

A comparison of carbon based ammonia excretion rates between gelatinous and non-gelatinous zooplankton: implications and consequences

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Abstract. About 560 literature data on weight-specific ammonia excretion rates of gelatinous zooplankton (cnidarians, ctenophores and salps) and non-gelatinous zooplankton (mainly crustacea) were converted to carbon based units to enable a better comparison between both groups. If carbon is used as body-mass unit ammonia excretion rates of gelatinous zooplankton are in the same range as values obtained for other zooplankton taxa, indicating a similar nitrogen output per unit of organic matter in both groups. These results suggest nutrient regeneration potential to be the same in gelatinous and non-gelatinous zooplankton, and that nutrient regeneration within the pelagic system depends more upon the carbon biomass ratio between gelatinous and other zooplankton than on physiological differences.

Introduction

It is well known that nitrogen is an essential element in phytoplankton primary production. This element is available to the algal cells mainly in the forms of $\text{NO}_3\text{-N}$ or $\text{NH}_4\text{-N}$, but the ratio between these components is quite variable. In situations like spring blooms nitrate will be the dominant N-donor, whereas in other seasons ammonia is more important. Dugdale and Goering (1967) termed primary production based on nitrate “new production”, “regenerated production” being associated with ammonia. In general, new production dominates turbulent systems, where nitrate is mixed from deeper water layers into the euphotic zone (e.g. spring blooms, upwellings, tidal mixed coastal areas). Regenerated production, which is mainly sustained by bacterial decay processes and the excretion of zooplankton, can be attributed to steady state conditions in pelagic systems (stratified summer situations, anticyclonic gyres and so on). A large body of literature deals with excretion rates of zooplankton and its relation to phytoplankton nutrient demands (e.g. Eppeley et al. 1973, Jawed 1973, Biggs 1977, Smith and Whitledge 1977, Smith 1978, Båmstedt 1985,

Verity 1985, Weisse 1985). Ammonia excretion of meso- and macrozooplankton sustains nitrogen requirements of primary production from a few percent to nearly 100%, depending on area and season.

Studies on mass-specific metabolic rates of different zooplankton groups show excretion of gelatinous zooplankton (cnidarians, ctenophores and salps) to be about one order of magnitude lower than in other taxa like copepods or euphausiids (e.g. Jawed 1973, Ikeda 1974) if dry weight is used as body-mass unit. The results of these studies imply gelatinous organisms to play a minor role in nutrient cycling within the pelagic system. However, we know carbon content (expressed as % of dry weight) to be much lower in gelatinous zooplankton compared with crustacea and other taxa (summarized in Schneider 1989a). When assuming organic content to be roughly twice the carbon content (Cushing et al. 1958), it can be calculated that in zooplankton, like copepods and euphausiids, 80 to 90% of dry material are organic matter and about 10 to 20% are inorganic salts. The reverse will be calculated for gelatinous zooplankton. Since the ratio dry weight : organic matter varies strongly between these different groups, dry weight is not a useful biomass unit when comparing physiological rates. Therefore, comparisons of metabolic rates of individuals with the same dry weight result in comparisons of different amounts of living matter. The aim of this paper is to compare ammonia excretion rates of gelatinous and non-gelatinous zooplankton on a carbon basis and to discuss some consequences.

Treatment of data

Data on ammonia excretion rates of zooplankton, including representatives of all major ocean regions, were taken from 21 articles published between 1975 and 1989. Table 1 lists all investigations used for this compilation, and provides some information on experimental conditions; Tables 2 and 3 give ranges and units of original measurements.

