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Carbon, nitrogen and phosphorus stoichiometry of crustacean zooplankton in the Baltic Sea: implications for nutrient recycling

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Abstract. The carbon (C), nitrogen (N) and phosphorus (P) contents (% of dry weight) of some crustacean zooplankton were studied in the Baltic Sea. The copepod *Acartia* sp. had a stable C and N content (48.3 ± 0.8% C, 12.4 ± 0.2% N, C:N ratio 4.5 ± 0.1). The P content was variable (1–2%), probably depending on developmental stage and season. Copepods accumulating fat, like *Pseudocalanus minutus elongatus*, had higher and more variable C content (50–60%), and lower N and P content (7–12% N, 0.6–1.5% P). The highest C and lowest N and P contents were found in adult *Limnocalanus macrurus*. However, the N:P ratio was apparently independent of fat content and between 14 and 27 for all copepods. The cladocerans *Bosmina longispina maritima* and *Evadne nordmanni* had lower N content (9.3–10.8%) and higher C:N ratio (5.1–5.7) than *Acartia* sp. The P content (1.2–1.4%) was similar to *Acartia* sp. and the N:P ratios (16–19) were in the lower range of that found for the copepods. The N:P ratio was generally somewhat higher in the copepods than in seston, which most of the year had nearly Redfield C:N:P ratios. Potentially, nutrient recycling from crustacean zooplankton could enhance N limitation of phytoplankton, but small stoichiometric differences suggest that this effect is probably weak. The extent is dependent on the structure of the zooplankton community and the gross growth efficiencies. *Acartia* copepodites, which had nearly Redfield N:P ratios, would have the opposite effect and enhance P limitation in late summer when seston N:P ratios increased.

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Introduction

In planktonic food webs, zooplankton function both as a sink and a source for nutrients, by simultaneous incorporation into biomass and release of dissolved nutrients (e.g. Lehman, 1980). Stoichiometric theory predicts that differences in carbon:nitrogen:phosphorus (C:N:P) elemental ratios between zooplankton and their food should influence the relative role of zooplankton as a sink or source of N and P (Sterner, 1990; Sterner and Hessen, 1994). At maximal growth rate, phytoplankton C:N:P ratios are generally close to Redfield ratios ($C_{106}N_{16}P_1$) (Goldman, 1979), but can deviate substantially depending on the degree of nutrient limitation (Hecky and Kilham, 1988). The relatively stable elemental composition of zooplankton compared to phytoplankton (Hessen, 1990; Andersen and Hessen, 1991) means that they accumulate elements from the food in a relatively constant ratio. To maintain stoichiometric balance with a food that has a high C:N, C:P or N:P ratio, zooplankton must adjust their growth efficiency, so that the element in short supply is effectively incorporated, while elements in surplus are disposed of (Sterner, 1990). In this way, zooplankton may accentuate nutrient limitation of phytoplankton by being an effective sink for the element in greatest shortage (Hessen and Andersen, 1992).

Zooplankton with different body N:P ratios can be expected to differ in their relative rate of recycling of N and P (Sterner, 1990; Sterner *et al.*, 1992). Andersen and Hessen (1991) and Hessen and Lyche (1991) found large differences in P content between some freshwater zooplankton species. Herbivorous cladocerans,

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especially *Daphnia*, had a high P content and low N:P ratio, while copepods had lower P content and higher N:P ratios. This difference between copepods and cladocerans in elemental composition, and thus in expected recycling of N and P according to the stoichiometric model, has been suggested to explain observed shifts in the limiting nutrient in experiments and in the field (Elser *et al.*, 1988; Sterner *et al.*, 1992). The high N:P ratio recycled by *Daphnia* could also explain suppression of N fixation by cyanobacteria (MacKay and Elser, 1998), which are known to benefit from a low N:P ratio (Smith, 1983).

Only scarce data are available on P content, and thus N:P ratio, in zooplankton and especially copepods. While some data on marine species support the observations by Hessen and Lyche (1991) and Andersen and Hessen (1991), showing low P content and high N:P ratios in copepods (Mayzaud and Martin, 1975; Ikeda and Mitchell, 1982), others are contradictory (reviewed by Corner and Davies, 1971; Uye and Matsuda, 1988; Gismervik, 1997).

