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Production of dissolved organic carbon by sloppy feeding in the copepods *Acartia tonsa*, *Centropages typicus*, and *Temora longicornis*

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Abstract

With ^{14}C-labeled phytoplankton as tracer, dissolved organic carbon (DOC) produced by sloppy feeding was measured for three species of marine copepods (*Acartia tonsa*, *Centropages typicus*, and *Temora longicornis*) grazing on the differently sized phytoplankton (*Rhodomonas salina*, *Heterocapsa rotundata*, and *Ditylum brightwelli*). DOC production per prey cleared was not dependent on prey concentration, whereas the relative size of the prey was important. When the prey was more than 39 times smaller than the copepod (measured as equivalent spherical diameter) no DOC production by sloppy feeding was measured. When the prey was larger, the fraction of carbon cleared that was lost as DOC by sloppy feeding was a function of the copepod–prey size ratio. The DOC production by the three species could be predicted from a common regression.

On a global scale, the pool of dissolved organic matter (DOM) is of about the same magnitude as the atmospheric CO_2 (Siegenthaler and Sarmiento 1993). The major part of the DOM is present in the ocean and most is autochthonous, i.e., produced in the marine environment (Opsahl and Benner 1997). Ultimately, all the autochthonous produced DOM originates from phytoplankton. However, only about half the carbon requirement of the bacterioplankton can be met directly by extracellular release from phytoplankton (Baines and Pace 1991) and sources like virus lysis and protozooplankton and metazooplankton grazing therefore need to be taken into account (Nagata 2000).

Copepods have been shown to produce considerable amounts of DOM through sloppy feeding, leakage from fecal pellets, and excretion (Hasegawa et al. 2001; Møller et al. 2003; Steinberg et al. 2004). However, the possibility of predicting when the DOM production is of significance is still limited because of the scarcity of quantitative experiments. Excretion and leakage from fecal pellets are related to the quality and concentration of the food experienced by the copepod and operate to release elements in excess of requirements (Jumars et al. 1989; Anderson et al. 2005). In contrast, sloppy feeding is probably independent of these factors and has instead been suggested to depend on the shape and size of the prey (Møller 2005). This prediction is, however, based mainly on indirect evidence from literature data on apparent gross growth efficiency and copepod–prey size ratio.

In this study, dissolved organic carbon (DOC) produced by sloppy feeding is measured for three species of marine copepods *Acartia tonsa*, *Centropages typicus*, and *Temora longicornis* grazing on the differently sized phytoplankton *Rhodomonas salina*, *Heterocapsa rotundata*, and *Ditylum brightwelli* to test experimentally whether the size ratio between the copepod and its prey can be used to predict the DOC production by sloppy feeding.

Methods

Cultures—The phytoplankton *R. salina* (haptophyte), *H. rotundata* (dinoflagellate), and *D. brightwelli* (diatom) were cultivated at 18°C in a B1 medium prepared on filtered seawater (Hansen 1989). Silicate was added to the diatom medium. Light was provided by cool white fluorescent bulbs set on a 14 : 10 light : dark cycle. Irradiance was around 50–70 μmol quanta m^{-2} s^{-1}. To obtain phytoplankton labeled with ^{14}C, phytoplankton cultures were incubated for 3–4 d with $NaH^{14}CO_3$ at 740–1,480 kBq L^{-1} in air sealed bottles, allowing 4–5 doublings to ensure uniform labeling (Nielsen and Olsen 1989). Cohorts of the copepods *A. tonsa*, *C. typicus*, and *T. longicornis* were reared on *R. salina* or a mixture of *R. salina*, *H. rotundata*, and *Thalassiosira weissflogii* at 18°C.

Before each experiment copepods and phytoplankton were rinsed to reduce bacteria that could take up produced DOC and for the phytoplankton cultures to reduce the background level of DO^{14}C and DI^{14}C. Copepods were transferred twice to 0.2-μm filtered seawater to allow them to empty their guts 3–4 h before the experiment. Phytoplankton cultures were placed in a 600-mL chamber with a 2-μm filter in the bottom. The culture was drained until ~60 mL was left while it was gently stirred from above with a magnetic stirrer. The chamber was then filled with 0.2-μm filtered seawater and the procedure repeated three times causing ~1,000 times dilution of everything smaller than 2 μm. Even with this dilution some bacteria will unavoidably be left, and the DOC production by the copepods may therefore be considered a conservative estimate. The DO^{14}C : PO^{14}C ratio at the beginning of experiment was always below 0.05.