Prior to presentation of carbon-specific excretion rates, it may be useful to compare dry weight-specific rates of both zooplankton

groups (gelatinous and non-gelatinous zooplankton), showing the afore-mentioned difference in rates to be a general phenomenon. For this reason, data from 16 studies were converted to $\mu\text{mol NH}_4\text{-N g}^{-1}\text{ DW d}^{-1}$ (in the remaining five investigations, dry weight values of experimental individuals were not given). Since experimental temperatures were quite different (Table 1), all data were additionally standardized to 15°C using the well known Q_{10} law:

$$Q_{10} = (k_1/k_2)^{10/(t_1-t_2)},$$

Table 1. List of studies used for this contribution. Types of organisms investigated: (n) non-gelatinous zooplankton; (g) gelatinous zooplankton. Experimental temperatures (T °C) and duration of incubations (h) also given

Source	Type	T °C	Duration (h)
Polar waters (Arctic and Antarctic)			
Biggs (1982)	n	-1°, 10°	1 to 4
Ikeda and Bruce (1986)	n, g	-1.8° to -0.8°	24
Ikeda and Mitchell (1982)	n, g	-1.3° to -0.8°	24
Ikeda and Skjoldahl (1989)	n, g	-0.5° to 1.1°	24
Boreal and temperate waters			
Båmstedt (1985)	n, g	4° to 6°	5
Ikeda (1974)	n, g	4.3° to 17.5°	4 to 24
Jawed (1973)	n, g	11.5° to 15.2°	2 to 4
Kremer (1977)	g	10.4° to 24.5°	12 to 26
Kroll (1979)	n	10°	12 to 24
Schneider (1989b)	g	15°	17 to 27
Weisse (1985)	n	15°	4 to 18
Subtropical and tropical waters			
Biggs (1977)	g	26°	1 to 6
Cetta et al. (1986)	g	13.5° to 28.5°	1 to 8
Eppley et al. (1973)	n	20°	2
Ikeda (1974)	n, g	19.7° to 28.5°	4 to 24
Kremer (1982)	g	22°	3 to 10
Kremer et al. (1986)	g	25°	3 to 5
Muscantine and Marian (1982)	g	31°	1.5
Roger (1988)	n	12°, 17°	17
Verity (1985)	n	21° to 29°	2 to 3
Upwelling areas			
Smith (1978)	n	19°	4 to 6
Smith and Whitledge (1977)	n	17° to 22°	2 to 4

where k_1 and k_2 are metabolic rates corresponding to temperatures t_1 and t_2 , respectively. According to Ikeda (1985) a constant Q_{10} of 2 was used for all data.

The second step was to convert all data (from 21 publications) to $\mu\text{mol NH}_4\text{-N g}^{-1}\text{C d}^{-1}$. In nine studies (Ikeda 1974, Ikeda and Mitchell 1982, Kremer 1982, Verity 1985, Ikeda and Bruce 1986, Kremer et al. 1986, Roger 1988, Ikeda and Skjoldahl 1989, Schneider 1989b) carbon content of experimental specimens was actually measured. The obtained values were used to relate excretion rates to carbon body mass unit. An exception is the excretion rates of salps in Ikeda (1974) because no carbon data for salps are given. Therefore, an average carbon content of 8.1% of dry weight was assumed (Schneider 1989a). For conversions of rates of the ctenophore *Mnemiopsis leidyi* presented in Kremer (1977) the carbon content of this species (1.7% of DW) given in Kremer (1976) was adopted.

Excretion rates obtained by Biggs (1977), Muscatine and Marian (1982) and Båmstedt (1985) are based on protein as body-mass unit. Since both protein and carbon make up roughly one half of total organic matter each (Raymont 1983, Cushing et al. 1958, respectively), protein-based excretion rates can be equalized with carbon-based rates.

For dry weight-specific rates without further information on carbon content of experimental individuals, appropriate average conversion factors have to be used. Copepod data of Kroll (1979) were converted by assuming carbon contributing 46% of dry weight (Schneider 1989a), and for conversion of ammonia excretion rates of predominately non-gelatinous mixed zooplankton (Eppley et al. 1973, Jawed 1973, Smith and Whitledge 1977, Smith 1978, Weisse 1985) a carbon content of 40% of dry weight was used (Hårdstedt-Roméo 1982). The "jellyfish" data of Jawed (1973) were related to carbon with $C=9.7\%$ of dry weight (Schneider 1989a). The rates presented by Biggs (1982) are on a wet weight basis. To relate this to carbon we have to take into account that dry weight of non-gelatinous organisms amounts to 20% of wet weight (Omori 1969). Since carbon makes up 40% of dry weight, it will constitute 8% of wet weight.

