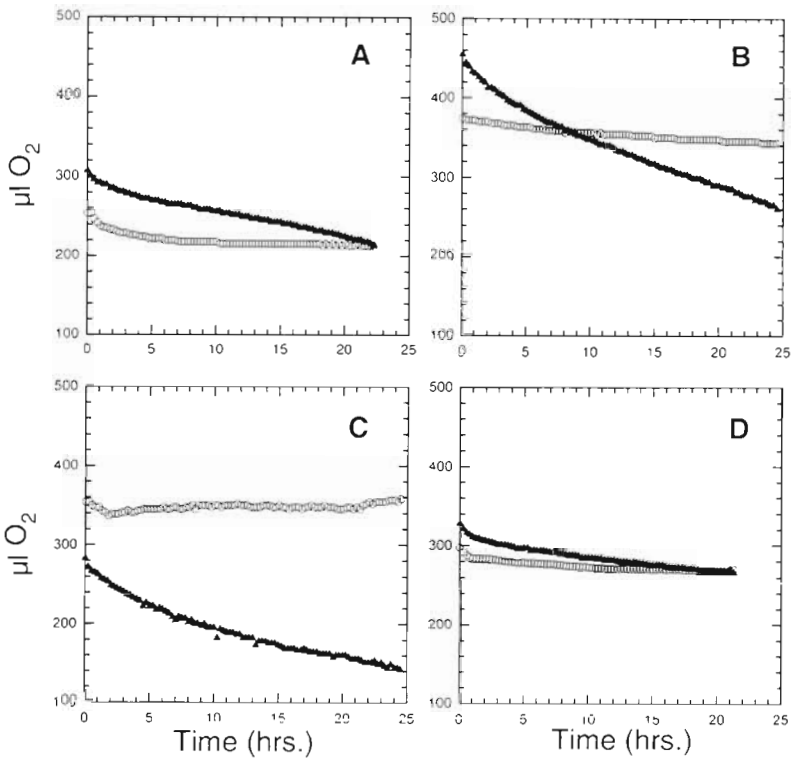

Fig. 1. Traces of oxygen consumption versus time for 4 different paired house (▲) and control (o; ambient water) samples. Dates (given as mo/d/yr) of sample collection and a and b correspond to Table 1: (A) 6/12/92 b, (B) 10/22/92 a, (C) 10/22/92 b, (D) 1/29/93 a

thus, the initial time point for an incubation was considered to be when organisms assumed a steady O_2 consumption rate (determined graphically from profiles), 1 to 5 h after the incubation began. Total house community respiration (as well as the number of metazoans house^{-1}) was determined by subtracting corresponding controls from houses, and then correcting for the fraction of the house sampled (estimated visually during house collection, mean % house sampled = 76%, range = 25 to 100%, n = 17), yielding a house community respiration (µl O_2 house^{-1} d^{-1}) as follows:

$$\frac{\text{house respiration} - \text{control respiration}}{\text{fraction of house sampled}} \quad (1)$$

Carbon requirements for respiration were determined from oxygen consumption rates using the appropriate stoichiometry (Parsons et al. 1984) and assuming a respiratory quotient (RQ) of 0.97 (Gnaiger 1983, Ikeda & Skjoldal 1989, Bochdansky & Herndl 1992) as follows:

$$\text{µg C utilized d}^{-1} = \text{µl O}_2 \text{ consumed d}^{-1} \times (12/22.4) \times 0.97 \quad (2)$$

where 12/22.4 is the weight (12 g) of C in 1 mol (22.4 l) of carbon dioxide.

At the end of the incubation, all house and control bottles were inspected for dead zooplankton. (Mortality rarely occurred during incubations.) A portion (usually 10%) of each house sample was removed for counts of microorganisms (bacteria, algae, and protozoans) and preserved in 2% glutaraldehyde (Silver & Gowing 1991). [Bacteria slides were prepared and frozen within 24 h of collection, as recommended by Turley & Hughes (1992) and counted within 6 mo of preparation.] The remainder of the bottle contents was then preserved in buffered 4% formaldehyde. Zooplankton were removed from the house samples and later identified and counted (Steinberg et al. 1994). The entire contents of the control bottles were preserved in 2% glutaraldehyde, and microorganisms and metazoans later enumerated. House organic C was measured by the procedure described in Pilskaln & Paduan (1992), Pilskaln et al. (1996), after zooplankton were removed from houses. Mean house C:N ratios of 9 (range = 6 to 17, n = 69; Pilskaln unpubl. data) measured on other giant larvacean house samples indicate houses resemble typical marine detritus (e.g. Alldredge & Silver 1988).

Conversion of respiration rate to carbon consumed. Respiration rates measure only the C an organism needs for maintenance, but C is used for many additional activities (growth, reproduction, etc.) (Parsons et al. 1984), resulting in a greater C requirement, which is usually supplied by food consumption in heterotrophs. Of the C consumed by zooplankton, some is assimilated (the 'usable' part for the organism) and the rest is egested as feces or lost as dissolved organic carbon (DOC). Of the C that is assimilated, some is respired (i.e. remineralized), some excreted as DOC, and some used for growth and reproduction.

Particle consumption (ingestion) rates were estimated from back-calculations from the measured respiration rates. To convert % house C respired d^{-1} into % house C consumed d^{-1} we used the following equation:

$$\%\text{ house C consumed d}^{-1} = \frac{\%\text{ house C respired d}^{-1}}{R \times AE} \quad (3)$$

where R is the fraction of assimilated C respired, and AE is the assimilation efficiency, or fraction of C consumed that was assimilated. Values of R and AE were taken from the literature.

Estimates of R for crustacean zooplankton generally range from 40 to 85% (Parsons et al. 1984). R for estuarine and coastal copepods feeding on detritus and phytoplankton ranges from 32 to 81% (Chervin 1978, calculated from Table 3 therein). Hargrave (1971) found an R of 49% for a deposit-feeding amphipod, and Dagg (1993) estimated an R of approximately 50% for *Neocalanus cristatus* in the subarctic Pacific Ocean (calculated from Table 1 in Dagg 1993). We use an R of 50%, an intermediate value within the range reported from the literature.

The most appropriate AE value for house-feeding copepods is that for a detritivore, because their food is mostly detritus (Steinberg 1995). Similar assumptions have been made for benthic boundary layer zooplankton (Wishner & Gowing 1987). Although few measurements of AE exist for detritivorous zooplankton, marine detritivores generally have a lower AE than do crustacean carnivores (AE ~90 to 95%) and herbivores (AE ~60 to 95%) (Valiela 1984). For example, mysids feeding on detritus have an AE of 10 to 50% for algal detritus and cellulose (C. F. Ferguson in Raymont 1983). Gowing & Wishner (1986) used an AE of 14% for calculating an energy budget for benthic boundary layer zooplankton. Estimates of AE for deposit-feeding invertebrates include 15% for a deposit-feeding amphipod (Hargrave 1971), and values of 60% have been assumed for typical deposit feeders (Cammen 1989). We chose a conservative high-end detritivore/low-end herbivore AE of 60% based on our knowledge of copepod feeding habits on houses (Steinberg 1995).

