

Feeding by the euphausiid *Euphausia pacifica* and the copepod *Calanus pacificus* on marine snow

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ABSTRACT: Consumption and assimilation rates of marine zooplankton feeding on large, abundant aggregates, known as marine snow, were measured for the first time. Two common zooplankton species, the euphausiid *Euphausia pacifica* and the copepod *Calanus pacificus*, consumed diverse types of field-collected marine snow, including diatom flocs, abandoned larvacean houses, and dinoflagellate aggregates, regardless of their composition, C:N ratio, age, or the availability of alternate dispersed food. Ingestion rates of aggregates by *E. pacifica* increased with increasing marine snow concentration, although *in situ* concentrations of aggregates were not sufficient to elicit a maximum ingestion rate. Ingestion rates of aggregates by *E. pacifica* at higher aggregate concentrations were from 9 to 15 $\mu\text{g C euphausiid}^{-1} \text{ h}^{-1}$. Assimilation efficiencies of euphausiids grazing on marine snow were 83 % (dinoflagellate snow) and 64 to 75 % (diatom/larvacean house snow). These results indicate that marine snow can be an important food source for marine zooplankton and that consumption of large aggregates is likely to play a role in the cycling of carbon and the structure of food webs in the pelagic zone of the ocean.

KEY WORDS: Marine snow · Grazing · *Euphausia pacifica* · *Calanus pacificus*

INTRODUCTION

Organic aggregates >0.5 mm in diameter, known as marine snow, are formed by the coagulation of smaller particles such as phytoplankton and fecal pellets, or directly by gelatinous zooplankton as discarded mucous feeding structures (Alldredge & Silver 1988). Marine snow sinks rapidly from the surface ocean to the deep sea (100 to 1000 m d^{-1}), forming a crucial link in the ocean's carbon cycle (Fowler & Knauer 1986). It has been hypothesized that the observed decrease in particulate flux with depth may be partially caused by ingestion of sinking aggregates by macrozooplankton (Karl et al. 1988).

Aggregates can contain diverse microbial communities, including bacteria, flagellates and protozoans (reviewed in Alldredge & Silver 1988), as well as phytoplankton and fecal pellets. Marine snow is ubiquitous, and can comprise up to 63 % of the total particulate organic carbon in neritic waters (Alldredge & Silver 1988). Marine snow, therefore, represents a relatively large, localized concentration of edible material, suggesting that it is potentially an important food source for larger zooplankton (Alldredge & Silver 1988).

Direct evidence that macrozooplankton consume marine snow is rare. Most authors have inferred that zooplankton ingest marine snow from gut contents, but it is nearly impossible to distinguish marine snow from other sources of food in the water column (although see Lampitt et al. 1993 for an exception). Lampitt et al. (1993) demonstrated through gut content analyses and feeding experiments that the ostracods *Concoecia hadoni* and *C. lophura*, the copepods *Gaetanus pileatus*

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and *Oncaea* sp., and the amphipod *Themisto compressa* ingested aggregates in the mid-water zone in the North Atlantic. Another midwater organism, the polychaete *Poeobius meseres*, intercepted and consumed sinking particles, most likely including aggregates, in Monterey Bay, California, USA (Uttal & Buck 1996). Epipelagic polychaete larvae utilized marine snow as both a source of food and for transport (Shanks & Edmonson 1990, Bochdansky & Herndl 1992). Gut content analyses indicated that the copepod *Neocalanus cristatus* in the North Pacific and larvae of *Euphausia pacifica* in the Western Pacific fed on marine snow (Suh et al. 1991, Dagg 1993). Copepod nauplii, ostracods, cladocerans, pelecypods, and ascidian larvae have also been found to be associated with marine snow in the Gulf of Mexico (Green & Dagg 1997). A few species of copepods have been observed *in situ* feeding on a particular type of marine snow, larvacean houses, by several authors (Alldredge 1972, 1976, Ohtsuka & Kubo 1991, Steinberg et al. 1994, Steinberg 1995). *Oncaea mediterranea*, a poecilostomatid copepod, fed on larvacean houses in the laboratory as well (Alldredge 1972). Juvenile white mullet ingested marine snow made in the laboratory, and may supplement their diet with aggregates in the natural environment (Larson & Shanks 1996). Consumption rates of zooplankton on natural marine snow and the factors affecting those rates, however, have never been investigated.

We chose 2 common species of macrozooplankton abundant off the California coast, the euphausiid *Euphausia pacifica* and the copepod *Calanus pacificus*, to directly test whether they can consume marine snow. Euphausiids, particularly *E. pacifica*, are relatively large, abundant members of the plankton in the Southern California Bight (Brooks & Mullin 1983). Many species of euphausiids are omnivorous and exhibit plasticity in feeding mode, being able to filter-feed using 'compression filtration' or to feed raptorially on zooplankton (Hamner 1988, Price et al. 1988). Some species, such as *E. pacifica*, vertically migrate from depth to the surface each night to feed (Brinton 1967) and have the potential to decrease the abundance of large, rapidly sinking particles in the epipelagic zone. *C. pacificus* is one of the dominant copepod species in the Southern California Bight and also migrates vertically, although to a lesser extent than *E. pacifica* (Brooks & Mullin 1983). While *C. pacificus* is thought of primarily as a filter-feeding herbivore (Frost 1977), it can also feed raptorially on small zooplankton (Landry 1981).

The purpose of this study was to obtain direct evidence that zooplankton can feed on field-collected marine snow, to quantify ingestion rates, and to investigate some of the variables potentially affecting inges-

tion, including aggregate concentration, composition and age, and the availability of alternate dispersed food.

METHODS

Methodological rationale. A number of unique challenges had to be overcome in order to document and quantify feeding on natural marine snow. Marine snow is operationally defined as biogenic aggregates larger than 0.5 mm in diameter (Alldredge & Silver 1988). A particle defined as marine snow can include a variety of material of algal, microbial or animal origin, often reflecting the diverse components available in the water column that form it. Because of its heterogeneous character and similarity in composition to non-aggregated components of the water column, marine snow is usually almost impossible to distinguish in natural fecal pellet or gut content samples.

The main difficulty presented by the heterogeneous nature of marine snow is finding a standard method for measuring feeding rates. Traditional methods for measuring ingestion rate, including counting food particles or measuring chlorophyll before and after feeding, marking food with dye or polystyrene beads, and measurement of gut fluorescence, were attempted and subsequently rejected for various reasons. It was difficult to obtain a consistent relationship of aggregate size to either chlorophyll or marker particles such as polystyrene beads, and early attempts to video-tape aggregates before and after experiments to determine size changes were unsuccessful (Dilling unpubl. data). Thus, methods such as labeling food or estimating feeding rates from gut fluorescence were unsuccessful.