The publication of Cetta et al. (1986) provides 11 regressions between individual ammonia excretion rates and individual carbon weights of salps. For each of these regressions I calculated two carbon specific excretion rates, one associated with a carbon weight of $500 \mu\text{g C ind.}^{-1}$ and one referring to a weight of $5000 \mu\text{g C ind.}^{-1}$. These weight values correspond roughly to the lower and upper limits of the regressions.

After conversion of original excretion values to carbon as body mass unit, all data were standardized to 15°C as described above. On the whole, for non-gelatinous zooplankton a total of 421 data, representing 1434 measurements were evaluated. For gelatinous

Table 2. Original ammonia nitrogen excretion rates of non-gelatinous zooplankton. Symbols are: (DW) dry weight; (WW) wet weight; (ind.) individual (dry weight of experimental individuals are given separately in the original sources); (prot.) protein. For number of data see Table 5

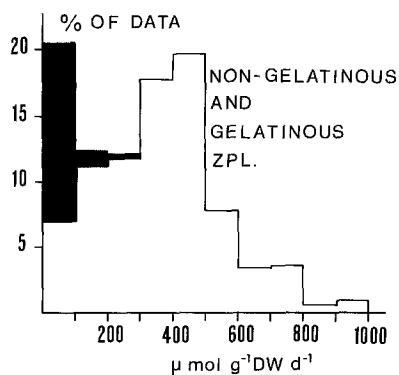
Zooplankton	Range	Original units			Source
Copepods	0.01 – 1.03	μg	$\text{mg}^{-1}\text{ DW}$	h^{-1}	Ikeda (1974)
Copepods	0.19 – 0.40	$\mu\text{g-at.}$	$\text{mg}^{-1}\text{ DW}$	d^{-1}	Kroll (1979)
Copepods	0.16 – 2.48	μg	ind.^{-1}	d^{-1}	Verity (1985)
Euphausiids	0.03 – 0.90	μg	$\text{mg}^{-1}\text{ DW}$	h^{-1}	Ikeda (1974)
Crustacea + 1 Cephalopod	0.36 – 4.09	μg	ind.^{-1}	h^{-1}	Ikeda and Bruce (1986)
Crustacea	0.08 – 0.20	$\mu\text{g-at.}$	$\text{mg}^{-1}\text{ DW}$	d^{-1}	Roger (1988)
Zooplankton	0.16 – 0.6	$\mu\text{g-at.}$	$\text{mg}^{-1}\text{ DW}$	d^{-1}	Jawed (1973)
Zooplankton	8 – 54	ng-at.	$\text{mg}^{-1}\text{ DW}$	h^{-1}	Eppley et al. (1973)
Zooplankton	0.002– 0.016	$\mu\text{g-at.}$	$\text{mg}^{-1}\text{ DW}$	h^{-1}	Smith and Whitledge (1977)
Zooplankton	0.016– 0.069	$\mu\text{g-at.}$	$\text{mg}^{-1}\text{ DW}$	h^{-1}	Smith (1978)
Zooplankton	0.2 – 6.1	$\mu\text{g-at.}$	$\text{g}^{-1}\text{ WW}$	h^{-1}	Biggs (1982)
Zooplankton	1.85 – 79.86	nmol	$\text{mg}^{-1}\text{ prot.}$	h^{-1}	Båmstedt (1985)
Zooplankton	0.02 – 10.28	μg	ind.^{-1}	h^{-1}	Ikeda and Mitchell (1982)
Zooplankton	0.98 – 9.75	μmol	$\text{g}^{-1}\text{ DW}$	h^{-1}	Weisse (1985)
Zooplankton	0.01 – 0.86	μg	ind.^{-1}	h^{-1}	Ikeda and Skjoldahl (1989)