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Table 1. Size and concentration of phytoplankton used in the experiments. Organisms were sized for each experiment performed, but just the average is presented here.

Phytoplankton species	Length (μm)	Width (μm)	Volume (μm^3)	ESD (μm)	Experimental concentration (cells mL^{-1})
Rhodomonas salina	9	6	180	7	2,000–8,000
Heterocapsa rotundata	20	13	1,800	15	800–2,500
Ditylum brightwelli	63	25	31,000	39	150–600

Measurements—Samples for ^{14}C measurements were preserved with 0.5 mL of 23% formaldehyde. Inorganic ^{14}C was removed by adding 200 μL HCl (1 mol L^{-1}), leaving the vials without lids for 24 h prior to the addition of 10 mL of Packard Ultima Gold XR scintillation cocktail. The activity was assessed by liquid scintillation counting in LKB Wallac Rack Beta counter.

The sizes of phytoplankton and copepods were measured every time an experiment was performed. The phytoplankton linear dimensions were measured and cell volumes were estimated assuming simple geometric shapes (Table 1). The copepod length (Table 2) was measured and the biomass calculated on the basis of length-carbon regressions from the literature: *A. tonsa* from Berggreen et al. (1988), *T. longicornis* from Hay et al. (1991), and *C. typicus* from Klein Breteler et al. (1982), assuming the carbon content to be 50% of the dry weight. To convert copepod carbon to volume, a conversion factor of 0.13 pg C μm^{-3} (Berggren et al., 1988) was used. The sizes of the organisms are also expressed as the equivalent spherical diameter (ESD) calculated from the volume.

The isotopic activity of the samples (dpm) was converted to organic carbon (μgC) by dividing with the specific activity of the washed phytoplankton (dpm μgC^{-1}). The specific activity of the washed phytoplankton was calculated by dividing the measured activity in initial phytoplankton samples with the corresponding carbon content. The carbon content was obtained via phytoplankton counts and volume measurements converted to biomass according to the carbon-to-volume relationship for protist plankton provided by Menden-Deuer and Lessard (2000).

DOC production by sloppy feeding—DOC production by sloppy feeding was measured by individual short time incubations of *A. tonsa*, *C. typicus*, and *T. longicornis* with *R. salina*, *H. rotundata*, or *D. brightwelli* following the procedure described below. For *A. tonsa* experiments were carried out at 3–4 different concentrations for each phytoplankton species (Table 1), while for *C. typicus* and *T. longicornis* one concentration was used (~4,000 *R. salina* mL^{-1}, ~1,500 *H. rotundata* mL^{-1}, and ~300 *D. brightwelli* mL^{-1}). All experiments were carried out at 16–18°C.

Table 2. Size of copepods used in the experiments. Organisms were sized for each experiment performed, but just the average is presented here.

Copepod species	Length (μm)	ESD (μm)
Acartia tonsa	712	327
Centropages typicus	971	495
Temora longicornis	631	484

The rinsed phytoplankton suspension was distributed in 20-mL vials. Then two to three copepods were added to between six and ten of them. Another six vials served as controls; three were immediately stopped and three incubated for the same time as the copepod vials. With the copepods 1 mL of water was added. The same amount of water from the copepod culture but without copepods was added to the controls.

The experiments ran for 20–30 min, a time period short enough to avoid defecation by the copepods. To stop the experiment, the content of the vial was poured through a 200-μm screen to remove the copepods (and for the control to test the amount of phytoplankton removed by this procedure) and subsequently filtered on a GF/F filter under low vacuum pressure. The screen was rinsed twice and backwashed to a vial for measurement of ingestion and phytoplankton removed. The GF/F filter and the filtrate were measured for $PO^{14}C$ and $DO^{14}C$.