Because these more traditional methods to measure feeding rate on marine snow proved unsatisfactory, the less widely used method of fecal pellet production was used (Honjo & Roman 1978, Paffenhöfer & Knowles 1979). Production of fecal pellets clearly demonstrates feeding, and fecal pellets can be recovered and measured to quantify egestion, which can then be converted to ingestion if the assimilation efficiency is known. The disadvantage of this technique is that animals may ingest or break apart their own fecal pellets, resulting in an underestimation of feeding rate (Noji et al. 1991). The majority of experiments reported here are fecal pellet production experiments. Ingestion and assimilation efficiency were also directly determined in 2 direct ingestion rate experiments using POC (particulate organic carbon) concentration.

Collection of animals and marine snow. Larvae and adult *Euphausia pacifica*, adult *Calanus pacificus*, and samples of marine snow were collected on cruises in

the Santa Barbara Channel and off Point Conception, California, in 1990, 1993, 1994, and 1995 on the RVs 'Pt. Sur' and 'New Horizon'. Zooplankton were collected by vertical tows from 80 m using a 1 m diameter, 333 μm mesh net after nightfall (*E. pacifica*) or during both the night and day (*C. pacificus*). Both euphausiids and copepods were starved 12 to 24 h in 0.45 μm filtered seawater before being used in experiments.

Marine snow was collected by SCUBA divers using hand-held syringes capable of holding 10 to 50 aggregates per syringe (Alldredge 1991). Syringes containing marine snow were kept at 15°C up to a maximum of 6 h before use. Because collection tended to disrupt the aggregates, the contents of each bulk syringe were reaggregated in 285 ml centrifuge bottles containing 0.45 μm filtered seawater on rotating rollers as described by Shanks & Edmonson (1989). Aggregates usually re-formed within 2 h. The composition of aggregates was determined using light microscopy to identify the dominant components. Aggregates used in this study were categorized as diatom, dinoflagellate, or larvacean house, if one of these components was clearly dominant. If there was not a majority of any one component, the 2 main components were used to categorize the aggregate (e.g. diatom/larvacean) or the aggregates were categorized as miscellaneous. Aggre-

gates dominated by fecal pellets were not used in this study.

Experimental protocol. Several different experimental protocols were followed (see below and Table 1 for summary). The experimental set-up used depended on the animal (euphausiid or copepod) and the variable being manipulated (aggregate concentration, background particle presence/absence, age of aggregate). Specific experiments are described below, although all experiments contained common elements. Controls in each case consisted of animals alone, and aggregates alone, and were checked for the presence of fecal pellets. In all cases experiments were conducted in the dark in environmental chambers set to *in situ* temperatures (12 to 16°C). Euphausiids fed for 12 h overnight in darkness. *Calanus pacificus* fed from 4 to 12 h in darkness, but experiments were conducted during both the day and night. Most experimental treatments were run in triplicate, with the exception of experiments in April 1994, with 2 replicates of each concentration.

Aggregate concentration: Euphausiids and copepods were given a range of marine snow concentrations to determine the concentration at which the maximum feeding rate occurred. Experiments were conducted on several cruises (Table 1). Two series of

Table 1. Summary of experimental methods. Fecal pellets in experiments with copepods *Calanus pacificus* and juvenile euphausiids *Euphausia pacifica* were sized under the dissecting scope, and converted to carbon using factors in Silver & Gowing (1991). Fecal pellets in experiments with adult euphausiids were filtered onto pre-weighed 0.4 μm Nuclepore filters, dried at 60°C and weighed. [Agg.] = aggregate concentration

Type of experiment	Date	Container volume (l)	Back-ground seawater ^c	Species	No. of animals container ⁻¹	[Agg.] ($\mu\text{g C l}^{-1}$)	Type of aggs. ^e
Aggregate concentration	Sep 1994 ^a	4.3	F	<i>E. pacifica</i>	4	0–80	DT, L
	Dec 1994, Jun 1995	4.3	F	<i>E. pacifica</i>	4 or 6	0, 200–400	DN, DT/L
	Apr 1994 ^{a, b} , Jun 1995 ^{a, b}	0.05	F	<i>C. pacificus</i>	3	0–2,800 0–1,600	DT, L C
Dispersed food availability	Dec 1994	4.3	F, S	<i>E. pacifica</i>	6	380	DN
	Apr 1990 ^{b, d}	1	R, F	<i>E. pacifica</i>	4–7	(25) ^f	L
	Apr 1990 ^{a, b}	0.5	R, F	<i>C. pacificus</i>	5–6	(15) ^f	L
Aged aggregates	Apr 1994 ^{a, b}	0.05	R, F	<i>C. pacificus</i>	2	322 aged, 460 fresh	DT
Ingestion/assimilation efficiency	Dec 1994, Jun 1995	4.3	F, S	<i>E. pacifica</i>	4 or 6	200–400	DN, DT/L

^a Experimental containers were not rotated in these experiments. All other experiments used rotating containers
^b Animals were separated from their fecal pellets by 500 μm or 333 μm mesh (for euphausiids and copepods, respectively)
^c R = raw seawater, F = 0.45 μm filtered seawater, S = 100 μm screened seawater
^d Juvenile euphausiids were used in this experiment; all others were adult *E. pacifica*
^e L = larvacean houses, DT = natural diatom aggregates, DN = dinoflagellate aggregates, C = aggregates generated from cultures of *Nitzschia angularis*
^f Number of aggregates per container; no carbon estimate available

experiments were conducted with euphausiids: one with a range of snow concentrations approximating *in situ* conditions, and one with a snow concentration near and above *Euphausia pacifica*'s critical food concentration, as measured in carbon (Ohman 1984). Both diver-collected marine snow and aggregates formed from diatom cultures were fed to animals. To generate diatom aggregates in the laboratory, *Nitzschia angularis* was grown in F/2 plus silica media using standard culture techniques (Guillard 1975), and aggregated in 285 ml centrifuge bottles on rotating rollers (Shanks & Edmonson 1989). The diatoms were used after 3 d growth (exponential phase) and after 10 d growth (stationary phase). Aggregates formed from diatoms in stationary phase had a higher carbon content.

Dispersed food availability: In order to measure the effect of suspended background food particles on ingestion by *Euphausia pacifica* adults and juveniles, and *Calanus pacificus* adults, aggregates were added to sea water processed in 2 different ways. In one treatment, sea water was screened through a 100 μm mesh to remove large particles, and in the other, sea water was filtered through a 0.45 μm cartridge filtration system (Table 1).