Table 3. Original ammonia nitrogen excretion rates of gelatinous zooplankton. Symbols as in Table 2. For number of data see Table 6

Zooplankton	Range	Original units			Source
"Jellyfish"	0.02 – 0.06	$\mu\text{g-at.}$	$\text{mg}^{-1} \text{DW}$	d^{-1}	Jawed (1973)
Ctenophores, 3 species	1.0 – 1.2	μg	$\text{mg}^{-1} \text{prot.}$	h^{-1}	Biggs (1977)
2 species	4.76 – 22.87	nmol	$\text{mg}^{-1} \text{prot.}$	h^{-1}	Båmstedt (1985)
4 species	0.46 – 2.27	$\mu\text{g-at.}$	$\text{g}^{-1} \text{DW}$	h^{-1}	Kremer et al. (1986)
2 species	0.80 – 3.30	μg	ind.^{-1}	h^{-1}	Ikeda and Bruce (1986)
<i>Mnemiopsis leidyi</i>	9.9 – 35.6	$\mu\text{g-at.}$	$\text{g}^{-1} \text{DW}$	d^{-1}	Kremer (1977)
<i>M. maccradyi</i>	0.42 – 1.80	$\mu\text{g-at.}$	$\text{g}^{-1} \text{DW}$	h^{-1}	Kremer (1982)
<i>Beroe</i> sp.	2.213	μg	ind.^{-1}	h^{-1}	Ikeda and Mitchell (1982)
<i>B. cucumis</i>	0.022 – 0.025	μg	$\text{mg}^{-1} \text{DW}$	h^{-1}	Ikeda (1974)
Scyphomedusae, 2 species	0.2 – 1.2	μg	$\text{mg}^{-1} \text{prot.}$	h^{-1}	Biggs (1977)
<i>Aurelia aurita</i>	76	$\mu\text{g-at.}$	$\text{g}^{-1} \text{prot.}$	h^{-1}	Muscantine and Marian (1982)
<i>A. aurita</i>	28.8 – 94.4	μmol	$\text{g}^{-1} \text{DW}$	d^{-1}	Schneider (1989 b)
Hydromedusae, 3 species	0.4 – 1.5	μg	$\text{mg}^{-1} \text{prot.}$	h^{-1}	Biggs (1977)
2 species	0.031 – 0.074	μg	$\text{mg}^{-1} \text{DW}$	h^{-1}	Ikeda (1974)
<i>Aglantha digitale</i>	0.08	μg	ind.^{-1}	h^{-1}	Ikeda and Skjoldahl (1989)
Siphonophores, 2 species	0.027 – 0.063	μg	$\text{mg}^{-1} \text{DW}$	h^{-1}	Ikeda (1974)
21 species	0.1 – 2.7	μg	$\text{mg}^{-1} \text{prot.}$	h^{-1}	Biggs (1977)
<i>Diphyes antarctica</i>	0.11 – 0.24	μg	ind.^{-1}	h^{-1}	Ikeda and Bruce (1986)
Salps, 5 species	0.04 – 0.14	μg	$\text{mg}^{-1} \text{DW}$	h^{-1}	Ikeda (1974)
4 species	0.8 – 3.1	μg	$\text{mg}^{-1} \text{prot.}$	h^{-1}	Biggs (1977)
2 species	0.15 – 0.81	μg	ind.^{-1}	h^{-1}	Ikeda and Mitchell (1982)
7 species	0.01 – 1.00	$\mu\text{g-at.}$	ind.^{-1}	h^{-1}	Cetta et al. (1986)
<i>Salpa thompsoni</i>	2.31 – 4.33	μg	ind.^{-1}	h^{-1}	Ikeda and Bruce (1986)