Using values of 50% for R and 60% for AE in Eq. (2), the amount of C respired by copepods on larvacean houses is estimated to be approximately 30% of the C consumed. This is a conservative value because it minimizes the C estimated to be consumed, based on measured respiration rates.

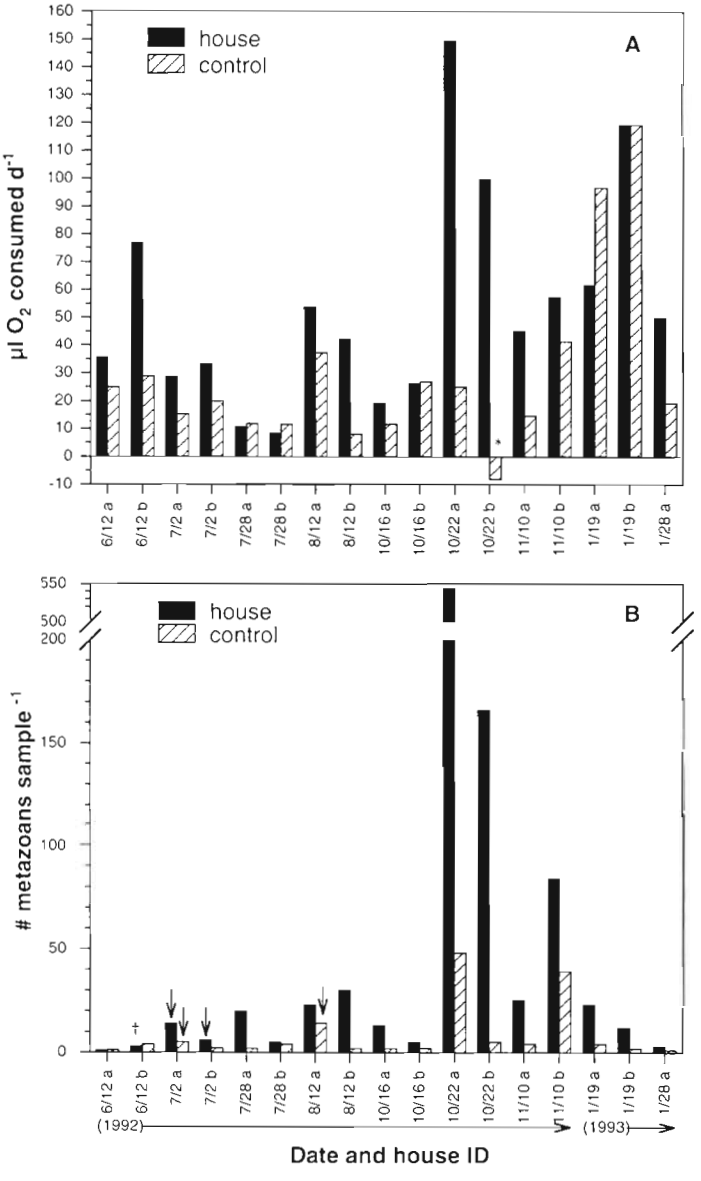

Fig. 2. Oxygen consumption and number of metazoans in house and control (ambient water) samples collected between June 1992 and January 1993 (date of collection shown as mo/d). (A) Community oxygen consumption on house samples compared with oxygen consumption in water taken adjacent to houses. n = 17 paired samples. $p < 0.05$ [Student's t-test on $\log(x+1)$-transformed values]. House mean ± SE = 54 ± 9 µl O_2 d^{-1}; Control mean ± SE = 29 ± 7 µl O_2 d^{-1} (B) Number of metazoans associated with house samples compared with the number in water sampled adjacent to houses. n = 17 paired samples. $p < 0.05$ [Student's t-test on $\log(x+1)$-transformed values]. House mean ± SE = 58 ± 32 metazoans; Control mean ± SE = 8 ± 3 metazoans. (*) Negative value indicates oxygen increased slightly during the incubation, for which we have no explanation: there were no visible bubbles in the bottle and no photosynthesis, since samples were kept in the dark; (†) this sample contained thousands of small (<100 µm) eggs; (↓) these samples contained large diatoms (*Coscinodiscus* sp.)

RESULTS

Both respiration rates and metazoan numbers on houses were significantly higher than those in corresponding water controls [Student's t-test on $\log(x+1)$-transformed values, $p < 0.05$] (Fig. 2A, B). (Note: as between-day differences might bias results, we also conducted a 2-way ANOVA which again showed significant differences between houses and controls independent of the between-day differences.) The highest respiration rate was 150 µl O_2 d^{-1} (Fig. 2A). Metazoan communities on incubated houses were typical of those described in Steinberg et al. (1994). Small (~1 mm) poecilostoma-

toid copepods of the genus *Oncaea* were the most numerous metazoans on houses. *Oncaea* spp. numbers were extremely high on 2 house samples, Sample 22 Oct a with 523 *Oncaea* spp. house sample^{-1}, and Sample 22 Oct b with 152 *Oncaea* spp. house sample^{-1}. The calanoid copepod *Scopalatum vorax* (Ferrari & Steinberg 1993, Steinberg et al. 1994, Steinberg 1995) occurred on many houses (max. 7 house^{-1}). Other calanoid copepods, crustacean nauplii, polychaetes, and amphipods were occasionally present.

Control values were occasionally higher than house values (Fig. 2A, B). Although the number of metazoans in controls were almost always lower than the number on houses, some controls may have contained larger metazoans or other smaller organisms that were more concentrated in the surrounding water, accounting for elevated respiration in some controls.

The microplankton community on incubated houses was typical of numerous other houses we have sampled (Silver et al. unpubl.). Heterotrophic bacteria averaged 3.0×10^8 house^{-1} ($\pm$SE = 8.5×10^7, range = 4.3×10^7 to 7.8×10^8, n = 10). Several of the incubated houses had high numbers of the large centric diatoms *Coscinodiscus* sp. as indicated in Fig. 2B (arrows). Large sarcodine protozoans, such as phaeodarian radiolarians and foraminifera, were occasionally present, and numbers of ciliates, sarcodines, and other small protozoans (between ~20 and 100 µm) were low (total protozoan mean $\pm$ SE = $1 \times 10^3 \pm 4.7 \times 10^3$ house^{-1}, range = 0 to 8×10^3, n = 17). Silver et al. (unpubl.) found houses are enriched in microorganisms with respect to the surrounding seawater, with enrichment factors of 8 for bacteria, 3×10^1 for ciliates, 2.2×10^1 (upwelling season) and 3.8×10^2 (non-upwelling season) for sarcodine protozoa, and 1.3×10^2 (upwelling) and 1.7×10^3 (non-upwelling) for diatoms. Non-living material such as fecal pellets and crustacean molts was often abundant on houses. One house contained thousands of small (<100 µm) eggs (Fig. 2B, indicated by †), possibly causing the elevated respiration of that sample (Fig. 2A).