Aged marine snow: Natural diatom aggregates were collected in April 1994, and aged in the laboratory to determine the effect of aggregate age on feeding. The aggregates were split into 2 aliquots, one of which was fed immediately to *Calanus pacificus*, and the other used after it had been aged in the laboratory at 12°C for 8 d (Table 1).

Ingestion rate: Ingestion rate and assimilation efficiency were measured directly by measuring the change in POC concentration before and after an experiment with *Euphausia pacifica* adults and by quantifying fecal pellet production (Omori & Ikeda 1984). It was only possible to measure ingestion rate with this method in experiments with treatments using higher than natural concentrations of marine snow, because of the sensitivity of the CHN analyzer. Only 2 experiments could be conducted because of the limitations of SCUBA collection time.

Triplicate 2 l samples of seawater and aggregates at initial concentrations were filtered onto combusted 25 mm GF/F filters to estimate initial POC concentration (C_0). At the conclusion of the experiment fecal pellets were removed by screening and sorting. After fecal pellets were removed, aggregates and other debris (excluding molts) captured by the screen were combined with the entire contents of each bottle and filtered onto combusted GF/F filters. The entire bottle was filtered in each treatment, because aggregates were inhomogeneously distributed. Sorted fecal pellets were twice transferred by pipette into filtered seawater

to exclude as much non-fecal matter as possible, and then filtered onto GF/F filters. Rinse water used in the sorting of fecal pellets was added to filters containing entire bottle contents. All samples were dried at 65°C, and stored in a dessiccator before elemental analysis with a Leeman Labs Inc. CE CHN Analyzer (Model 440) and calculation of the egestion rate (E).

Ingestion rates (I) were calculated from these measurements for each bottle following the equations of Marin et al. (1986), assuming no growth in aggregate-only controls. It was also assumed that initial food concentration (C_0) was higher than the euphausiids' critical food concentration (C_c) for most treatments ($C_0 > C_c$) (Eq. 1), except in the lower concentration experiment in June 1995, where the assumption was $C_0 \leq C_c$ (Eq. 2):

$$I = \frac{V}{Nt} (C_0 - C_t) \quad (1)$$

$$I = \frac{V}{Nt} \ln(C_0 / C_t) C_0 \quad (2)$$

where V = volume of the experimental container, N = number of animals in the container, C_t = food concentration at the end of the experiment, and t = duration of the experiment (Marin et al 1986). Changes in the total amount of carbon in the treatments unrelated to ingestion by euphausiids were accounted for using the animal and seawater controls. Assimilation efficiencies (AE) were calculated using the formula, $AE = (I - E)/I$ for each bottle (Omori & Ikeda 1984).

Chemical analyses: At the end of experiments, animals were removed, rinsed onto pre-weighed 0.4 μm Nuclepore filters, and dried in a 65°C oven. The contents of the bottles were gently poured through a 35 μm mesh screen to collect fecal pellets. Fecal pellets were sorted under a dissecting microscope (6× or 25× magnification), rinsed in filtered seawater, and filtered onto pre-weighed 0.4 μm Nuclepore filters or GF/F filters if enough material was present. An amount of filtered seawater equal to the amount used in rinsing was also filtered and subtracted as a blank from the final pellet sample weight. Nuclepore filters were dried and re-weighed on a CAHN electrobalance (model 4600). GF/F filters were dried and analyzed for POC and PON (particulate organic nitrogen) with a Leeman Labs Inc. CE CHN Analyzer (Model 440) (Sharp 1991). For experiments with *Calanus pacificus* adults and *Euphausia pacifica* juveniles, fecal pellets were sized under the dissecting scope, and converted to carbon as described in Silver & Gowing (1991). Aggregates were filtered onto combusted GF/F filters, dried at 65°C, and analyzed for POC and PON (Sharp 1991). Dry weight samples were filtered onto pre-weighed Nuclepore filters, rinsed well with nanopure water, dried at 60°C, and weighed.

Table 2. *Euphausia pacifica*. Mean fecal pellet production of euphausiids feeding on each type of aggregate tested. Natural concentrations: maximum observed *in situ* concentrations; high concentrations: concentrations over 300 $\mu\text{g C l}^{-1}$. Values are mean \pm 1 SD

Date	Type of aggregate	Fecal pellet production ($\mu\text{g dry wt euph.}^{-1} \text{ h}^{-1}$)	Fecal pellet production ($\mu\text{g dry wt mg}^{-1} \text{ euph. h}^{-1}$)	Aggregate C:N (by weight)
Sep 1994 (natural concentrations)				
9 Sep	Diatom	0.5 ± 0.3	0.35 ± 0.3	13.14
10 Sep	Diatom	2.1 ± 1.7	0.55 ± 0.4	11.15
12 Sep	Larvacean houses	1.9 ± 0.5	0.36 ± 0.3	6.82
13 Sep	Diatom	1.1 ± 0.6	0.41 ± 0.2	4.7
14 Sep	Diatom	1.6 ± 1.3	0.32 ± 0.3	7.6
Dec 1994 (high concentrations)				
3 Dec	Dinoflagellate	11.3 ± 2.8	2.6 ± 0.6	8.0
4 Dec	Dinoflagellate	7.5 ± 3.1	2.1 ± 0.8	8.75
Jun 1995 (high concentrations)				
19 Jun	Diatom/larvacean	28.7 ± 6.7	2.6 ± 0.8	6.9

RESULTS

Both *Euphausia pacifica* and *Calanus pacificus* consumed all types of marine snow tested at high rates. Fecal pellet production successfully indicated feeding on all types of marine snow used. Controls containing animals incubated without marine snow did not contain fecal pellets, indicating that starvation time of animals before each experiment was adequate.

Aggregate concentration and type

At *in situ* concentrations of marine snow, *Euphausia pacifica* produced a maximum of 2.1 $\mu\text{g dry weight of pellets euphausiid}^{-1} \text{ h}^{-1}$ (Table 2). This was not a maximum fecal pellet production rate, however, since at higher marine snow concentrations, *E. pacifica* produced up to 28 $\mu\text{g dry weight of pellets euphausiid}^{-1} \text{ h}^{-1}$. These higher fecal pellet production rates may also have been due to factors such as the different types of snow, or physiological differences among animals. All aggregates tested were consumed, including diatom, aged diatom, larvacean, and dinoflagellate, regardless of type or C:N ratio (Table 2).