Table 4. Dry weight-specific ammonia excretion rates of gelatinous zooplankton in the range 0 to 100 $\mu\text{mol NH}_4\text{-N g}^{-1} \text{DW d}^{-1}$ at 15°C (n =number of data; total=56 data; see also Fig. 1)

Range ($\mu\text{mol g}^{-1} \text{DW d}^{-1}$)	n	% of total
0– 25	23	41.1
>25– 50	19	33.9
>50– 75	7	12.5
>75–100	2	3.6
Total	51	91.1

**Fig. 1.** Frequency distribution of dry weight-specific ammonia excretion rates ($\mu\text{mol NH}_4\text{-N g}^{-1} \text{DW d}^{-1}$) of gelatinous (filled area) and non-gelatinous (open area) zooplankton. Excretion rates between 0 and 100 $\mu\text{mol NH}_4\text{-N g}^{-1} \text{DW d}^{-1}$ for gelatinous zooplankton are given in greater detail in Table 4. Total number of data: 354, 56 for gelatinous zooplankton and 298 for non-gelatinous zooplankton. Twelve data (=4% of total) are higher than 1000 $\mu\text{mol NH}_4\text{-N g}^{-1} \text{DW d}^{-1}$ and are not included in the figure

zooplankton 140 data (=718 measurements) were related to carbon as body-mass unit. Among the latter group 58 data (=41% of total) were derived from the publication of Biggs (1977), and all other data are from 12 investigations. This predominance of one investigation seems adequate for this compilation, since the study of Biggs (1977) is the most comprehensive one dealing with ammonia excretion rates of gelatinous zooplankton up to now.

Results and discussion

Dry weight-specific ammonia excretion rates of total zooplankton (gelatinous and non-gelatinous combined) range from 6 to more than 1000 $\mu\text{mol NH}_4\text{-N g}^{-1} \text{DW d}^{-1}$. As is evident from Fig. 1, the frequency distribution of all data shows two distinct peaks: one between 0 and 100 $\mu\text{mol NH}_4\text{-N g}^{-1} \text{DW d}^{-1}$ and a second one between 300 and 500 $\mu\text{mol NH}_4\text{-N g}^{-1} \text{DW d}^{-1}$. Filled areas in Fig. 1 indicate data obtained for gelatinous zooplankton. It appears that this group is responsible to a large extent for the first peak. The second peak is exclusively made up by rates of non-gelatinous zooplankton. Among gelatinous zooplankton 91% of all data are lower than 100 $\mu\text{mol NH}_4\text{-N g}^{-1} \text{DW d}^{-1}$, and 75% are lower than 50 $\mu\text{mol NH}_4\text{-N g}^{-1} \text{DW d}^{-1}$ (Table 4). Among non-gelatinous zooplankton only few data are below 100 $\mu\text{mol NH}_4\text{-N g}^{-1} \text{DW d}^{-1}$ and no data are below 50 $\mu\text{mol NH}_4\text{-N g}^{-1} \text{DW d}^{-1}$.

On the whole, the comparison demonstrates that excretion rates of gelatinous zooplankton appear to be generally much lower than rates of non-gelatinous zooplankton if dry weight is used as body-mass unit. In some cases, however, comparatively high rates can be found in the former and low rates in the latter. This is probably due to

Table 5. Carbon-specific ammonia excretion rates ($\mu\text{mol NH}_4\text{-N g}^{-1} \text{C d}^{-1}$) of non-gelatinous zooplankton standardized to 15°C. Symbols are: (DW) dry weight; (WW) wet weight; (C) carbon; (n) no. data representing n^* measurements