The highest community oxygen consumption rates occurred on the 2 houses with the greatest number of metazoans (Fig. 3). The highest respiration rates were

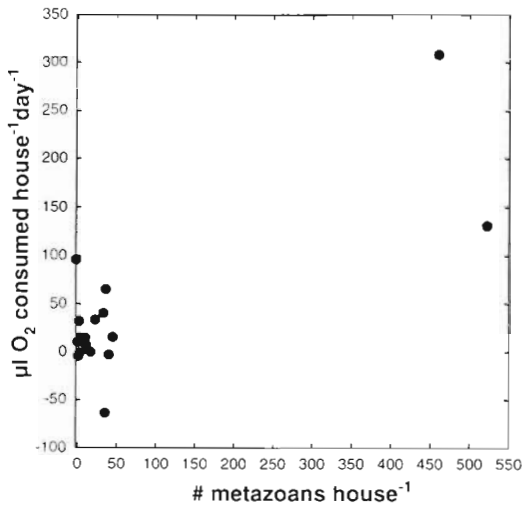

Fig. 3. Community oxygen consumption on houses compared with number of metazoans house^{-1}. Community oxygen consumption: mean $\pm$ SE = 41 $\pm$ 20 µl O_2 house^{-1} d^{-1}, range = <0 to 309 (n = 17). Number of metazoans house^{-1}: mean $\pm$ SE = 73 $\pm$ 38 metazoans house^{-1}, range = <0 to 522 (n = 17). Note: both community respiration rates and number of metazoans house^{-1} were determined by subtracting paired controls from house values (Fig. 1), and dividing by the fraction of the house collected (see text)

309 and 132 µl O_2 d^{-1} for houses containing 460 and 522 metazoans, respectively. The mean respiration rate for all houses was 41 µl O_2 d^{-1}, and the mean number of metazoans was 73 house^{-1} (n = 17). Several houses had 'negative' respiration rates or numbers of metazoans due to higher values in control samples (Fig. 3). As indicated above, this may be due to higher concentrations of smaller organisms, or an occasional large metazoan, in control water. These 'negative' values are assumed to be zero in further calculations.

To estimate the amount of house C required to support community respiration for 1 d, we converted house community metabolism into organic C requirements for respiration (Table 2). Estimates average 1% house C remineralized d^{-1} (corresponding to 105 d for C turnover on a house), with a maximum of 8% d^{-1} (12 d for C turnover on a house).

Table 2. Conversion of house community metabolism (oxygen consumed) to organic carbon requirements for respiration (carbon respired)

House	Oxygen consumed (µl house^{-1} d^{-1})	Carbon respired[a] (mg house^{-1} d^{-1})	Days to remineralize house carbon[b]	% house carbon remineralized (d^{-1})[b]
Mean (n = 17)	41	0.02	105	1
Range	(0–309)	(0–0.17)	(∞–12)	(0–8)

[a]Calculated using appropriate stoichiometry (Parsons et al. 1984), assuming RQ = 0.97 (see 'Materials and methods')
[b]Based on a mean house organic carbon of 2.1 mg (measured at end of experiment)

The metazoan contribution to house respiration is estimated from numbers of copepods on houses, which are mostly small *Oncaea* spp. We used a respiration rate of 1 µl O_2 copepod^{-1} d^{-1}, based on published rates measured for copepods of this genus or size (1 mm) at comparable temperatures, as well as our measured rates of O_2 consumption in 2 control samples that contained numbers of *Oncaea* spp. Gaudy & Baucher (1983) report *Oncaea venusta* respires 1.92 µl O_2 d^{-1} at 20°C. Using their determined Q_{10} of 2.15, *Oncaea* spp. would respire 0.8 µl O_2 d^{-1} at 8°C. Similarly, regression of respiration rates of temperate zooplankton as a function of body dry weight (= 20 µg for *O. venusta*; Gaudy & Baucher 1983) yields a respiration rate of 1.4 µl O_2 d^{-1} (from Ikeda 1974 in Raymont 1983, Fig. 6.28). Same-size copepods such as *Acartia* sp. respire 0.8 to 1.4 µl O_2 d^{-1} at 10°C (Raymont 1983, Table 6.21 therein). We also calculated copepod respiration from 2 controls containing *Oncaea* spp. We could not use an average of all the controls for determining copepod respiration as the assemblage of zooplankton on houses is unique; the same species are not necessarily found in the surrounding water. A control sample from 22 Oct 1992 contained 22 *Oncaea* spp. and a total control water respiration rate of 24.8 µl O_2 d^{-1}. This sample also contained 17 tiny *Oithona* sp., which have low respiration rates (<0.1 µl O_2 copepod^{-1} d^{-1} at 10°C, Lampitt 1978, Lampitt & Gamble 1982) and should have not added appreciably to the O_2 consumption in the sample. This gives a respiration rate for *Oncaea* spp. of ~1 µl O_2 copepod^{-1} d^{-1}. A control sample from 10 Nov 1992 contained 28 *Oncaea* spp. and a total control water respiration rate of 41.5 µl O_2 d^{-1}. This sample also contained 4 tiny *Oithona* sp., and 6 small (1 mm) calanoid copepods. At ~1 µl O_2 copepod^{-1} d^{-1} *Oncaea* spp. would account for ~70% of the respiraton in this sample, a reasonable estimate in light of the other copepods present.

With a respiration rate of 1 µl O_2 copepod^{-1}d^{-1} and a mean house organic C of 2.1 mg house^{-1} (n = 17 houses), we calculate that metazoans respire an average of 1.9% (max. 13%) of the house C d^{-1} (Table 3).

From the respiration rate measurements, the C consumption rates can be estimated for the metazoan community on houses. As noted above, C consumption always exceeds respiration, and better represents C loss or transformation than does respiration alone. Assuming an *AE* of 60% and an *R* of 50% (see 'Materials and methods'), the copepods could be consuming on average 6% and up to 43% of the house d^{-1} (Table 3), based on a mean of 1.9% and maximum of 13% of house C respired d^{-1}.

DISCUSSION

Degradation of organic matter has been described in the literature in many ways. The inconsistent use of terms and the different types of measurements used to represent the underlying processes responsible for decomposition makes it easy to misinterpret the differences among studies. In an attempt to clarify these underlying processes, we use 'decomposition' as a general term that includes both 'remineralization' (i.e. transformation of POC into its inorganic constituents, Fig. 4a) and 'alteration' (includes consumption, fecal pellet production, fragmentation, and production of DOC, Fig. 4b).