The aim of the present study was to evaluate whether there are stoichiometric differences between zooplankton and their food, and thus a potential for skewed recycling of N and P from zooplankton, in the brackish Baltic Sea. Content of C, N and P was measured in the common taxa of crustacean zooplankton, and in seston. In the Baltic proper, the phytoplankton community is usually N limited, and summer blooms of N-fixing cyanobacteria occur regularly (Granéli *et al.*, 1990). There is the possibility that the blooms are influenced by the recycling of an imbalanced N:P ratio from zooplankton, and that different zooplankton species could have contrasting effects. In the Baltic proper, copepods usually dominate the zooplankton community in terms of biomass (Hernroth and Ackefors, 1979). Especially abundant in the open sea are *Acartia bifilosa* and *Pseudocalanus minutus elongatus* (Viitasalo, 1992). In summer, the cladoceran *Bosmina longispina maritima* can become very abundant (Viitasalo, 1992). We have analysed the stoichiometry of major Baltic proper copepods and cladocerans during their main growth season, and in bulk seston as an indicator of food quality.

Method

Field collection

Zooplankton were collected with a WP2 net (90 μm) at three open-sea stations and two coastal stations (Table I) in the Baltic proper in 1995–1997. The plankton samples were transferred to 10 or 20 l containers filled with sea water from the sampling station, transported to the laboratory within 6 h, and stored in a cold room overnight (5°C) before sorting, or sorted immediately on board the vessel (stations BY15 and 030).

Seston samples were taken at station BY31 (Landsort Deep) in the Baltic Sea in 1998, with a time interval of 1–4 weeks, depending on season. Integrated samples were collected with 5 l water bottles at 0, 5, 10, 15 and 20 m depth, mixed, and filtered onto four pre-combusted and acid-washed Whatman GF/F glass fibre filters (duplicates for each analysis).

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Table I. Sampling stations

	Station	Position	Sampling depth	Station depth
BY31	Landsort Depth	58°35′N, 18°14′E	0–100 m	440 m
BY15	E. Gotland Depth	57°18′N, 20°04′E	0–100 m	250 m
030	S. Baltic proper	54°43′N, 12°47′E	0–20 m	22 m
B1	Askö	58°49′N, 17°36′E	h.t.	40 m
H4	Himmerfjärden Bay	58°59′N, 17°44′E	h.t.	40 m

h.t., horizontal tow (5–10 m depth).

Sorting procedure

In the laboratory, the zooplankton were concentrated on 90–250 µm sieves and placed in filtered sea water. Some samples were further separated using the positive phototaxis of the zooplankton (*Acartia* and *Eurytemora*). Using a stereomicroscope, different species or taxa were sorted with a suction pipette and temporarily placed in 5 ml containers with filtered sea water. If necessary, the zooplankton were narcotized with a few drops of carbonated water (*Acartia* and *Eurytemora*). Only live individuals were selected. Cladocerans trapped in the water surface were transferred onto a glass surface and a blunt needle was used to sort the cladocerans while they were still on the glass. If possible, copepods were separated by developmental stage, but sometimes mixtures of stages were needed to obtain sufficient material (Table II).

In some samples, the thoracic length of the copepods and maximum length of the cladocerans were measured under a stereomicroscope with ×10–40 magnification (precision ±0.01–0.05 mm), depending on the size of the animals.

When a sufficient number of animals had been obtained, they were collected on a fine plankton net and rinsed briefly with filtered sea water and deionized water to remove salts. From the net, the zooplankton were transferred with a needle to delicate pre-weighed tin capsules for C and N analysis. For P analysis, pre-weighed quarters of acid-washed GF/F filters (1995 samples) or similarly treated small coverslips (1996 and 1997 samples) were used.

Drying and weighing

Samples were dried at 60°C for at least 3 days, to a constant weight, and weighed on a Sartorius M3P microbalance (precision ±0.001 mg). Blank capsules, filters and coverslips were also weighed, but blank corrections were only necessary for the filters used in 1995. The weight of the samples ranged from 0.1 to 1 mg dry weight, but was usually between 0.2 and 0.5 mg. The number of animals weighed depended on their size and ranged from one (*Limnocalanus macrurus*) to around 200 (*B.longispina maritima*). Individual weight was estimated by weighing a known number of animals on coverslips.