The average $PO^{14}C$ concentration ($PO^{14}C_{avg}$, dpm mL^{-1}) was calculated following the method of Frost (1972) simplified by Kiørboe et al. (1982) in the control ($PO^{14}C_{P\text{-}avg}$) and copepod-containing bottles ($PO^{14}C_{C\text{-}avg}$) from the POC concentration at the start ($PO^{14}C_{start}$) and the end ($PO^{14}C_{end}$) of the incubation:

$$PO^{14}C_{average} = \frac{PO^{14}C_{end} - PO^{14}C_{start}}{\ln(PO^{14}C_{end}) - \ln(PO^{14}C_{start})} \quad (1)$$

The $DO^{14}C$ production rate by phytoplankton, i.e., the amount of $DO^{14}C$ produced per $PO^{14}C$ per time ($DO^{14}C_P$, [dpm dpm^{-1}] h^{-1}) was calculated from the total $DO^{14}C$ production ($DO^{14}C_T$, dpm mL^{-1} h^{-1}) in the control bottles as

$$DO^{14}C_P = \frac{DO^{14}C_T}{PO^{14}C_{P-average}} \quad (2)$$

$DO^{14}C$ production by the copepods, i.e., the amount of $DO^{14}C$ produced due to grazing per unit volume of water per unit time ($DO^{14}C_C$, dpm mL^{-1} h^{-1}) was calculated taking into account the $DO^{14}C$ production by phytoplankton in the copepod-containing bottle:

$$DO^{14}C_C = DO^{14}C_T - DO^{14}C_P \times PO^{14}C_{C-avg} \quad (3)$$

It was tested whether the $DO^{14}C$ production was significant (*t*-test, $p = 0.05$). Any $DO^{14}C$ production by the copepods was then compared either to ingestion or to the amount of carbon removed from suspension (RFS). Ingestion rate (I),

i.e., the amount of ^{14}C-carbon accumulated in the copepod gut per volume of water per unit time (I, dpm mL^{-1} h^{-1}) was calculated from the isotopic activity of the copepods minus the activity recovered in phytoplankton in the control. RFS (dpm mL^{-1} h^{-1}) is equal to the ingestion (I) (=gut content) plus the DOC produced by grazing (DO^{14}C$_C$).

Control for adsorption/absorption and bacterial uptake of DOC—To control for any adsorption/absorption to the copepods or uptake of DOC by bacteria associated with the copepods in the sloppy feeding experiments two different experiments were performed. In one, the uptake/adsorption of ^{14}C from a 0.2-μm filtrate from a ^{14}C-labeled *R. salina* culture was evaluated. The experiment was carried out both with and without addition of unlabeled *R. salina* to test whether feeding affected the absorption/uptake. Each subset contained five 20-ml vials with three *A. tonsa* in each, while three others served as controls. After 0.5 h the samples were recovered on GF/F filters and radioactivity was measured following the procedure described above. In another experiment the bacterial production associated with *A. tonsa* was measured during 0.5-h incubations with ^{3}H-thymidine. Eight vials were filled with 0.2-μm filtered seawater; to five vials three *A. tonsa* were added, while the remaining three served as control. Neither of the two experiments showed any adsorption to the copepods or bacterial uptake, and no further data will be presented.

Results

The ingestion of *A. tonsa* increased at increasing prey concentration for all three phytoplankton species, and for *H. rotundata* and *D. brightwelli* it seemed that the ingestion saturated at the highest concentrations (Fig. 1). No DOC production could be measured when *A. tonsa* was grazing on the smallest phytoplankton *R. salina*, while the grazing on the larger species *H. rotundata* and *D. brightwelli* resulted in increased DOC production with increasing prey concentrations (Fig. 1). However, the prey concentration did not influence the size of the fraction of what *A. tonsa* cleared that was lost by sloppy feeding. Grazing on *H. rotundata* led to 10–19% loss of what the copepod removed from suspension, while a significantly higher loss of 27–36% (t-test, $p < 0.05$) was found when *A. tonsa* was grazing the largest species, *D. brightwelli* (Fig. 2).

As for *A. tonsa*, no DOC production was found when *T. longicornis* was grazing on *R. salina*, whereas the grazing on *H. rotundata* and *D. brightwelli* both led to approximately the same loss of 13% and 15% (not significantly different, t-test) (Fig. 2).

C. typicus did not graze *R. salina*. The grazing on *H. rotundata* and *D. brightwelli* caused a DOC production of 7% and 20% of what they removed from suspension, respectively (significantly different, t-test, $p < 0.01$) (Fig. 2).