The role of zooplankton in the decomposer community is the focus of this paper. Most studies of pelagic detritus degradation have only considered bacterial decomposition or enhanced decomposition by bacteria in the presence of protozoans. However, here we include zooplankton consumption of detritus based on ratios of consumption to respiration. Thus, 2 estimates of detrital degradation were obtained: the amount potentially remineralized (measured by respiration) (Fig. 4a), and the amount consumed by zooplankton (Fig. 4b). Consumption necessarily uses more substrate than remineralization, and is seldom included in measurements of particle decomposition because zooplankton are rarely considered part of the decomposer community. Their exclusion results from the difficulty of assessing whether a given metazoan is a true detri-

Table 3. Estimated respiration and consumption rates of copepods feeding on larvacean house aggregates

	Copepod abundance (no. ind. house^{-1})	C respired (mg house^{-1} d^{-1})[a]	% house carbon respired due to copepods (d^{-1})[b]	% house carbon consumed (d^{-1})[c]
Mean (n = 17)	73	0.04	1.9	6
Range	(0–522)	(0–0.27)	(0–13)	(0–43)

[a]Calculated by assuming a 1 mm copepod respires ~1 µl O_2 d^{-1} (see 'Results') and using appropriate stoichiometry (Parsons et al. 1984), assuming RQ = 0.97
[b]Based on a mean house organic carbon of 2.1 mg (measured at end of experiment)
[c]Assuming assimilation efficiency = 60%, and respiration of assimilated carbon = 50% (see 'Materials and methods')

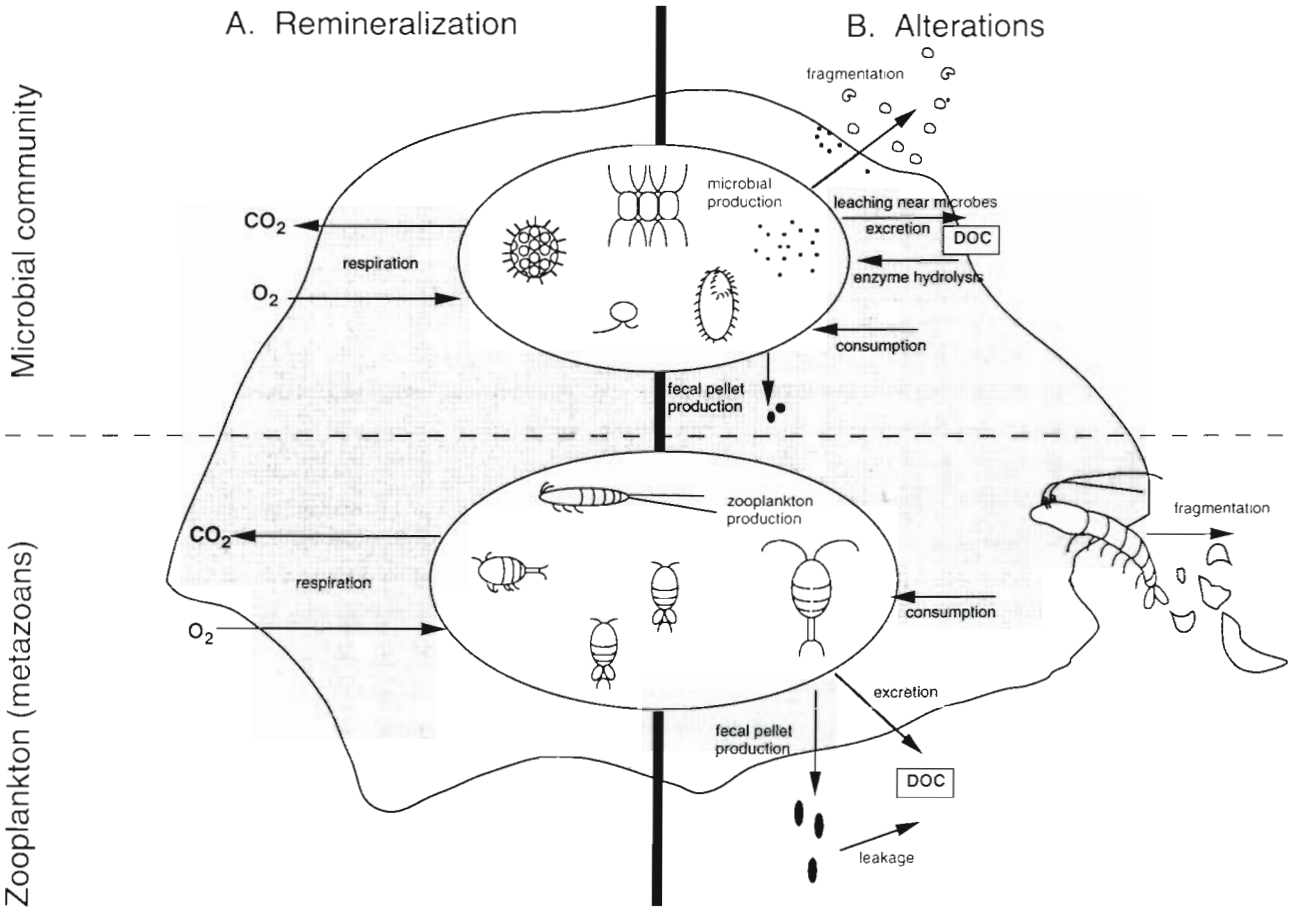

Fig. 4. Biologically mediated decomposition of particulate organic carbon. (A) Remineralization. Remineralization by both the microbial (e.g. clockwise from top: algae, bacteria, ciliates, flagellates, radiolarians) and metazoan (e.g. copepods) communities associated with particles involves the transformation of POC into its inorganic constituents. This can be equated with the C demand for respiration. (B) Alterations. Zooplankton: When detritus is consumed by a metazoan, a portion of the C is allocated to production (growth and reproduction). Other fates are to be excreted as DOC, or repackaged as fecal pellets, which may also leak DOC. In addition, particle fragmentation results from grazing, or disruption via swimming action as represented by the euphausiid. Microbial community: When detritus is consumed by protozoans or hydrolyzed by bacteria, a portion of the C is allocated to production (growth and reproduction). Enzyme hydrolysis of the particle ('consumption') by bacteria and subsequent uptake of DOC can also lead to particle fragmentation and leaching of DOC (the latter by algae as well). Consumption by protozoans essentially alters the particle as does that by zooplankton, but on a greatly reduced scale. Protozoans may also produce tiny fecal pellets, including minipellets (Gowing & Silver 1985), excrete DOC, and fragment particles via their feeding activities

tal associate and from the difficulty of capturing the larger, mobile forms.