Fecal pellet production increased with increasing aggregate concentration in all experiments (Fig. 1); however, only 2 of the 5 experiments showed a statistically significant increase ($p < 0.05$ regressions plotted on Fig. 1). Although aggregates were visible at the conclusion of each 12 h experiment, in some experiments up to 30 % of the aggregates were likely consumed, based on calculations assuming a 70 % assimilation efficiency. It is therefore likely that these fecal pellet production rates (and by conversion, ingestion rates) were minimal estimates. At all aggregate concentrations, fecal pellet production was highly variable.

Calanus pacificus also ingested all types of natural aggregates tested, including diatom aggregates, larvacean houses and combinations of the two (Table 3). Maximum pellet production rates for feeding on natural marine snow ranged from 0.3 to 1.5 $\mu\text{g dry weight copepod}^{-1} \text{ h}^{-1}$. These are most likely maximum fecal pellet production rates for feeding on marine snow, since concentrations were well above critical concentrations and food supply never decreased significantly during the course of the experiments. Feeding rates on natural aggregates were highly variable (Fig. 2). The maximum fecal pellet production rate was approximately 1.5 $\mu\text{g dry weight copepod}^{-1} \text{ h}^{-1}$, and was reached at concentrations of diatom/larvacean house aggregates as low as 500 $\mu\text{g C l}^{-1}$.

Fecal pellet production rates for copepods feeding on aggregates made from cultures of *Nitzschia angularis* were less variable than for natural aggregates (Fig. 3). With the exception of one high value, fecal pellet production rates reached a maximum of approximately 1 $\mu\text{g dry weight animal}^{-1} \text{ h}^{-1}$. This maximum fecal pel-

Table 3. *Calanus pacificus*. Mean fecal pellet production of copepods feeding on each type of aggregate tested. Values are mean \pm 1 SD

Date	Type of snow	Fecal pellet production ($\mu\text{g dry wt copepod}^{-1} \text{ h}^{-1}$)	Aggregate C:N (by weight)
Apr 1994			
5 Apr	Diatom	1.1 ± 0.2	5.14
21 Apr	Diatom culture	1.9 ± 0.2	5.59
Jun 1995			
17 Jun	Diatom/larvacean	1.5 ± 0.9	5.8
19 Jun	Larvacean	0.3 ± 0.1	6.0
20 Jun	Diatom/larvacean	1.3 ± 0.7	7.7

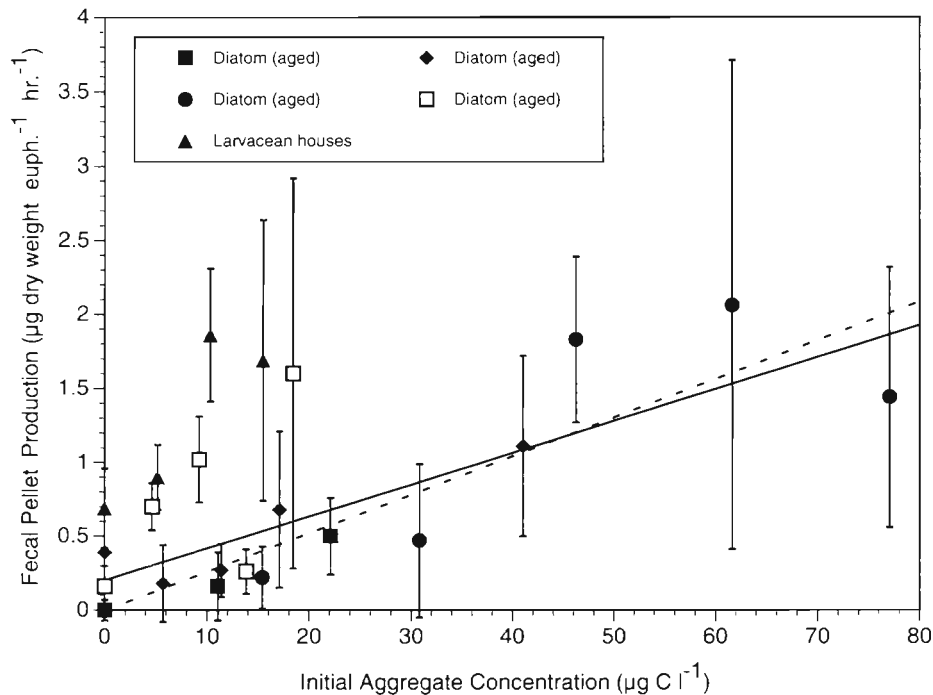


Fig. 1. *Euphausia pacifica*. Fecal pellet production of euphausiids feeding on natural marine snow in filtered seawater. Marine snow concentration spanned the range of typical *in situ* conditions. Symbols represent experiments conducted on separate days (aggregates were often of the same type from day to day, but components may have varied slightly, so experiments are represented separately). Values are mean \pm 1 SD, $n = 3$. Two experiments (indicated by \bullet and \blacklozenge) with aged diatom snow showed a significant increase in feeding rate with increasing concentration. Regression lines are plotted for these 2 experiments (\bullet with a dashed line: $y = 0.026x - 0.0024$, $r^2 = 0.73$, $p = 0.03$; \blacklozenge with a solid line: $y = 0.022x + 0.2$, $r^2 = 0.82$, $p = 0.03$)

let production rate was reached at an aggregate concentration of approximately $400 \mu\text{g C l}^{-1}$.

Dispersed food availability

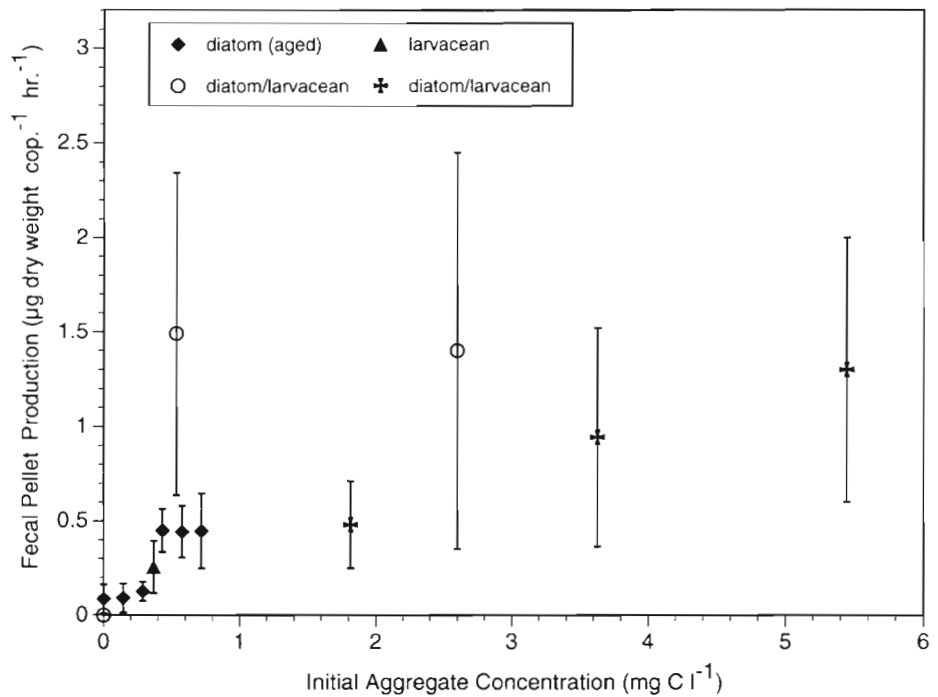
Ingestion of marine snow by euphausiids as measured by carbon was not significantly different in filtered seawater than in the presence of background particles less than $100 \mu\text{m}$ in size (Table 4). However, euphausiids produced significantly heavier fecal pellets (as measured by dry weight) in seawater containing background particles