Plotting all the data on relative DOC production against the size ratio (ESD : ESD) between the copepod and its prey showed that the size of the prey was clearly important for the DOC production. The largest prey caused the highest relative DOC production (Fig. 3). The relative DOC production by sloppy feeding (DOC$_{SF}$) could be predicted from the copepod–prey size ratio (SR, $8 < SR < 33$) by the regression:

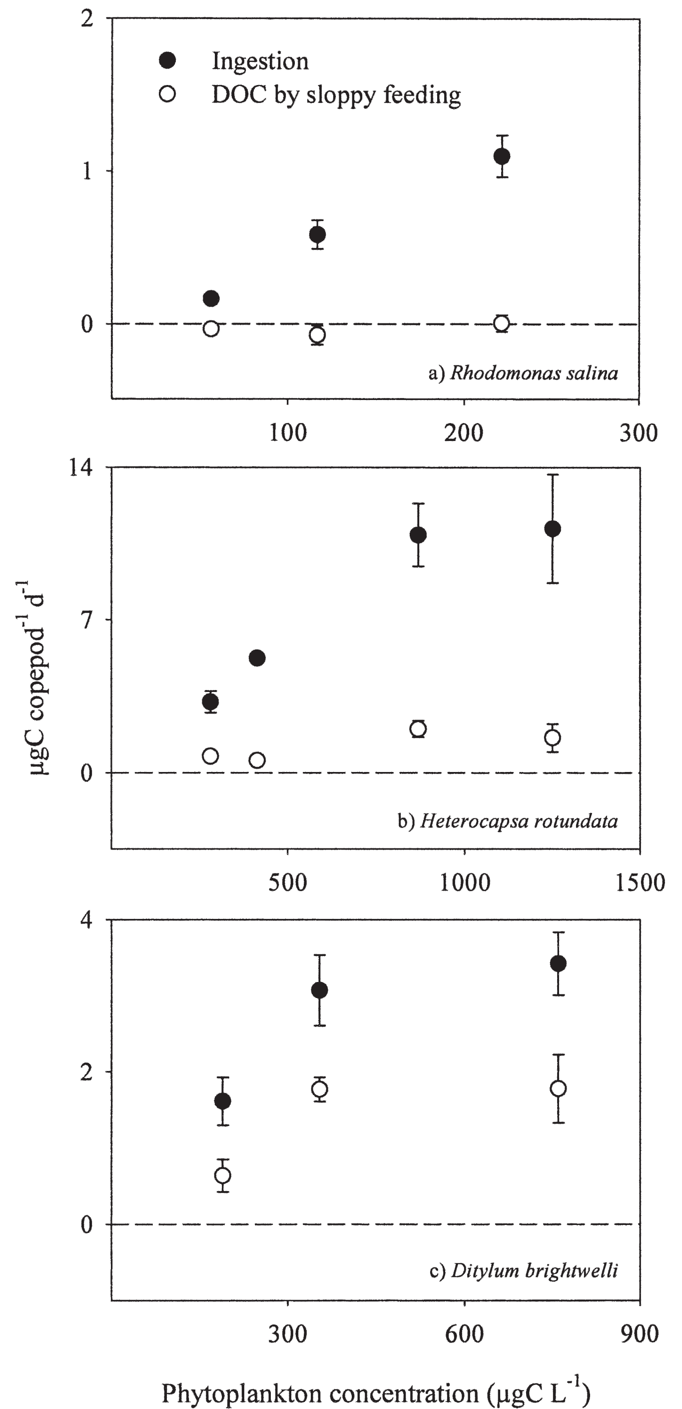

Fig. 1. POC ingestion and DOC production by sloppy feeding (±SE) by *A. tonsa* grazing on (a) *R. salina*, (b) *H. rotundata*, and (c) *D. brightwelli*.

$$DOC_{SF} = 0.368 \pm 0.038 - 0.009 \pm 0.002 \times SR, \quad r^2 = 0.70, p < 0.005 \tag{4}$$