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Table II. Carbon, nitrogen and phosphorus content of analysed zooplankton as a percentage of dry weight (±1 SD). Stations are described in Table I. Stage refers to copepodite stages, with the adult as stage VI. Numbers (*n*) are given for C/N, P, length and weight measurements. Numbers of weight determinations, as well as the mean number of individuals in each weight determination, are given in parentheses. All ratios are atomic. Length is thoracic length (copepods) or maximum length (cladocerans)

Species	Date	Station	Stage	C% ± SD (*n* C/N)	N% ± SD	P% ± SD (*n* P)	C:N	C:P	N:P	Length (mm) ± SD (*n*)	Weight (μg ind.$^{-1}$) ± SD (*n*)
Pseu.	Jan 97	BY31	IV	53.9 ± 1.0 (13)	10.4 ± 0.3	–	6.0	–	–	0.66 ± 0.06 (64)	3.4 ± 0.7 (4; 44)
	Jan 97	BY31	V	56.8 ± 0.1 (3)	9.0 ± 0.1	–	7.4	–	–	0.83 ± 0.07 (24)	8.4 (1; 35)
	April 97	BY31	V	55.2 ± 0.8 (2)	10.2 ± 0.4	1.18 ± 0.03 (2)	6.3	121	19	0.82 ± 0.04 (16)	9.0 (1; 30)
	April 97	BY31	VI female	49.7 ± 0.7 (9)	12.3 ± 0.2	1.52 ± 0.07 (9)	4.7	84	18	0.98 ± 0.07 (39)	10.1 ± 0.7 (18; 15)
	Aug 96	BY15	III–IV	60.1 ± 1.2 (6)	8.3 ± 0.4	0.82 ± 0.02 (7)	8.4	188	22	0.69 ± 0.11 (34)	–
	Sep 95	BY31	IV–V	58.3 ± 1.4 (11)	7.4 ± 1.5	0.63 ± 0.03 (12)	9.6	240	26	–	20.0 (1; 30)
	Oct 96	BY31	IV–V	60.0 ± 0.7 (5)	7.0 ± 0.2	0.80 ± 0.05 (4)	10.0	195	20	–	–
Limn.	Sep 95	BY31	VI	62.5 ± 1.2 (8)	5.3 ± 0.5	0.43 ± 0.05 (5)	13.8	373	27	–	106 (1; 3)
	Oct 96	BY31	VI	64.2 ± 2.5 (12)	5.3 ± 0.3	0.57 ± 0.08 (6)	14.2	289	20	1.91 ± 0.18 (18)	154 ± 52 (18; 1)
Eury.	Sep 96	BY31	VI	48.5 ± 0.6 (5)	12.7 ± 0.2	1.37 ± 0.04 (4)	4.5	91	21	0.58 ± 0.05 (10)	–
	Oct 95	H4	IV–VI	49.1 ± 0.4 (10)	12.0 ± 0.2	1.05 ± 0.08 (10)	4.8	121	25	–	–
Acartia	April 97	B1	I–IV	48.7 ± 0.4 (5)	12.6 ± 0.1	2.02 ± 0.05 (6)	4.5	62	14	0.48 ± 0.08 (31)	1.6 ± 0.2 (3; 110)
	April 97	B1	IV–VI	49.0 ± 0.4 (11)	12.7 ± 0.3	1.95 ± 0.05 (14)	4.5	65	14	0.65 ± 0.10 (24)	2.8 ± 0.2 (3; 118)
	June 97	BY31	IV–V	48.4 ± 0.2 (2)	12.1 ± 0.1	1.70 ± 0.05 (2)	4.7	74	16	0.58 ± 0.07 (23)	1.9 ± 0.2 (2; 65)
	June 97	BY31	VI	47.9 ± 0.4 (6)	12.3 ± 0.2	1.33 ± 0.10 (5)	4.5	93	21	0.76 ± 0.04 (22)	4.8 ± 0.6 (4; 76)
	July 97	BY31	III–V	47.9 ± 1.3 (3)	12.4 ± 0.2	1.71 ± 0.03 (3)	4.5	73	16	0.49 ± 0.07 (29)	1.6 ± 0.2 (3; 117)
	July 97	BY31	VI	46.6 ± 0.3 (4)	12.2 ± 0.2	1.48 ± 0.04 (5)	4.4	81	18	0.68 ± 0.07 (29)	3.1 ± 0.1 (3; 103)
	Aug 96	BY15	VI	48.7 ± 1.3 (16)	12.6 ± 0.5	1.09 ± 0.18 (15)	4.5	116	26	0.65 ± 0.03 (8)	3.3 ± 0.3 (2; 65)
	Oct 95	B1	V–VI	49.1 ± 1.4 (16)	12.2 ± 0.7	1.24 ± 0.18 (19)	4.7	102	22	–	3.0 ± 0.1 (3; 110)
Bosmina	Aug 96	030	–	49.9 ± 0.8 (10)	10.2 ± 0.4	1.19 ± 0.05 (6)	5.7	109	19	–	–
	Aug 96	BY15	–	48.6 ± 0.8 (8)	10.6 ± 0.2	1.29 ± 0.02 (5)	5.4	98	18	0.39 ± 0.04 (8)	–
	Sep 96	BY31	–	49.4 ± 0.9 (3)	10.8 ± 0.2	1.27 ± 0.05 (5)	5.3	101	19	0.38 ± 0.06 (10)	2.1 ± 0.1 (2; 100)
	Aug 97	BY15	–	44.8 ± 1.0 (5)	9.8 ± 0.3	1.19 ± 0.03 (5)	5.3	97	18	–	2.2 ± 0.1 (2; 159)
Evadne	Aug 96	030	–	46.2 ± 0.8 (5)	9.3 ± 0.3	1.17 ± 0.04 (3)	5.8	102	17	–	–
	Aug 96	BY15	–	45.2 ± 1.1 (3)	10.3 ± 0.3	1.34 ± 0.03 (3)	5.1	88	17	0.70 ± 0.08 (6)	–
	Aug 97	BY31	–	42.5 ± 0.9 (3)	9.4 ± 0.3	1.29 ± 0.06 (2)	5.3	85	16	–	1.7