than in filtered seawater (Fig. 4A). Production of fecal carbon was not significantly different in the 2 treatments; the carbon:dry weight ratio in fecal pellets was higher in the filtered seawater treatment, although this difference was not statistically significant ($p > 0.05$). The presence of background particles did not significantly affect fecal pellet production for larval euphausiids or *Calanus pacificus* (t -test, $p > 0.05$) (Fig. 4B, C). Fecal pellet production in seawater and filtered seawater alone was negligible in euphausiid adult and larvae experiments; some feeding did occur in the unfiltered treatment in the copepod experiment.

Table 4. *Euphausia pacifica*. Results of ingestion experiments using carbon as a measure of ingestion rate and assimilation efficiency. Values are mean \pm 1 SD

Type of aggregate	Seawater condition	Initial food conc. ($\mu\text{g C l}^{-1}$)	Animal weight (mg C)	Ingestion rate ($\mu\text{g C euph.}^{-1} \text{ h}^{-1}$)	Assimilation efficiency for C (%)	Clearance rates ($\text{ml euph.}^{-1} \text{ h}^{-1}$)
Dinoflagellate	100 μm screened	380	1.7 ± 0.2	13.5 ± 7	76 ± 20	35.5
Dinoflagellate	0.45 μm filtered	380	1.6 ± 0.1	15.2 ± 4	83 ± 2	40.0
Diatom/larvacean	0.45 μm filtered	200	5.3 ± 0.3	9.4 ± 4	64 ± 6	47.0
Diatom/larvacean	0.45 μm filtered	400	4.7 ± 0.6	11.3 ± 8	75 ± 2	28.2

Fig. 2. *Calanus pacificus*. Fecal pellet production of copepods feeding on natural marine snow in filtered seawater. Aggregate concentrations were higher than natural conditions. Values are mean ± 1 SD, $n = 3$

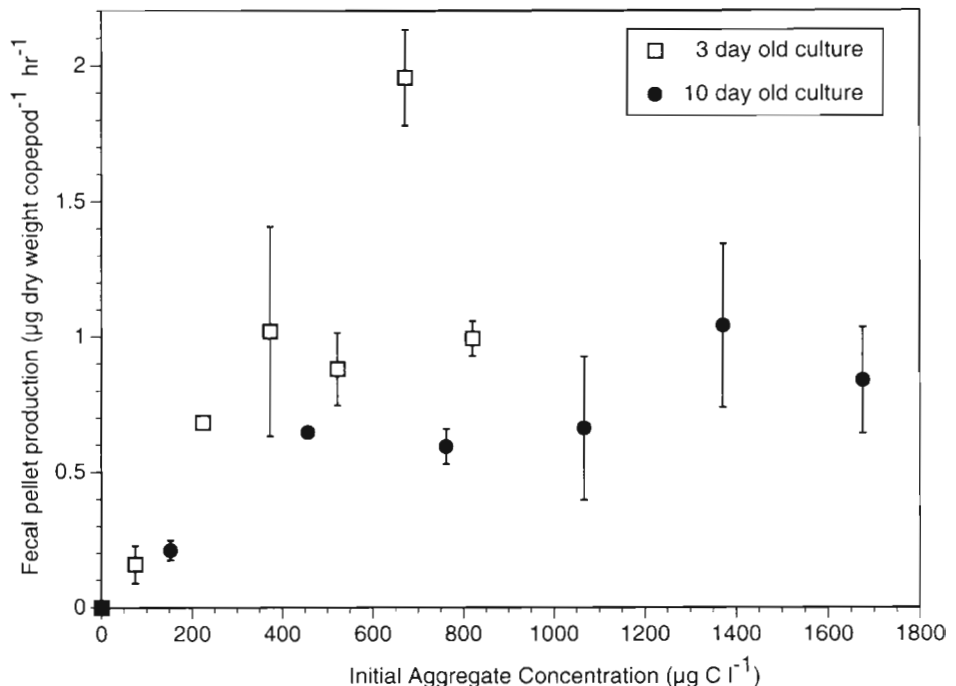


Aged snow

Calanus pacificus feeding on aged aggregates produced fewer pellets than when feeding on fresh aggregates, although these results were not statistically significant (t -test, $p > 0.05$, Fig. 5). Aggregate C:N ratio only increased slightly as a result of aging in the labo-

ratory, from 5.1 to 5.3 ± 0.2 . Ingestion in filtered seawater controls (without aggregates) was negligible in both aged and fresh marine snow experiments. Fecal pellet production was significantly higher in treatments with aggregates and filtered or raw seawater than without aggregates (t -test, $p < 0.05$), indicating that the great majority of fecal pellet production was

Fig. 3. *Calanus pacificus*. Fecal pellet production of copepods feeding on aggregates formed from cultures of *Nitzschia angularis* in the laboratory. Aggregates were formed from cultures at Day 3 after inoculation and Day 10. Aggregate C:N ratio increased from 5.6 ± 0.4 to 6.5 ± 1.0 over the 8 d aging process. Values are mean ± 1 SD, $n = 3$