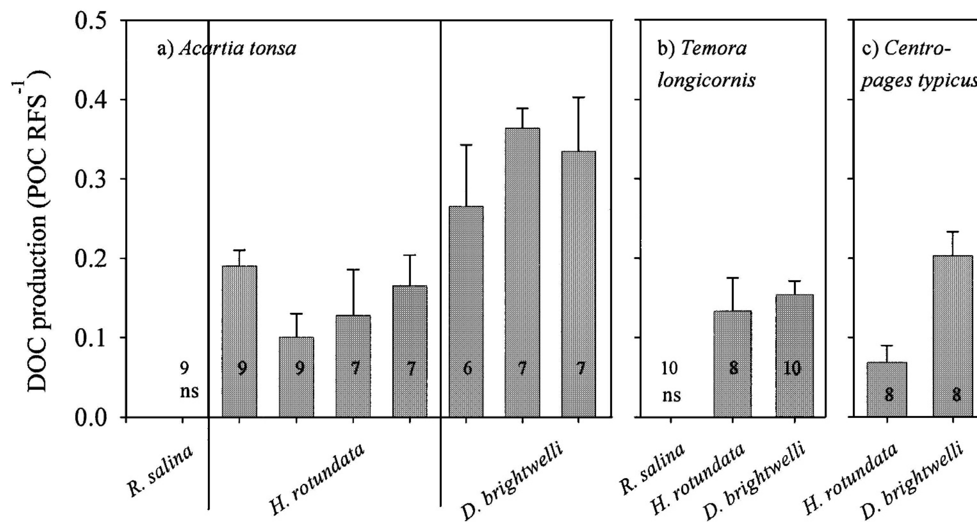

Fig. 2. DOC production by sloppy feeding as a fraction of POC removed from suspension (RFS) (±SE) by (a) *A. tonsa* (b) *C. typicus*, and (c) *T. longicornis* grazing on *R. salina*, *H. rotundata*, and *D. brightwelli*. Numbers on the bars are the number of samples in each experiment.

This regression was created using the data where DOC production was actually measured. If it is assumed that it is linear also for higher copepod–prey size ratios, it can be used to predict that above a copepod–prey size ratio of 39 there will be no DOC production by sloppy feeding. In agreement, the two measurements of no DOC production were both above this ratio (Fig. 3).

Discussion

The present study is the first to clearly demonstrate experimentally that the DOC production by sloppy feeding depends on the relative size of the prey. Until now only few quantitative studies of DOC production by copepods have been made (Roy et al. 1989; Strom et al. 1997; Møller and Nielsen 2001). Most did not separate the DOC production by sloppy feeding, leakage from fecal pellets, and excretion. Yet, copepods feeding on very large prey seem to produce large amounts of DOC (Roy et al. 1989; Hasegawa et al. 2001; Møller et al. 2003), while no DOC is produced when the prey is small relative to the copepod (Strom et al. 1997; Møller and Nielsen 2001). Generally, earlier estimates of DOC production have been somewhat higher than in the present study. *Calanus helgolandicus* grazing on prey 5.4 times smaller than itself lost 95% of what it cleared as dissolved and particulate debris, while *T. longicornis* was shown to lose 79% when the prey was 2.4 times smaller (Roy et al. 1989). *A. tonsa* lost ~60% as DOC when the prey was 25–30 times smaller than the copepod (Møller and Nielsen 2001). The latter study, however, did not measure DOC production directly, but recalculated increases in bacterial biomass to potential DOC production by assuming bacterial growth efficiency.

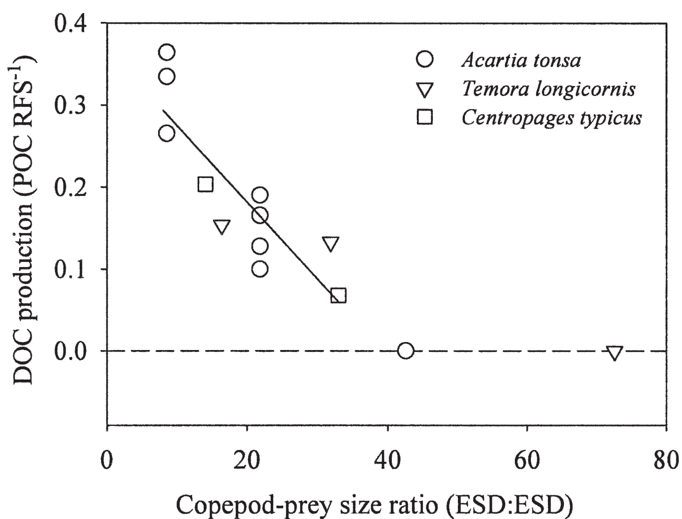

Fig. 3. DOC production by sloppy feeding as a fraction of POC removed from suspension (RFS) as a function of copepod–prey size ratio (ESD : ESD). For copepod–prey size ratios (SR) between 8 and 33 the relative DOC production by sloppy feeding (DOC_{SF}) could be predicted by the regression $DOC_{SF} = 0.368 \pm 0.038 - 0.009 \pm 0.002 \times SR$, $r^2 = 0.70$, $p < 0.005$.