Zooplankton	n	n*	Excretion rate	Conversion to C	Source
Copepods	68	68	57–3727	C=measured	Ikeda (1974)
Copepods	91	91	717–1271	C=46% of DW	Kroll (1979)
Copepods	20	20	545–3005	C=measured	Verity (1985)
Euphausiids	25	25	117–1588	C=measured	Ikeda (1974)
Crustacea + 1 Cephalopod	11	107	75–742	C=measured	Ikeda and Bruce (1986)
Crustacea	10	247	188–643	C=measured	Roger (1988)
Zooplankton	27	27	459–1723	C=40% of DW	Jawed (1973)
Zooplankton	10	10	240–1620	C=40% of DW	Eppeley et al. (1973)
Zooplankton	4	49	227–4365	C=40% of DW	Smith and Whitledge (1977)
Zooplankton	17	271	9–5683	C=40% of DW	Smith (1978)
Zooplankton	60	60	181–2745	C=8% of WW	Biggs (1982)
Zooplankton	35	35	88–3832	C=protein	Båmstedt (1985)
Zooplankton	19	176	243–1191	C=measured	Ikeda and Mitchell (1982)
Zooplankton	11	183	311–4515	C=40% of DW	Weisse (1985)
Zooplankton	14	100	27–662	C=measured	Ikeda and Skjoldahl (1989)

Table 6. Carbon-specific ammonia excretion rates ($\mu\text{mol NH}_4\text{-N g}^{-1} \text{C d}^{-1}$) of gelatinous zooplankton standardized to 15°C. Symbols as in Table 5

Zooplankton	n	n*	Excretion rate	Conversion to C	Source
“Jellyfish”	4	4	240–721	C=9.7% of DW	Jawed (1973)
Ctenophores, 3 species	5	5	780–2319	C=protein	Biggs (1977)
2 species	3	3	230–1010	C=protein	Båmstedt (1985)
4 species	4	92	476–628	C=measured	Kremer et al. (1986)
2 species	3	19	110–390	C=measured	Ikeda and Bruce (1986)
<i>Mnemiopsis leidyi</i>	6	117	551–1047	C=1.7% of DW	Kremer (1977)
<i>M. mccradyi</i>	4	79	434–1437	C=measured	Kremer (1982)
<i>Beroe</i> sp.	1	1	330	C=measured	Ikeda and Mitchell (1982)
<i>B. cucumis</i>	3	3	334–379	C=measured	Ikeda (1974)
Scyphomedusae, 2 species	3	5	160–960	C=protein	Biggs (1977)
<i>Aurelia aurita</i>	1	1	602	C=protein	Muscantine and Marian (1982)
<i>A. aurita</i>	2	23	1006–1074	C=measured	Schneider (1989b)
Hydromedusae, 3 species	5	12	342–1371	C=protein	Biggs (1977)
2 species	4	4	77–693	C=measured	Ikeda (1974)
<i>Aglantha digitale</i>	1	8	158	C=measured	Ikeda and Skjoldahl (1989)
Siphonophores, 2 species	2	2	129–296	C=measured	Ikeda (1974)
21 species	36	135	80–2639	C=protein	Biggs (1977)
<i>Diphyes antarctica</i>	3	3	123–154	C=measured	Ikeda and Bruce (1986)
Salps, 5 species	15	15	359–1289	C=8.1% of DW	Ikeda (1974)
4 species	9	41	640–2479	C=protein	Biggs (1977)
2 species	2	16	700–776	C=measured	Ikeda and Mitchell (1982)
7 species	22	119	265–5319	C=500 and 5000 μg	Cetta et al. (1986)
<i>Salpa thompsoni</i>	2	18	421–543	C=measured	Ikeda and Bruce (1986)

similar carbon : dry weight ratios of some representatives of both groups. Some non-gelatinous organisms have a comparatively low carbon content, whereas in some gelatinous species carbon content is close to values reported from crustaceans (e.g. Ikeda 1974, Larson 1986).

For carbon based excretion rates the reader is referred to Table 5, Table 6 and Fig. 2. Rates range from 9 to 5683 $\mu\text{mol NH}_4\text{-N g}^{-1} \text{C d}^{-1}$ for non-gelatinous zooplankton (Table 5) and from 77 to 5319 $\mu\text{mol NH}_4\text{-N g}^{-1} \text{C d}^{-1}$ for gelatinous zooplankton (Table 6). Despite this large variability, most data (roughly 82%) of each

group are below 1250 $\mu\text{mol NH}_4\text{-N g}^{-1} \text{C d}^{-1}$ (Fig. 2), and the two frequency distributions of data are strikingly similar to each other. This indicates that ammonia excretion rates of gelatinous zooplankton are in the same range as other zooplankton if carbon is used as body-mass unit. Slight differences in the shape of the histograms are of minor importance in this context.