Pseu., *Pseudocalanus minutus elongatus*; *Limn.*, *Limnocalanus macrurus*; *Eury.*, *Eurytemora affinis.*

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Analyses

Carbon and N in zooplankton and seston were analysed in a CHN analyser (CHN-900, 600-800-300, Leco corporation), with EDTA as standard. Phosphorus was determined somewhat differently in 1995 and 1996–98. In 1995, the samples were digested in 5 ml persulphate solution (20 g l^{-1}, 1 h, 120°C) in 50 ml Pyrex flasks. In 1996–98, the samples were combusted (550°C, 2 h) before digestion in 6 ml persulphate solution in 15 ml glass tubes. Blanks were carried through the same procedure. Standards were prepared by adding stock phosphate solution to the persulphate solution before digestion. The digest was analysed for molybdate-reactive orthophosphate with a flow injection system (Lachat Instruments, QuikChem Method 31-115-01-3-A). Since neither of the methods used for P analysis dissolves the samples completely, they were tested against complete dissolution in acid (2 ml mixture of 25% concentrated H_2SO_4, 20% HNO_3 and 5% H_3ClO_4 by volume) heated to 355°C. The pre-combustion and acid digestion methods gave similar results, but the persulphate method without pre-combustion, used in 1995, gave a lower recovery (up to 10% lower) when sample size was large (>1 mg). We estimate the error for the samples analysed here, which were <0.4 mg, to be <5%.

Statistics

Non-parametric comparisons were made with the Mann–Whitney *U*-test, using Statistica software (StatSoft, Inc., 1998). Linear regression analysis was performed only for the N:P ratio versus carbon content, since C, N and P contents per dry weight are not independent.

Models for estimation of N:P ratio of nutrients recycled from zooplankton

The N:P ratio recycled by zooplankton was estimated using the equations formulated by Sterner (1990) and further described by Elser and Urabe (1999). The alternative model proposed by Schindler and Eby (1997) was also used.

In the model by Sterner (1990), the recycled N:P ratio is calculated by:

$$\mathrm{N{:}P}_{\mathrm{recycled}} = \mathrm{N{:}P}_{\mathrm{food}}/(1 - L) - \mathrm{N{:}P}_{\mathrm{zoopl}} \times \mathrm{L}/(1 - L) \text{ when } \mathrm{N{:}P}_{\mathrm{food}} > \mathrm{N{:}P}_{\mathrm{zoopl}}$$

and

$$\mathrm{N{:}P}_{\mathrm{recycled}} = \mathrm{N{:}P}_{\mathrm{food}} \times (1 - L)/(1 - L \times \mathrm{N{:}P}_{\mathrm{food}}/\mathrm{N{:}P}_{\mathrm{zoopl}}) \text{ when } \mathrm{N{:}P}_{\mathrm{food}} \le \mathrm{N{:}P}_{\mathrm{zoopl}}$$

where L is the 'maximum accumulation efficiency' of N or P (the fraction of N and P that is allocated to growth).