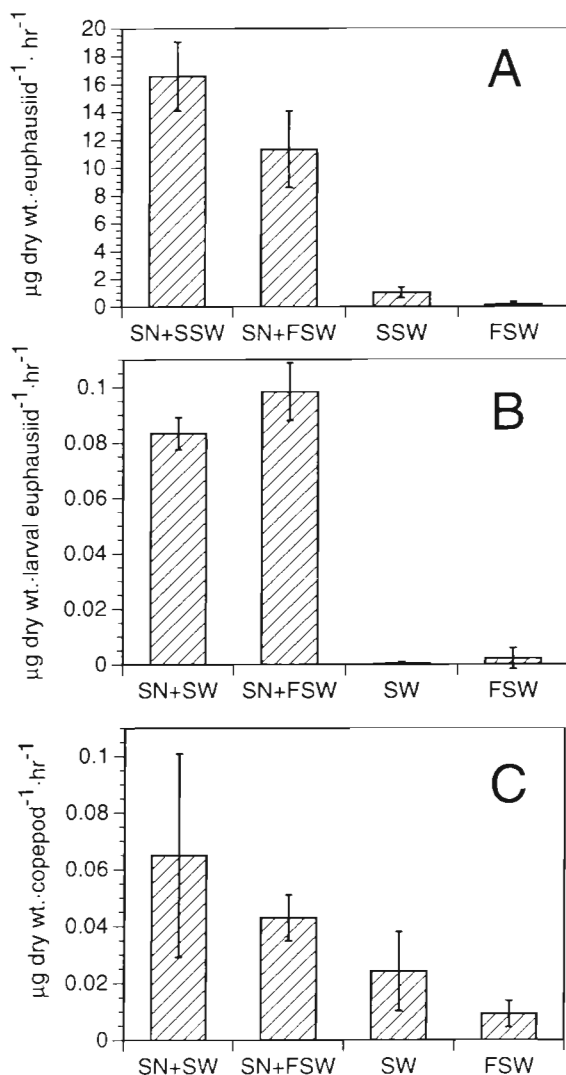


Fig. 4. Fecal pellet production by zooplankters under different background particle conditions. (A) Adult *Euphausia pacifica* feeding on dinoflagellate snow. (B) Larval *E. pacifica* feeding on larvacean houses. (C) Adult *Calanus pacificus* feeding on larvacean houses. SN: animals plus marine snow; SSW: 100 µm screened seawater; FSW: 0.45 µm filtered seawater; SW: un-filtered seawater. Values are mean \pm 1 SD, n = 2 or 3

due to feeding on marine snow. In the treatment with fresh marine snow, however, copepods produced almost as many fecal pellets in raw seawater alone as with aggregates present, suggesting that fecal pellet production in aggregate treatments was likely due to feeding on suspended material as well as marine snow. In the experiment with aged marine snow and raw seawater, however, feeding in seawater alone was negligible, implying that fecal pellet production in aggregate treatments was primarily due to feeding on aged aggregates (*t*-test, $p = 0.029$). Seawater was collected once at the beginning of both experiments, and stored in carboys at *in situ* temperature in the dark until used.

The difference in feeding in raw seawater alone between the 2 experiments was likely due to loss of edible suspended material in the water during its 8 d storage.

Ingestion rate

Ingestion rates of *Euphausia pacifica* feeding on marine snow as measured by POC ranged from 9 to 15 µg C euphausiid⁻¹ h⁻¹ (Table 4). There was a negligible change in POC in aggregate only controls, but quite a large increase, around 55 µg C l⁻¹, in bottles containing euphausiids but no snow. This increase was factored in when calculating ingestion rates. Since few or no fecal pellets were produced in controls with euphausiids and filtered or screened seawater only, it was assumed that all ingestion represented feeding on aggregates. Assimilation efficiencies ranged from 64 to 83%. Clearance rates ranged from 29 ± 15 to 47 ± 19.7 ml euphausiid⁻¹ h⁻¹ (Table 4).

DISCUSSION

Discussion of methods

While Alldredge (1972) used fecal pellet production to demonstrate feeding by copepods on marine snow, most other comparable studies in the laboratory have used either natural or artificial tracers to demonstrate consumption of marine snow (Bochdansky & Herndl 1992, Lampitt et al. 1993, Larson & Shanks 1996). Larson & Shanks (1996) obtained a consumption rate for juvenile mullet using artificial fluorescent polystyrene spheres; however, we found polystyrene spheres were incorporated into natural particles at a widely varying rate, and this method was judged to be not sufficiently quantitative for use with zooplankton. In addition, euphausiids appeared to be able to ingest even very small microspheres (1 µm) individually; thus it was not clear whether ingested microspheres came from marine snow particles or from individual suspended microspheres sloughed off into the water.

The fecal pellet production method used here was variable, however. Variation in feeding rates was high among replicates, both in experiments which measured fecal pellet production and in experiments which measured ingestion directly through changes in POC concentration. Several sources may account for this variability. First, initial food concentration was variable. At higher concentrations, the standard deviation of the mean initial food concentration was around 10%. At lower concentrations, the standard deviation was higher, sometimes reaching 40%. This variability is ex-

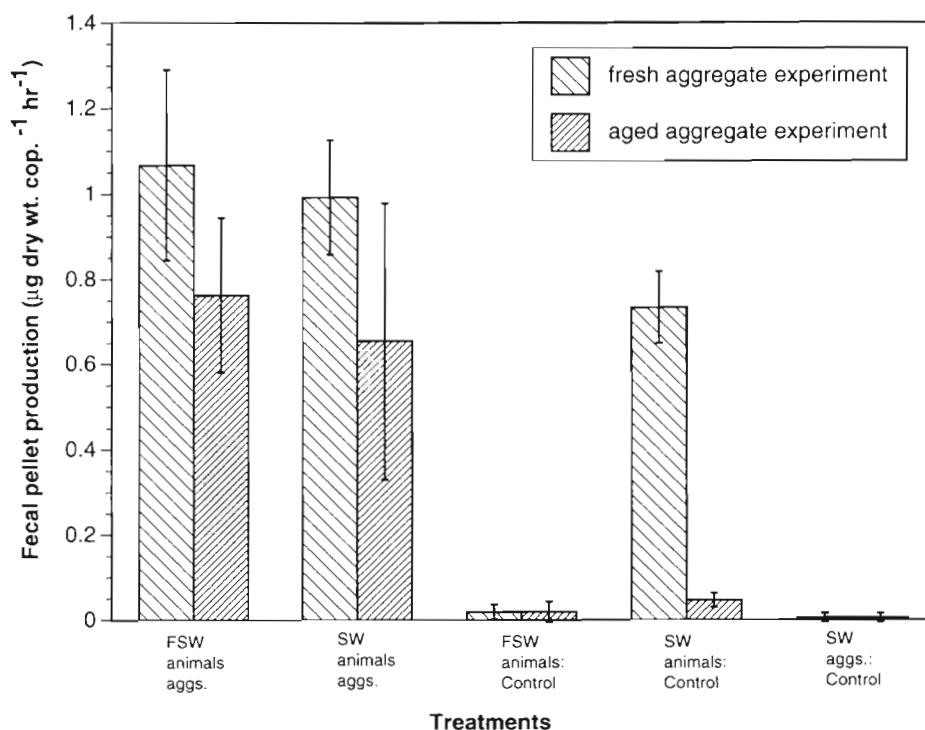


Fig. 5. *Calanus pacificus*. Fecal pellet production of copepods feeding on natural diatom snow immediately after collection and after aging in laboratory for 8 d. Values are mean \pm 1 SD, $n = 2$. SW: unfiltered seawater; FSW: 0.45 μ m filtered seawater