Thus, the large differences observed in dry weight-based excretion rates between both groups of zooplankton result simply from comparisons where a misleading body mass unit (dry weight) was used.

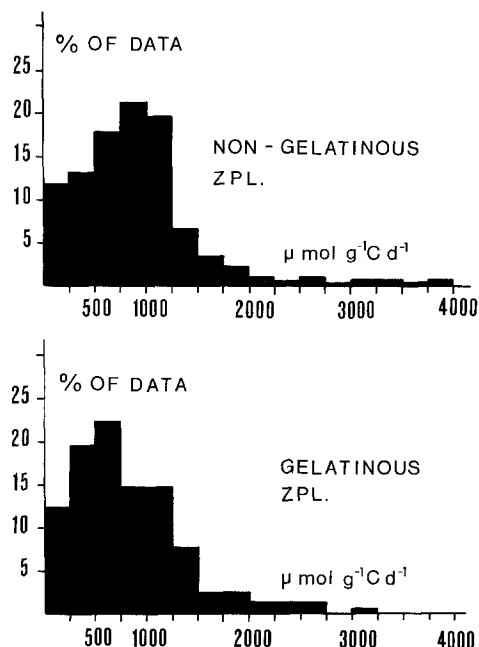


Fig. 2. Frequency distribution of carbon specific ammonia excretion rates ($\mu\text{mol NH}_4\text{-N g}^{-1} \text{C d}^{-1}$) of non-gelatinous (upper) and gelatinous (lower) zooplankton. Number of non-gelatinous data: 421, with 8 data (=1.9% of total) being higher than 4000 $\mu\text{mol NH}_4\text{-N g}^{-1} \text{C d}^{-1}$ which are not included in the figure. Total number of gelatinous data: 140, one of which (=0.7% of total) exceeds 4000 $\mu\text{mol NH}_4\text{-N g}^{-1} \text{C d}^{-1}$ and is not included in the figure

Ikeda and Mitchell (1982) reported euphausiid respiration to be 17 times higher than in salps on a wet weight basis and four times higher on a dry weight basis. Using carbon as body-mass unit, however, the ratio between euphausiid and salp metabolism becomes 0.8, which is close to unity. Ikeda (1985) pointed out that the choice of body-mass unit in mass-scaled metabolism studies influences the interpretation of results, and he stated explicitly that "carbon and nitrogen units reduce phylogenetic variability in metabolic rates". Thus, the rate of nutrient regeneration in the environment seems to depend primarily upon the carbon ratio between gelatinous and non-gelatinous zooplankton and less on physiological differences.

Since gelatinous organisms are generally larger than most non-gelatinous species, the similarity in carbon-specific excretion rates seems to be contradictory to the well known law of metabolism reduction with increasing body size. On the other hand, allometric exponents (usually abbreviated with "b"), relating weight-specific metabolic rates to individual weight, were found to be very close to unity in several studies (e.g. Krüger 1968, Kremer 1977, Kremer 1982, Kremer et al. 1986, Schneider 1989 b). Weight-specific metabolic rates of gelatinous species, therefore, seem to be independent of body weight. However, Biggs (1977) as well as Cetta et al. (1986) showed that allometric exponents of gelatinous zooplankton may be well less than 1 in one species or stage, but may be close to or larger than 1 in another species or stage. Moreover, Ikeda and Mitchell (1982) demonstrated that b-values may depend upon the body-mass unit. For example, salps have b-values for ammonia excretion of 0.682 and 0.685

on a fresh weight and dry weight basis, respectively, whereas values of 0.922 and 0.963 were obtained if carbon and nitrogen serves as body-mass unit. General conclusions on this topic are obviously difficult to obtain for gelatinous species. However, some variability may be introduced into the data sets by body-mass effects, and may partially explain the large range of data mentioned above.