In the model by Schindler and Eby (1997), which was developed for fish, the recycled N:P ratio is described by:

$$\mathrm{N{:}P}_{\mathrm{recycled}} = (K_2 \times \mathrm{N{:}C}_{\mathrm{food}} - K_1 \times \mathrm{N{:}C}_{\mathrm{zoopl}})/(K_2 \times \mathrm{P{:}C}_{\mathrm{food}} - K_1 \times \mathrm{P{:}C}_{\mathrm{zoopl}})$$

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where K_2 is the assimilation efficiency (fraction of ingested nutrients not lost in faeces) and K_1 is the gross growth efficiency (growth/consumption). In this form, nutrients in the faeces are excluded and the $N:P_{recycled}$ is the ratio of excreted nutrients. For simplicity, we set $K_2 = 1$ to look at the N:P ratio of totally recycled nutrients, as in Sterner (1990).

Results

Zooplankton

Four of the dominant copepods and two of the cladocerans in the Baltic proper were analysed for C, N and P content (Table II). Sampling was concentrated to summer and autumn due to the pronounced seasonal occurrence of zooplankton (Viitasalo *et al*., 1995). Two species, *Acartia* sp. (mainly *A.bifilosa*) and *P.minutus elongatus*, were present in sufficient numbers for analysis in all seasons. The calanoid copepod *Acartia* sp. had a stable C and N content (48.3 ± 0.8% C and 12.4 ± 0.2% N), and consequently a stable C:N ratio (4.5 ± 0.1 by atoms) (Table II, Figure 1A), despite different developmental stages, seasons and sampling stations. Autumn specimens of *Eurytemora affinis* had a similar composition. *Pseudocalanus*, however, showed strong variations in C, N and P content (Table II, Figure 1A and B), most likely related to the seasonal accumulation of lipids. In contrast to the other copepod species, large lipid droplets (cf. Sargent and Henderson, 1986) were observed when *Pseudocalanus* were rich in C, but poor in N and P. The C content and C:N ratio of late *Pseudocalanus* copepodite stages were high in the autumn and lower during the winter (data from station BY31; Table II, Figure 1A). Between stage V copepodites and adult females, the C content fell drastically and the composition of females closely approached that of copepods not accumulating fat, e.g. *Acartia* sp. The large copepod *L.macrurus* also had large fat deposits and the highest C and the lowest N and P content of all studied zooplankton, and consequently high C:N and C:P ratios.

The copepod N:P ratio (14–27 by atoms) was apparently independent of the C content ($r^2 = 0.18$, $P = 0.09$, $n = 17$; linear regression not shown), and was mostly higher than the Redfield ratio (16) (Table II, Figure 1C). The high P content of a few *Acartia* samples is the main reason why the relationship is close to significance. In contrast to the stable C and N content, the P content and consequently the N:P ratio was very variable in *Acartia* sp. (Table II, Figure 1B and C). *Acartia* copepodites from the coastal station (B1) in spring had a P content as high as 2.0% of dry weight. On two occasions, when adults and copepodites were successfully separated (station BY31), copepodites seemed to have higher P content than adults (Table II), which was significant on one occasion and nearly significant on the other one ($P = 0.025$ and 0.053 respectively; Mann–Whitney *U*-test).

The cladocerans *B.longispina maritima* and *Evadne nordmanni* had similar N contents (10.3 ± 0.4 and 9.7 ± 0.6%; $P = 0.16$, Mann–Whitney *U*-test) and C:N ratios (5.4 ± 0.2 and 5.4 ± 0.4; $P = 0.75$, Mann–Whitney *U*-test). The N content in *Bosmina* and *Evadne* was lower ($P = 0.007$ and $P = 0.014$) and the C:N ratio higher ($P = 0.007$ and $P = 0.014$, respectively) than in *Acartia*. *Bosmina* had a C content similar to *Acartia* (49.3 ± 0.7%), except for one occasion (44.8% C). On this