Previously, an attempt has been made to predict DOC production by sloppy feeding indirectly from literature data on apparent gross growth efficiency ($GGE_{apparent}$) and copepod–prey size ratio (Møller 2005). This prediction and the one of the present study follow the same shape, although the predictions by Møller (2005) are considerable higher than the present ($DOC_{SF} = 0.714 - 0.013 \times SR$). The indirect prediction in Møller (2005), however, is based on two assumptions. The first assumption concerns the copepod–prey size ratio above which DOC is not produced by sloppy feeding, and was assumed to be 55 in Møller (2005). Secondly, in Møller (2005) it was assumed that all other factors than the size of the prey were optimal for the GGE in the studies used to create prediction, i.e., that the regression obtained from the collection of data on $GGE_{apparent}$ and the copepod–prey size ratio was not

below what could be considered a theoretical maximum. These two assumptions can be changed to evaluate whether Møller (2005) could have arrived at a result comparable to the actual measurements presented here. If the threshold copepod–prey size ratio is assumed to be the same as was actually measured in the present study (i.e., 39) and all measurements of $GGE_{apparent}$ are assumed to be below the theoretical maximum (i.e., assuming the intercept in Møller 2005 fig. 1 is three times higher) the prediction by Møller (2005) would have been $DOC_{SF} = 0.373 - 0.009 \times SR$. This prediction is not significantly different (*t*-test, $p < 0.01$) from the one of the present study (Eq. 4).

In the present study ESD has been used as a proxy for size. However, it is not likely that the size of the copepod determines the DOC production, but rather the dimensions of its mouth. Yet, the use of ESD produces a significant prediction of the DOC production for the three copepod species used. Moreover, it is a measure available from many other studies, therefore allowing evaluation of the potential DOC production in these. However, it could be speculated that copepods that are highly specialized for one prey type/size, e.g., purely carnivorous copepods, would have optimized their handling of the prey and that their DOC production, therefore, cannot be predicted by the general equation found in the present study. Another important factor for the generality of the prediction from the present study is the shape of the prey. In the present study the shape of the phytoplankton used were all more or less oval. However, the DOC production by sloppy feeding will not necessarily be the same if a prey with the same ESD was instead very elongated.

In addition to the DOC production by sloppy feeding, DOC will also be produced by excretion and leakage from fecal pellets (Urban-Rich 1999; Møller et al. 2003; Steinberg et al. 2004). The present study ran for only 20–30 min to minimize $DO^{14}C$ production by these sources, and visual inspection was carried out to ensure that no fecal pellets were produced during the experiment. Although production of $DO^{14}C$ by excretion cannot be completely ruled out, it is not likely to be large. If there had been a significant $DO^{14}C$ production by excretion, it should have been seen in the experiments when copepods were grazing *R. salina*. However, even though ingestion was evident, no $DO^{14}C$ production was measured. In general, there is no reason to believe that excretion and fecal pellet DOC production should be dependent on the copepod–prey size ratio, and the contribution from these in situ will therefore be relatively more important when prey cells are small.

When copepods lose some part of what they clear as DOC, it is obvious that it has implications for the food requirements of the copepods and for the food chain efficiency. Furthermore, it may also have an impact on the microbial community. The presence of zooplankton has been shown to increase bacterial productivity (Roman et al. 1988; Peduzzi and Herndl 1992; Hygum et al. 1997) indicating production of labile dissolved material. An evaluation of the potential importance of copepod-produced DOC to the total DOC pool and bacterial carbon consumption in situ can be made assuming, for instance, a typical concentration of 25 μg copepods L^{-1} and further assuming that they are grazing 50% their own body weight per day on prey 10 times smaller than themselves. The predicted DOC production would then be 3.5 μg C L^{-1} d^{-1}. In marine areas, DOC concentrations are between 1 and 5 mg L^{-1}, of which, generally, about 1/5 is labile (Søndergaard and Middelboe 1995). Hence, if DOC produced by sloppy feeding is primarily labile, the copepods could add less than 1% to the labile DOC pool each day. Compared to common levels of bacterial carbon consumption, in the range 3–13 μg C L^{-1} (del Giorgio and Cole 2000), a copepod DOC production of labile material of this order would, however, seem to be of significance. If, on the other hand, the copepod DOC production is not readily available for bacteria, the importance would seem to be minor.

Important questions in future investigations will be related to the quality of the different sources of copepod-produced DOM, e.g., lability, nutrient : carbon ratios, and optical properties, compared to other sources within the system (e.g., directly from phytoplankton or produced by protozooplankton grazing or viruses) and that produced outside (e.g., terrestrial) material.

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