Remineralization and alteration

Measurements of decomposition have used a variety of approaches, which we categorize as either remineralization or alteration of POC. Remineralization is loss of organic carbon to dissolved inorganic carbon (ΣCO_2), but is most conveniently measured as O_2 consumption, which results from respiration of the entire community. Here we equate remineralization with the C demand for respiration. (Fig. 4a). Alteration includes all the processes in Fig. 4b and is necessarily greater than remineralization; it can include production (growth and reproduction), consumption (or enzyme hydrolysis for bacteria), fecal pellet production, fragmentation, and production of DOC by microbes or metazoans (discussed in greater detail below).

Decomposition is often measured by biologists through bulk biomass changes (e.g. through ATP), or via growth rates or production of a community considered primarily responsible for remineralization, usually bacteria. These measurements are especially subject to bias, because the membership of deep-sea detrital communities is relatively poorly known, and only selected participants are typically considered.

Presumably, however, these decomposer communities contain the common membership of bacteria, microflagellates, ciliates, invertebrates, and other organisms. Bacteria are usually considered primarily responsible for decomposing the detrital matrix, but their consumers may be more important releasers of elemental constituents (e.g. nitrogen) than bacteria alone (Goldman et al. 1985). Remineralization could occur even in the absence of bacteria: community respiration could release CO_2 and consumption of the matrix or of other consumers would release other mineral constituents. Thus, estimates of population size or growth rates of particular taxa, especially bacteria, may not be linked with remineralization in a simple way.

Overall house community remineralization

Losses of POC due to remineralization, i.e. respiration by the total community of associated organisms, appear to be small in this study. Organic C remineralization of larvacean houses averaged approximately 1% of house C d^{-1} (C turnover time of 105 d), but was higher when large numbers of metazoans were present (8% of house C d^{-1}, C turnover time of 12 d).

The loss of sinking POC with depth, as measured by sediment traps, is often used to represent decomposition, though loss also occurs when particles are fragmented into smaller pieces or converted to dissolved organic material. We can calculate equivalent C loss rates for houses. Given average sinking rates of ~800 m d^{-1} for discarded houses (Hamner & Robison 1992), and a maximum of about 8% house C respired d^{-1} (present study), only about 4% of the house C will be fully remineralized before descending below the base of the 100 to 500 m *Bathochordaeus* spp. stratum we studied. If a house is typically used for a day by *Bathochordaeus* spp. before collapsing and sinking from the zone (Silver et al. unpubl.), a maximum of only about 12% of the house C would be remineralized before descending below 500 m (houses do reach the floor of the Monterey Canyon at depths ≥1600 m; Hamner & Robison 1992). Thus, even with maximum numbers of metazoans present, respiratory losses are not large.

We can cautiously compare our results to others in the literature. For example, decay rates, measured by weight loss of C for bulk material in sediment traps, can be approximately 1% d^{-1} (Gardner et al. 1983), ≤0.26% d^{-1} over a 6 mo period (Khripounoff & Crassous 1994), or 6% d^{-1} over a 5 d period (Lorenzen et al. 1983). These rates, however, reflect not only remineralization but also the additional alteration of organic matter (e.g. weight loss due to solubilization of organic matter). Bacterial carbon demand [BCD: the sum of respiration (i.e. remineralization) and bacterial production] also can be used to estimate an important source of C loss or transformation. Estimates of BCD show rates of 1 to 5% d^{-1} for surface marine snow aggregates (Simon et al. 1990).

A number of studies have shown that decomposition of detritus in the presence of natural microbial communities can occur rapidly. For example, C turnover times of only several days have been found for phytoplankton detritus (Newell et al. 1981), fecal pellets of pelagic tunicates (Pomeroy et al. 1984), and abandoned larvacean houses (Davoll & Silver 1986). The presence of protozoans and solubilization of labile organic material from the substrate may partially account for the comparatively high rates in these studies, which measure not only remineralization but also alterations of organic matter.

Contribution of zooplankton to community remineralization

The role of detritus-feeding zooplankton (metazoans) in remineralization at depth has largely been neglected. Yet the present study suggests that, at least for these large particles, zooplankton are important. When zooplankton were abundant on aggregates, the remineralization rate, measured by oxygen consumption of the entire community, reached approximately 8% d^{-1}, higher than the overall average of 1% d^{-1}. It is unlikely the higher respiration in these samples resulted from another component of the community covarying with the zooplankton numbers (i.e. some houses contain more food and thus more zooplankton), as Steinberg et al. (1994) found no relationship between numbers of potential food items (e.g. diatoms, ciliates) on houses and the numbers of copepods. Using respiration rates for zooplankton in our control bottles and from the literature we conclude that the observed numbers of associated zooplankton account for measured oxygen utilization (Fig. 3, Table 3). The estimated respiration d^{-1} by copepods (up to 13% of house C; Table 3) more than accounts for the measured total community rate of house C respired d^{-1} (up to 8%, Table 2). This discrepancy may be due to differences in respiration rates of copepods when they are associated with a house versus when they are free in the water.

Zooplankton members of the house community may contribute as much to house remineralization as the bacteria members. Our average estimated rates of zooplankton remineralization (1.9% C remineralized d^{-1}) are similar to bacteria remineralization rates suggested for sediment trap detritus (Ducklow et al. 1985) and copepod fecal pellets (Jacobsen & Azam 1984). Since the house community studied here is likely a few days old or less, the rates of bacteria remineralization may

be lower than for aged detritus with more fully developed communities.

Other studies have also shown zooplankton to play a significant role in remineralization. By comparing losses of sinking C measured by sediment traps with zooplankton respiratory requirements, Lampitt (1992) estimated 9% of remineralization between 1000 and 100 m above the seabed in the Madeira Abyssal Plain was due to the zooplankton community, and that zooplankton were likely responsible for more remineralization in shallower depths. Bochdansky & Herndl (1992) measured polychaete C respiration on surface marine snow. By translating respiration rates into C assimilation by the polychaetes, they found this polychaete 'C demand' could exceed BCD on the particles.

Other members of the detrital community

Thus far we have discussed zooplankton communities, with some comparison to the better known bacterial communities, on detritus. Members of the microbial community other than bacteria, such as algae and protozoans, may also contribute to remineralization of detritus. Algal metabolism does not remineralize the detrital matrix though algae are part of the detrital community/substrate and do respire their own C. Algae are not unique to larvacean houses, but are common to many types of marine detritus, especially in upwelling areas. Live algae are commonly exported from upwelling areas like our study site (Legendre 1990) and have been collected on marine snow particles in the deep sea (Silver & Alldredge 1981), although their importance declines with depth (Silver & Gowing 1991). Thus, algal metabolism in detrital communities will likely be highest in areas of high production and at shallower depths.

Protozoans are commonly important members of detrital communities (Caron et al. 1982, Silver et al. 1984, Silver & Gowing 1991), and have been shown to accelerate decomposition of detritus (Pomeroy et al. 1984, Taylor et al. 1986, Turley et al. 1988). There is also considerable evidence that bacterivorous protozoa are major regenerators of inorganic nitrogen and phosphorus in the sea (reviewed by Caron & Goldman 1990). Therefore, protozoans can play a major role in remineralization, but one we cannot adequately estimate from this study.