Another source of variability in excretion rates is the nutritional state of experimental individuals. Kremer (1982) clearly showed that prestarved ctenophores excreted much less ammonia than individuals which were offered food during incubation, and the actual excretion rate depended upon the amount of food available. Similar observations are reported by Ikeda (1977) for non-gelatinous zooplankton.

Thus, actual excretion rates depend upon experimental conditions, i.e. the time-lag between catch of individuals and start of experiments (a few hours in most studies used for this contribution), incubation period (e.g. Båmstedt 1985), nutritional state in the environment (food-depleted versus rich food) and so on.

On the whole, the potential variability of excretion data are probably too small to interfere with the overall message of Fig. 2 that carbon-based ammonia excretion rates are in the same range for both groups of zooplankton. Additionally, existing variations may be averaged out when large numbers of data are compiled. However, the inherent variability prevents prediction of particular rates from carbon weight and temperature data.

To elucidate the role of gelatinous zooplankton in pelagic nutrient cycling, data on abundances, animal size and actual excretion rates are needed. Our knowledge about neritic systems is more complete than for oceanic regions, where there are generally more delicate species. Harbison et al. (1978) demonstrated by SCUBA diving that gelatinous zooplankton was more abundant than previously thought because delicate organisms are destroyed by conventional zooplankton sampling methods. In contrast, observations by Biggs et al. (1981) showed abundance of gelatinous plankton to be very low in oceanic waters. However, results from one study area do not hold true for another due to patchiness as well as seasonal variations. For example, Wiebe et al. (1979) reported the occurrence of dense swarms of *Salpa aspera* in American slope waters with an average biomass value of 9 mg C m^{-3} in the upper 100 m. In the Bering Sea regularly spaced rows of medusae with densities up to 1000 ind. m^{-3} were observed (Hamner and Schneider 1986), and a similar phenomenon was observed by the author off NW-Africa in spring 1983. Bathmann (1988) showed that salp carbon biomass outweighed that of all other zooplankton groups west of Ireland in spring 1984. Nonetheless, as summarized by Alldredge (1984), quantitative data on abundance of open ocean gelatinous plankton are rare and contradictory and, therefore, the role of coelenterates and salps in open ocean nutrient cycling remains unknown.

More reliable data are available for neritic areas. Mass occurrences of coelenterates and salps are known from earliest studies in marine science (e.g. Haeckel 1879,

Haeckel 1890). Recent observations are summarized by Alldredge (1984) and Purcell (1985). Salp swarms are also recorded by Fraser (1961), Binet (1970), Hubbard and Percy (1971) and Andreu-Puyal et al. (1975). Direct comparisons showed that, for example, scyphomedusae carbon biomass contributes a large portion (25 to 80%) of total metazoan zooplankton biomass at particular times (Shenker 1984, Van der Veer and Oorthuysen 1985, Schneider 1989b).

Taking into account the similarity of carbon-specific excretion rates among different taxa, ammonia regeneration by gelatinous organisms during swarm periods may be comparable to that of other zooplankton.

Explicitly, Kremer (1976) reported ammonia release of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, USA, to be similar to ammonia regeneration by all other zooplankton groups during the season when *M. leidyi* was most abundant. The same observation was reported by Schneider (1989b) for the scyphomedusae *Aurelia aurita* in Kiel Bight.

The few examples mentioned here may demonstrate that in neritic seas the role of gelatinous zooplankton in nutrient cycling can be as important as other zooplankton taxa. Therefore, more detailed investigations of population dynamics, spatial and seasonal variations of cnidarians, ctenophores and salps are needed in both, neritic and oceanic waters. They require more sophisticated standing stock estimations (SCUBA divers, submersibles), particularly in oceanic regions.

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