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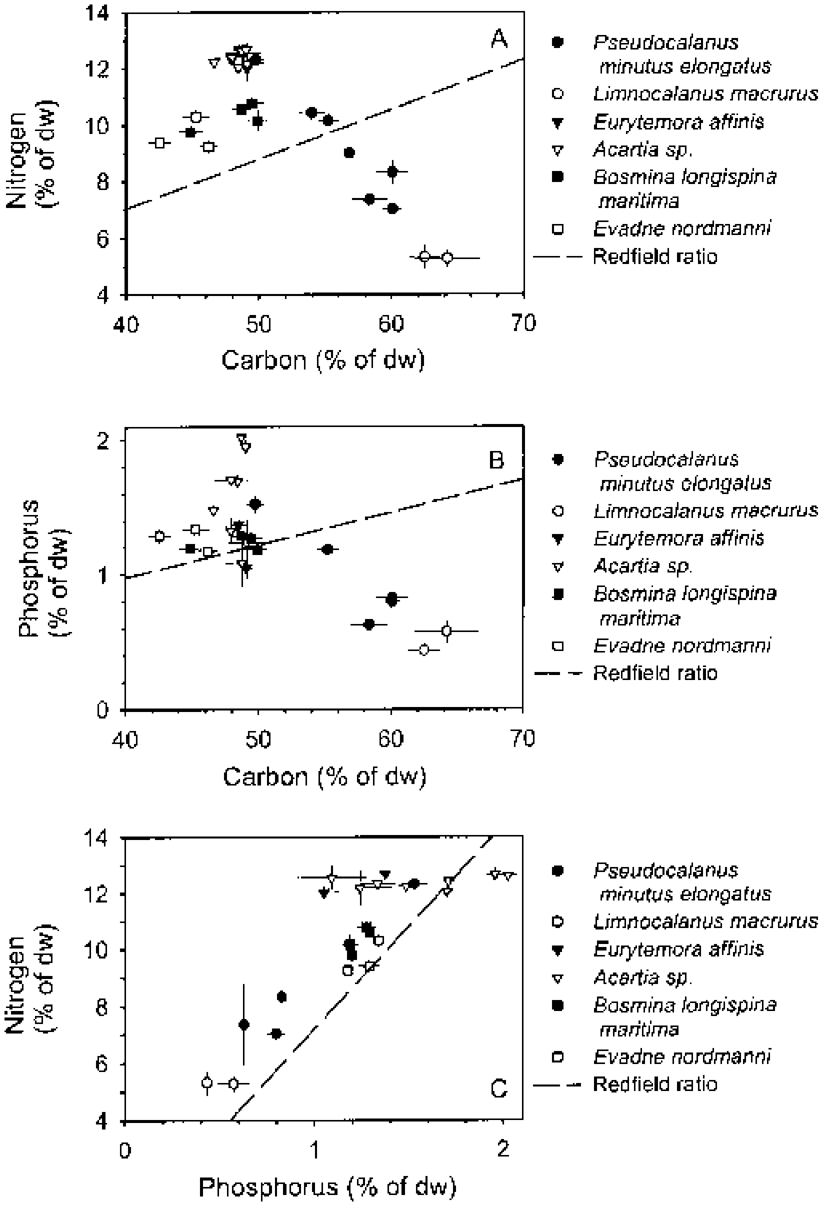

Fig. 1. (**A–C**) Carbon, nitrogen and phosphorus content of analysed zooplankton, as a percentage of dry weight. Error bars indicate 1 SD from the mean. The dashed line shows the Redfield ratio. More details are given in Table II.

occasion, the animals were not rinsed with deionized water prior to analysis, and sea salt could have contributed to the dry weight. That the element ratios of the *Bosmina* samples did not differ supports this conclusion. This observation could perhaps also explain a lower C content of *Evadne* compared to *Bosmina*, since

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Evadne should contain more water due to its large egg sac. The N:P ratio of the cladocerans (16–19) is in the lower range of that for copepods and close to the Redfield ratio (16). The N:P ratio of *Acartia* copepodites in spring was even lower than the ratio in the cladocerans, because of a very high P content.