Particle alteration by the detrital community

When detritus or its associated community is eaten, much more of it is altered or transformed from its original state than the portion that is respired (Fig. 4), likely hastening remineralization by members of the microbial community. Alteration by the community on particles is a continuum with zooplankton and bacteria at opposite ends, and protozoans as intermediates. Zooplankton and bacteria alter particles differently. Bacteria hydrolyze the particle substrate and take up the solubilized compounds (DOC). This can lead to particle fragmentation, and some of the DOC may be lost by leaching near microbes. Zooplankton alter particles on a larger scale. Consumption of the detrital matrix or of other associated organisms by larger zooplankton could fragment aggregates almost instantaneously. Within an hour, fecal pellets are produced by most copepod-sized consumers, further altering particulate material.

The microbial and zooplankton communities may play different roles in particle alteration at different stages of decomposition, and the likelihood of sampling all members of the community at one time on a particle may depend on the particle size. Zooplankton may only be present regularly on larger particles. With their greater food requirements, detrital-feeding zooplankton may require sufficiently large substrates to be regular associates. Zooplankton may also consume multiple smaller particles, thus spending less time on each, to obtain their daily food rations. In late stages when particles are fragmented, bacteria or protozoans may become more abundant (i.e. increased surface area relative to volume for their attachment; Johannes 1965).

Zooplankton-mediated alteration of particles

Evidence for a significant role for midwater zooplankton in the consumption of giant larvacean houses is provided by the large numbers of metazoans aggregated on houses and by their gut-contents which suggest feeding on house-associated organisms, and possibly the mucous matrix (Steinberg 1995). In other studies, gut composition of deep-sea copepods (e.g. Harding 1974, Gowing & Wishner 1986, 1992, Sasaki et al. 1988) and polychaetes (Uttal & Buck 1996) provides evidence for feeding on other forms of detritus in deep water.

In this study the estimated consumption rate of larvacean house detritus averages 6% and ranges up to 43% of the house d^{-1} (Table 3). Thus, a substantial part of the house could be ingested by detritus-feeding zooplankton before the house sinks from the mesopelagic zone. Other studies have compared depth-related losses measured by sediment trap C fluxes with estimated respiration rates of resident zooplankton communities and thereby predicted consumption due to

zooplankton. For example, Sasaki et al. (1988) estimated that 37% of the particles lost between 150 and 1000 m in the Oyashio current (northwestern Pacific Ocean) could be consumed by copepods, a value comparable to that found in our study.

Estimates of consumption of house detritus in this study are likely low. We measured the role of only the zooplankton consistently associated with giant larvacean house detritus and used conservative values to predict consumption from respiration. However, other types of zooplankton (e.g. euphausiids, which usually left when the ROV approached) may use houses but only visit them intermittantly. We also did not include the larvacean organism itself (*Bathochordaeus* spp.) in our estimates of community metabolism, since technically it is not a part of the house's 'detrital community'. However, larvaceans could consume large amounts of detritus concentrated by their feeding filters.

Many forms of particle alteration occur when a metazoan consumes detritus. One fate of consumed detritus is its repackaging into fecal pellets, a process by which new fecal pellet classes could be injected at depth (Honjo 1978, Urrere & Knauer 1981). Copepods feeding on houses or other large detrital particles may also deposit their pellets there, and these pellets may in turn be ingested by other members of the detrital community. In addition, a significant amount of the C consumed by crustacean zooplankton can be lost as DOC (e.g. Hargrave 1971, Dagg 1976). DOC is released during consumption by 'sloppy feeding' or diffuses from fecal pellets immediately after their release (Jumars et al. 1989) (Fig. 4). This DOC could then be rapidly hydrolyzed by free-living bacteria (Jumars et al. 1989, Banse 1990).

Zooplankton can fragment the house matrix, leaving smaller pieces for other zooplankton to consume whole, or for bacteria to solubilize. Many investigators have suggested that zooplankton may break up particles in the mesopelagic zone (Banse 1990, Taylor & Karl 1991, Lampitt 1992), but as yet there has been little direct evidence. We have observed (with the ROV video camera) zooplankton disrupting particles. Euphausiids approaching larvacean houses break apart the already fragile structure by the swimming action of their pleopods. Ctenophores and other gelatinous zooplankton occasionally become entangled in the house mucus and disrupt the house by the movement of their cilia or the pulsing of their swimming bells. We have not seen copepods breaking apart a house, but we have observed hundreds of *Oncaea* spp. copepods 'swarming' on houses and the calanoid copepod *Scopalatum vorax* picking at the mucous structure of a house, presumably while feeding. These observations suggest that copepods could contribute to house fragmentation.

Because most studies only measure a portion of the decomposition cycle, it is difficult to compare results among different studies. For example, the rapid loss of C with depth indicated by sediment trap studies (e.g. Karl et al. 1988, Taylor & Karl 1991) is not only due to remineralization, but also to alterations of POC. Our results likewise suggest that a substantial portion of house detritus is consumed and transformed into other forms of C, while only a small portion of the house C is likely fully remineralized during the few days or less that houses are suspended or sinking through the water. When broken into smaller particles or transformed into DOC, the house may be more readily degradable by bacteria (attached or free-living), or by other zooplankton. The rate and manner in which decomposition occurs depends on what kinds of organisms are present on detritus. Zooplankton accounted for a substantial portion of the community metabolism on houses in our study; thus, an important part of the decomposition cycle could be missed if zooplankton are not considered.

There are many other potentially remineralizing detritivores in the mesopelagic zone in addition to the particle-associated species investigated in this study. Whether zooplankton ingest entire small particles or pieces of larger particles, or intercept and ingest particles on mucous feeding webs or use food-concentrating filters, sinking detritus is likely an important food source for zooplankton in the mesopelagic zone. As others have expressed (e.g. Banse 1990, Taylor & Karl 1991), more attention to the mechanisms and rates of zooplankton-mediated remineralization of sinking detritus is needed to understand mechanisms of C recycling below the euphotic zone, and to elucidate the observed losses of sinking particles with depth.

Acknowledgements. We thank the crew and especially the ROV pilots, J. McFarlane, C. Grech, and C. Dawe, of the RV 'Pt. Lobos' for help with sample collection. Special thanks to G. Friederich and L. Codispoti for helpful suggestions on the methodology for metabolic measurements, and S. Coale and J. Paduan for technical assistance. A. Alldredge, D. Malmquist, D. Smith, A. Michaels, and 4 anonymous reviewers made helpful suggestions and comments on the manuscript. This work was supported in part by NSF grant OCE-9012340 to M.W.S., NSF grant OCE-9015602 and funding at MBARI from the David and Lucille Packard Foundation awarded to C.H.P., and a Dr. Earl H. Myers and Ethel M. Myers Oceanographic and Marine Biology Trust Fund grant to D.K.S.