pected considering that marine snow is heterogeneous in size and density. Second, some variation occurred in animal size among replicates, although in most experiments the standard deviation of animal dry weight was less than 15%. Third, some error undoubtedly lay in the collection and sorting of fecal pellets; although pellets were robust, some pellets could have been missed. Finally, differences in animal behavior may have introduced variability in ingestion and fecal pellet production rates. With only 4 or 6 animals in a treatment, small differences between animals, hunger levels, or stage in molting cycle could have had a large effect (Lasker 1966). Molts were noted, but did not consistently correlate with expected depressed feeding rates. Sources of error involving animals could be reduced in future experiments by increasing the experimental vessel size and number of animals in each vessel, although these changes may introduce other problems.

Measuring fecal pellet production is labor-intensive because pellets must be sorted from remaining aggregates. Because only marine snow with low levels of fecal material was used in experiments, pellets could be clearly distinguished from aggregates. In addition, newly formed pellets could be easily distinguished from older pellets originally in aggregates because new pellets were compact and had intact membranes. Copepods are known to ingest their own or other species' fecal pellets (Noji et al. 1991), but there is little published work on coprophagy by euphausiids. As euphausiids were not separated from their pellets during

experiments, they may have ingested some of them during the course of the experiment. However, coprophagy and coprorhexy were not evident, since pellets examined after experiments were not fragmented and were still intact in membranes. In addition, experiments were short, and food was relatively abundant, so any effect was likely minimal. In any case, if some pellets were consumed or fragmented during the course of experiments, the fecal pellet production rates measured would be conservative estimates.

Measuring changes in carbon concentration over the course of an experiment was a satisfactory method of determining ingestion rate, giving statistically significant results despite high variability. One unexplained result was the increase in POC in controls containing animals but no snow. No fecal pellets were observed in those controls, and all molts and animals were recovered, but it is possible that small pieces of molts or other debris escaped attention.

Our results are most likely conservative estimates of ingestion on different types of marine snow, because confining containers may decrease ingestion rates relative to *in situ* conditions. Feeding rates for the Antarctic krill *Euphausia superba* were much higher in 50 l tanks compared to 5 l containers (Price et al. 1988). Increasing density of krill also negatively affected filtration rates (Morris et al. 1983). *E. pacifica* is much smaller than *E. superba*, however, and it is not known to what degree the 4.3 l bottles used in the experiments affected natural feeding rates.

Zooplankton consumption of marine snow

Our results provide the first direct evidence that *Euphausia pacifica* and *Calanus pacificus*, both important macrozooplankton in coastal California waters, ingest natural marine snow. Moreover, these data are the first determination of consumption rates of marine snow by any zooplankton species, and suggest that feeding on marine snow may be common in the field. Comparable studies are few. While *E. pacifica* seemed a likely candidate for ingesting aggregates (Suh et al. 1991) and indeed did consume marine snow at high rates, we did not anticipate that *C. pacificus* would ingest aggregates in such appreciable amounts. An earlier study by Paffenhöfer & Strickland (1970) found that *C. helgolandicus* (conspecific with *C. pacificus*; Frost 1977) did not ingest artificial aggregates generated by concentration of seawater collected below the euphotic zone. In contrast, our data demonstrate feeding by *C. pacificus* on marine snow, and support evidence that *C. pacificus* is a flexible omnivore (Landry 1981), able to take advantage of several different food sources: phytoplankton (Frost 1972), zooplankton (Landry 1981) and aggregates. Bochdansky & Herndl (1992) found that the calanoid copepod *Acartia clausii* did not consume aggregates of *Nitzschia closterium*; however, a different calanoid species, *Temora stylifera*, did graze on aggregates. While no previous studies have directly examined feeding by *E. pacifica* or any euphausiid species on aggregates, *E. pacifica* can graze on diatoms, fish larvae, artemia and copepods (Ohman 1984). Grazing on, and preference for, marine snow may thus depend on the species and its flexibility in feeding.

The difficulty in working with marine snow both in the field and the laboratory may be one reason why feeding on marine snow is not more commonly observed. Marine snow is a heterogeneous, fragile food source that is usually not easily identified in gut contents. Field observations have noted epipelagic harpacticoid copepods, euphausiid larvae, copepod nauplii, polychaete larvae, and nematodes (Alldredge 1972, 1976, Shanks & Edmonson 1990, Green & Dagg 1997, Shanks & Carmen 1997, Shanks & Walters 1997) and midwater copepods, crustacean nauplii, and amphipods (Lampitt et al. 1993, Steinberg et al. 1994) directly associated with marine snow aggregates. Relatively few studies have observed or collected calanoid copepods or euphausiids associated with aggregates. These organisms swim relatively rapidly, and encounters between these types of organisms and marine snow may be short-lived in the field. Even if feeding on an aggregate, these organisms may not stay in its vicinity for long, reducing the chance that it will be seen by a diver or sampled during aggregate collec-

tion. However, our data shows that euphausiids and calanoid copepods are able to consume marine snow at a high rate, suggesting that they may be doing so in nature.

Aggregates may serve as a supplemental food source in the Santa Barbara Channel. Larson & Shanks (1996) found that juvenile mullet consumed both marine snow and *Artemia* sp. in the laboratory, although marine snow alone was not sufficient for growth. Mullet have different feeding modes and nutritional needs than zooplankton; however, this suggests that marine snow may at least act as a supplemental food source, especially in regions of low food availability. *Euphausia pacifica* does ingest marine snow at natural concentrations—these concentrations are not sufficient, however, to elicit a maximum feeding rate. The critical concentration, or concentration of food above which ingestion rate is maximal, is around $300 \mu\text{g C l}^{-1}$ for *E. pacifica* grazing on diatoms (Ross 1982, Ohman 1984). The concentration of marine snow and even total POC off the coast of California is therefore typically lower than the critical concentration for *E. pacifica*. This suggests that *E. pacifica* may be generally food-limited *in situ*, and likely to take advantage of a variety of food sources, including marine snow.