LITERATURE CITED

Alldredge AL (1979) The chemical composition of macroscopic aggregates in two neritic seas. Limnol Oceanogr 24: 855–866

Alldredge AL, Silver MW (1988) Characteristics, dynamics, and significance of marine snow. Prog Oceanogr 20:41–82

Alldredge AL, Youngbluth MJ (1985) The significance of macroscopic aggregates (marine snow) as sites for heterotrophic bacterial production in the mesopelagic zone of the subtropical Atlantic. Deep Sea Res 32:1445–1456

Angel MV (1989) Does mesopelagic biology affect the vertical flux? In: Berger WH, Smetacek VS, Wefer G (eds) Productivity of the ocean: present and past. John Wiley and Sons Limited, New York, p 155–173

Banse K (1990) New views on the degradation and disposition of organic particles as collected by sediment traps in the open sea. Deep Sea Res 37(7):1177–1195

Barham EG (1979) Giant larvacean houses: observations from deep submersibles. Science 205:1129–1131

Bianchi A, Garcin J (1993) In stratified waters the metabolic rate of deep-sea bacteria decreases with decompression. Deep Sea Res 40(8):1703–1710

Bochdansky AB, Herndl GJ (1992) Ecology of amorphous aggregations (marine snow) in the Northern Adriatic Sea. III. Zooplankton interactions with marine snow. Mar Ecol Prog Ser 87:135–146

Cammen LM (1989) The relationship between ingestion rate of deposit feeders and sediment nutritional value. In: Lopez G, Taghon G, Levinton J (eds) Ecology of marine deposit feeders. Springer-Verlag, New York, p 201–222

Caron DA, Davis PG, Madin LP, Sieburth JMcN (1982) Heterotrophic bacteria and bacterivorous protozoa in oceanic macroaggregates. Science 218:795–797

Caron DA, Goldman JC (1990) Protozoan nutrient regeneration. In: Capriulo GM (ed) The ecology of marine protozoa. Oxford University Press, New York, p 283–306

Chervin MB (1978) Assimilation of particulate organic carbon by estuarine and coastal copepods. Mar Biol 49:265–275

Childress JJ (1977) Physiological approaches to the biology of midwater organisms. In: Anderson NR, Zahuranac BJ (eds) Oceanic sound scattering and prediction. Plenum Press, New York, p 301–324

Childress JJ, Thuesen EV (1993) Effects of hydrostatic pressure on metabolic rates of six species of deep-sea gelatinous zooplankton. Limnol Oceanogr 38(3):665–670

Cho BC, Azam F (1988) Major role of bacteria in biogeochemical fluxes in the oceans' interior. Nature 32:441–443

Dagg M (1976) Complete carbon and nitrogen budgets for the carnivorous amphipod, *Calliopius laeviusculus* (Kroyer). Int Rev Ges Hydrobiol 61(3):297–357

Dagg M (1993) Sinking particles as a possible source of nutrition for the large calanoid copepod *Neocalanus cristatus* in the subarctic Pacific Ocean. Deep Sea Res 40(7): 1431–1445

Davoll PJ, Silver MW (1986) Marine snow aggregates: life history sequence and microbial community of abandoned larvacean houses from Monterey Bay, California. Mar Ecol Prog Ser 33:111–120

Davoll PJ, Youngbluth MJ (1990) Heterotrophic activity on appendicularian (Tunicata: Appendicularia) houses in mesopelagic regions and their potential contribution to particle flux. Deep Sea Res 37(2):285–294

Deibel D (1986) Feeding mechanism and house of the appendicularian *Oikopleura vanhoeffeni*. Mar Biol 93:429–436

Ducklow HW, Hill SM, Gardner ND (1985) Bacterial growth and the decomposition of particulate organic carbon collected in sediment traps. Cont Shelf Res 4(4):445–464

Ferrari FD, Steinberg DK (1993) *Scopalatum vorax* (Esterly, 1911) and *Scolecithricella lobophora* Park, 1970, calanoid copepods (Scolecitrichidae) associated with a pelagic tunicate in Monterey Bay. Proc Biol Soc Wash 106(3):467–489

Galt CP (1979) First records of a giant pelagic tunicate, *Bathochordaeus charon* (Urochordata, Larvacea), from the eastern Pacific Ocean, with notes on its biology. Fish Bull 77(2):514–519

Gardner WD, Hinga KR, Marra J (1983) Observations on the degradation of biogenic material in the deep ocean with implications on the accuracy of sediment trap fluxes. J Mar Res 41:195–214

Gaudy R, Baucher J (1983) Relation between respiration, excretion (ammonia and inorganic phosphorus) and activity of amylase and trypsin in different species of pelagic copepods from an Indian Ocean equatorial area. Mar Biol 75:37–45

Gnaiger E (1983) Calculation of energetic and biochemical equivalents of respiratory oxygen consumption. In: Gnaiger E, Forstner H (eds) Polarographic oxygen sensors. Springer-Verlag, Berlin, p 337–345

Goldman JC, Caron DA, Anderson OK, Dennet MR (1985) Nutrient cycling in a microflagellate food chain: I. Nitrogen dynamics. Mar Ecol Prog Ser 24:231–242

Gowing MM, Silver MW (1985) Minipellets: a new and abundant size class of marine fecal pellets. J Mar Res 43: 395–418

Gowing MM, Wishner KF (1986) Trophic relationships of deep-sea calanoid copepods from the benthic boundary layer of the Santa Catalina Basin, CA. Deep Sea Res 33: 939–961

Gowing MM, Wishner KF (1992) Feeding ecology of benthopelagic zooplankton on an eastern tropical Pacific seamount. Mar Biol 112:451–467

Hamner WM, Robison BH (1992) *In situ* observations of giant appendicularians in Monterey Bay. Deep Sea Res 39: 1299–1313

Harding GCH (1974) The food of deep sea copepods. J Mar Biol Ass UK 54:141–156

Hargrave BT (1971) An energy budget for a deposit feeding amphipod. Limnol Oceanogr 16(1):99–103

Honjo SH (1978) Sedimentation of materials in the Sargasso Sea at a 5,367 m deep station. J Mar Res 36:469–492

Ikeda T (1974) Nutritional ecology of marine zooplankton. Mem Fac Fish, Hokkaido Univ 22:1–97

Ikeda T, Skjoldal HR (1989) Metabolism and elemental composition of zooplankton from the Barents Sea during early Arctic summer. Mar Biol 100:173–183

Jackson GA (1993) Flux feeding as a mechanism for zooplankton grazing and its implications for vertical particulate flux. Limnol Oceanogr 38(6):1328–1331

Jacobsen TR, Azam F (1984) Role of bacteria in copepod fecal pellet decomposition: Colonization, growth rates and mineralization. Bull Mar Sci 35(3):495–502