Marine snow represents a previously underestimated food source because measurements of POC in the ocean using water bottles often miss rapidly settling particles, such as marine snow (Gardner 1977). The patchy distribution of marine snow may also lead to underestimates of its abundance. Marine snow tends to accumulate at density discontinuities and its abundance varies vertically in the water column (Lampitt et al. 1993, MacIntyre et al. 1995). Euphausiids can be vertically stratified based on prey concentration (Sameoto et al. 1987) or water column structure (Barange 1990), suggesting that euphausiids may be able to cue in on regions of high marine snow abundance.

The mechanism used by euphausiids for capture and ingestion of aggregates is not known. In the laboratory, we have observed euphausiids with large aggregates protruding from their feeding basket, suggesting that the animals do not necessarily break apart aggregates before capture. Jørgensen (1966) found that euphausiids use suspension feeding to capture cells less than $50 \mu\text{m}$ in size, and raptorial feeding for cells greater than $50 \mu\text{m}$, or for zooplankton prey. Since marine snow is larger than 0.5 mm , it would likely be captured raptorially. Regardless of the mechanism of ingestion, results in this study indicate that euphausiids and copepods are able to ingest the components of marine snow aggregates.

Because of the nature of the experimental set-up, *Calanus pacificus* fed on aggregates in these experi-

ments in a 'benthic feeding mode.' Aggregates were not encountered freely suspended in the water column, but rather sitting on a mesh screen near the bottom of the experimental container. However, this benthic mode is likely commonly employed by small zooplankton feeding on marine snow in the field. Field observations have shown that zooplankton 'rest' on marine snow as it descends through the water column, grazing on the aggregate matrix as well as smaller organisms imbedded in the matrix (Alldredge 1972, Steinberg et al. 1994, Steinberg 1995). Marine snow thus provides a surface in an otherwise surface-free environment. In this context, zooplankton smaller than the size of aggregates are not filter feeding, but benthic feeding. Fecal pellet production rates in copepod experiments presented here, therefore, should be considered maximum potential consumption rates of marine snow, since the food source was greatly in excess, and encounter rates were maximized due to the small size of the container and the unchanging location of the aggregates on the bottom of each container.

Euphausia pacifica assimilated natural marine snow with relatively high efficiency, similar to efficiencies for feeding on diatoms. Assimilation efficiencies on dinoflagellate snow (83%) and diatom/larvacean snow (64 to 75%) were slightly lower than those Ross (1982) found for *E. pacifica* feeding on *Thalassiosira angustii* ($\approx 83\%$). Ross' experiments were conducted at concentrations higher than $375 \mu\text{g C l}^{-1}$ for adult euphausiids at 12°C . The 2 types of marine snow used in experiments measuring assimilation efficiencies may have been particularly edible. The first experiment used dinoflagellate aggregates, and the second used diatom/larvacean aggregates; both were high in chlorophyll and appeared to be relatively 'fresh' (recently formed). Assimilation efficiencies on more detrital, refractory aggregates would most likely be lower.

Euphausia pacifica ingested all types of aggregates regardless of food quality as measured by C:N ratio. In addition, ingestion rate did not appear to vary with other measures of food quality, including chlorophyll *a* or protein to dry weight ratios (Dilling & Alldredge unpubl. data). These results, coupled with the observation that the natural concentration of food is generally lower than *E. pacifica*'s critical concentration, suggest that *E. pacifica* will ingest marine snow regardless of food quality. In these experiments, we offered euphausiids and copepods one type of marine snow at a time, so preferences for higher quality food were not measured directly. These results do not preclude food quality from affecting aggregate ingestion rates in nature where food is abundant, or where a choice of dispersed cells or several types of aggregates are present. Sticky aggregates may also reduce feeding rates.

We have observed marine snow sticking to and clogging the feeding appendages and antennae of *E. pacifica* and *Calanus pacificus* in the laboratory.

Although the ingestion rate, critical concentration, and assimilation efficiency for *Calanus pacificus* grazing on aggregates remain to be determined, we can convert fecal pellet production rates from our experiments to ingestion rates. Assuming a 70% assimilation efficiency (approximated from Hassett & Landry 1990 for *C. pacificus* feeding on the diatom *Thalassiosira weissflogii*), ingestion rates range from 0.3 to $1.8 \mu\text{g C copepod}^{-1} \text{ h}^{-1}$ for natural marine snow. The wide range of the estimates may indicate varying assimilation efficiencies as well as ingestion rates themselves. For comparison, *C. pacificus* ingests diatoms at a rate of $1.1 \pm 0.06 \mu\text{g C copepod}^{-1} \text{ h}^{-1}$ at cell densities above the copepods' critical concentration (Frost 1972).

Feeding by macrozooplankton on marine snow has implications for our understanding of food webs in the pelagic zone. Natural marine snow supports a rich community of protozoans and microbes (Alldredge & Silver 1988). By ingesting marine snow, macrozooplankton including amphipods (Lampitt et al. 1993) and copepods (Alldredge 1972, Dagg 1993, Steinberg et al. 1994, Steinberg 1995) can prey on these microscopic taxa which are not efficiently captured as individuals. Marine snow thus constitutes a 'food chain short-cut' by which picoplankton-sized organisms can be consumed by macrozooplankton (Alldredge 1972, Lampitt et al. 1993). In addition, marine snow represents a concentrated 'package' of food, with 1 to 3 orders of magnitude more phytoplankton, bacteria or protozoa than in an equivalent volume of sea water (Alldredge & Silver 1988).

Sinking of marine snow is the primary mechanism by which carbon and other materials are transported from the euphotic zone to the deep ocean (Fowler & Knauer 1986). By grazing on marine snow, zooplankton can diminish the flux of large particles out of the euphotic zone and may contribute to the widely observed decrease in POC flux with depth (Karl et al. 1988). Vertically-migrating zooplankton such as *Euphausia pacifica* would also release much of the carbon consumed through respiration at depth. Midwater communities of organisms associated with sinking marine snow may also contribute to remineralization of POC (Steinberg et al. 1997).

In conclusion, we have found that many types of marine snow are consumed by *Euphausia pacifica* and *Calanus pacificus*. Our results support gut content and other *in situ* studies which suggest that marine snow can be an important food source for copepods and euphausiids in nature (Ohtsuka & Kubo 1991, Suh et al. 1991, Dagg 1993, Steinberg 1995). The consumption rate of marine snow *in situ* remains to be deter-

mined, however. Consumption rates of marine snow in nature most likely depend on a complex combination of factors including encounter rate, handling time, availability of alternative food and composition of the marine snow aggregates themselves. Marine snow is abundant in many areas of the world's oceans (Alldredge & Silver 1988), and the ability to take advantage of this resource may help zooplankton survive in a spatially and temporally patchy food environment.

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