Johannes RE (1965) Influence of marine protozoa on nutrient regeneration. Limnol Oceanogr 10:434–442

Jumars PA, Penry DL, Baross JA, Perry MJ, Frost BW (1989) Closing the microbial loop: dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion, and absorption in animals. Deep Sea Res 36(4): 483–495

Karl DM, Knauer GA, Martin JH (1988) Downward flux of particulate organic matter in the ocean: a particle decomposition paradox. Nature 332:438–441

Khripounoff A, Crassous P (1994) Particulate material degradation in sediment traps at 2000 m depth on the Meriadzeck Terrace (Bay of Biscay). Deep Sea Res 41(5/6):821–829

Lampitt RS (1978) Carnivorous feeding by a small marine copepod. Limnol Oceanogr 23(6):1228–1231

Lampitt RS (1992) The contribution of deep-sea macroplankton to organic remineralization: results from sediment trap and zooplankton studies over the Madiera Abyssal Plain. Deep Sea Res 39(2):221–233

Lampitt RS, Gamble JC (1982) Diet and respiration of the small planktonic marine copepod *Oithona nana*. Mar Biol 66:185–190

Legendre L (1990) The significance of microalgal blooms for fisheries and for the export of particulate carbon in the oceans. J Plankton Res 12:681–699

Lorenzen CJ, Welschmeyer NA, Copping AE, Vernet M (1983) Sinking rates of organic particles. Limnol Oceanogr 28(4):766–769

Newell RC, Lucas MI, Linley EAS (1981) Rate of degradation and efficiency of conversion of phytoplankton debris by marine micro-organisms. Mar Ecol Prog Ser 6:123–136

Parsons TR, Takahashi M, Hargrave B (1984) Biological oceanographic processes. Pergamon Press, Oxford

Pilskaln CH, Paduan JB (1992) Laboratory techniques for the handling and geochemical analysis of water column particulate and surface sediment samples. Monterey Bay Aquarium Research Institute, Tech Rep No. 92–9

Pilskaln CH, Paduan JB, Chavez FP, Anderson RY, Berelson WM (1996) Carbon export and regeneration in the coastal upwelling system of Monterey Bay, central California. J Mar Res 54(6):1149–1178

Pilskaln CH, Silver MW, Davis DL, Murphy KM, Gritton B, Lowder S, Lewis L (1991) A quantitative study of marine aggregates in the mid-water column using specialized ROV instrumentation. Oceans '91 Proceedings 2. Institute of Electrical and Electronics Engineers (IEEE), Piscataway, NJ, p 1175–1182

Pomeroy LR, Hanson RB, McGillivary PA, Sherr BF, Kirchman D, Deibel D (1984) Microbiology and chemistry of fecal products of pelagic tunicates: rates and fates. Bull Mar Sci 35:426–439

Raymont JEG (1983) Plankton and productivity in the oceans, Vol 2. Zooplankton. Pergamon Press, Oxford

Saiz E, Alcaraz M (1992) Enhanced excretion rates induced by small-scale turbulence in Acartia (Copepoda: Calanoida). J Plankton Res 14(5):681–689

Sasaki H, Hattori H, Nishizawa S (1988) Downward flux of particulate organic matter and vertical distribution of calanoid copepods in the Oyashio Water in summer. Deep Sea Res 35:505–515

Silver MW, Alldredge AL (1981) Bathypelagic marine snow: deep-sea algal and detrital community. J Mar Res 39: 501–530

Silver MW, Gowing MM (1991) The 'particle' flux: origins and biological components. Prog Oceanogr 26:75–113

Silver MW, Gowing MM, Brownlee DC, Corliss JD (1984) Ciliated protozoa associated with oceanic sinking detritus. Nature 309:246–248

Simon M, Alldredge AL, Azam F (1990) Bacterial carbon dynamics on marine snow. Mar Ecol Prog Ser 65:205–211

Smith DC, Simon M , Alldredge AL, Azam F (1992) Intense hydrolytic enzyme activity on marine aggregates and implications for rapid particle dissolution. Science 359: 139–142

Steinberg DK (1995) Diet of copepods (*Scopalatum vorax*) associated with mesopelagic detritus (giant larvacean houses) in Monterey Bay, California. Mar Biol 122(4): 571–584

Steinberg DK, Silver MW, Pilskaln CH, Coale SL, Paduan JB (1994) Mid-water zooplankton communities on pelagic detritus (giant larvacean houses) in Monterey Bay, California. Limnol Oceanogr 39(7):1606–1620

Taguchi S (1982) Seasonal study of fecal pellets and discarded houses of appendicularia in a subtropical inlet, Kaneoha Bay, Hawaii. Estuar Coast Shelf Sci 14:545–555

Taylor GT, Karl DM (1991) Vertical fluxes of biogenic particles and associated biota in the Eastern North Pacific: Implications for biogeochemical cycling and productivity. Global Biogeochem Cycles 5(3):289–303

Taylor GT, Karl DM, Pace ML (1986) Impact of bacteria and zooflagellates on the composition of sinking particles: an *in situ* experiment. Mar Ecol Prog Ser 29:141–151

Torres JJ, Childress JJ (1983) The relationship of oxygen consumption to swimming speed in *Euphausia pacifica*. 1 The effects of temperature and pressure. Mar Biol 74: 79–86

Turley C, Hughes DJ (1992) Effects of storage on direct estimates of bacterial numbers of preserved seawater samples. Deep Sea Res 39:375–394

Turley CM, Lochte K, Patterson DJ (1988) A barophilic flagellate isolated from 4500 m in the mid-North Atlantic. Deep Sea Res 35(7):1079–1092

Urrere MA, Knauer GA (1981) Zooplankton fecal pellet fluxes and vertical transport of particulate organic material in the pelagic environment. J Plankton Res 3:369–387

Uttal L, Buck KR (1996) Dietary study of the midwater polychaete *Poeobius meseres* in Monterey Bay, California. Mar Biol 125(2):333–343

Valiela I (1984) Processing of consumed energy. Marine ecological processes. Springer-Verlag, New York, p 177–218

Wishner KF, Gowing MM (1987) *In situ* filtering and ingestion rates of deep-sea benthic boundary-layer zooplankton in the Santa Catalina Basin. Mar Biol 94:357–366

Yayanos AA (1986) Evolutional and ecological implications of the properties of deep-sea barophilic bacteria. Proc Natl Acad Sci USA 83: 9542–9546

Youngbluth MJ (1984) Water column ecology: *in situ* observations of marine zooplankton from a manned submersible. In: Fleming NC (ed) Divers, submersibles, and marine science. Occasional Papers in Biology, Vol 9, Memorial Univ Newfoundland, p 45–57

This article was submitted to the editor

Manuscript first received: August 23, 1996
Revised version accepted: December 4, 1996