Seston

Total seston concentrations peaked during the spring bloom and reached a maximum concentration of 36 µM C. A second, less pronounced, peak was found in late summer during the cyanobacterial bloom (Figure 2A). The same pattern was seen for N (Figure 2B) and, consequently, the C:N ratio (Figure 2D) was relatively stable over the year (7.2 ± 0.6). For P, the increase during the cyanobacterial bloom was smaller (Figure 2C). This was reflected in the C:P and N:P ratios, which increased somewhat in late summer (Figure 2E and F). The average C:P and N:P ratios (113 ± 15 and 15.6 ± 2.1) were close to Redfield (106 and 16). Because seston was analysed as total seston, zooplankton are included. This probably had a minor influence on the C:N:P ratios, since size-fractionated (<10 µm)

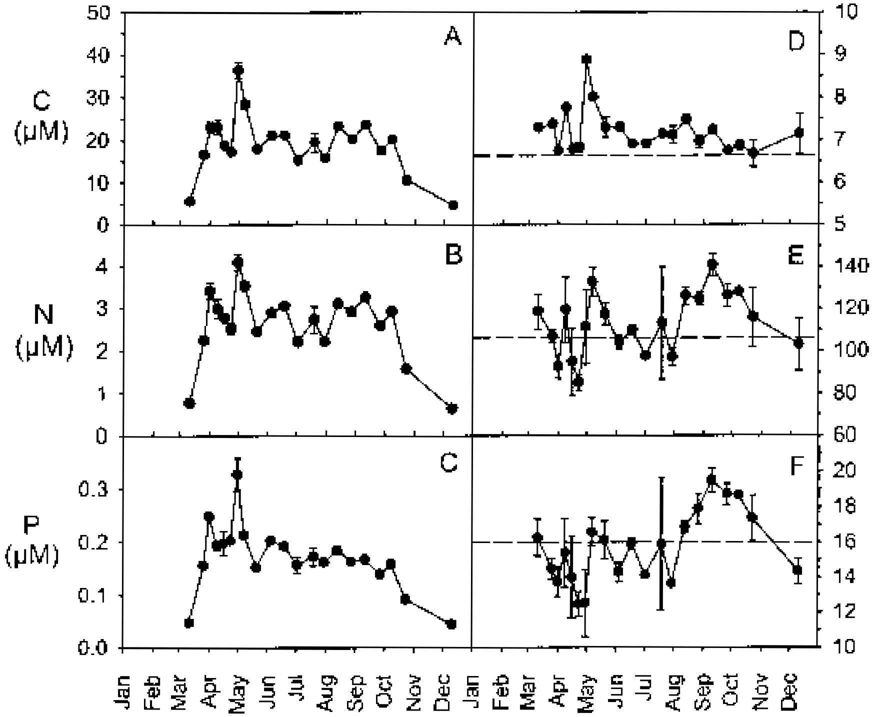

Fig. 2. (**A–F**) Seston C, N and P (µmol l^{-1}) integrated from 0–20 m, and corresponding C:N, C:P and N:P atomic ratios. Horizontal lines indicate Redfield ratios. Error bars on C, N, P and C:N indicate the range of duplicate samples. Error bars on C:P and N:P indicate maximum and minimum ratios calculated from extreme values.

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and total seston samples from the surface (5 m) differed by <10% (data not shown).

Nutrient recycling from zooplankton

We used the data on zooplankton and seston stoichiometry to explore potential imbalances in N and P recycling by applying both the Sterner (1990) and the Schindler and Eby (1997) models (Table III). In both models, the magnitude of the imbalances is largely dependent on assumed values for L and K_1. When the seston N:P ratio is close to Redfield, as during spring and early summer, *Acartia* copepodites will only marginally lower the recycled N:P ratio, while adults and the cladoceran *Bosmina* will have a more pronounced effect, particularly at high L and K_1. When seston N:P increase in late summer, *Acartia* copepodites will selectively retain P and recycle a relatively high N:P ratio, contrary to adults and *Bosmina*, which then have body N:P ratios similar to that in seston. Both models give the same direction of changes in imbalances, however with differences in magnitude.

Discussion

The C:N ratio of *Acartia* (4.5) is in the range (3.5–4.7) typical for many copepods (Båmstedt, 1986). *Pseudocalanus* showed strong variations in C, N and P content, which are related to the accumulation of fat, rich in C, but poor in N and P. A decreasing C content and C:N ratio during the winter are to be expected if lipids are metabolized during overwintering. The fall in C content between stage V copepodites and adult females is in agreement with studies on *Calanus* (Tande, 1982; Gismervik, 1997), and is explained by the use of fat for egg production (Sargent and Falk-Petersen, 1988). A high C content and low N and P contents in the lipid store have an interesting consequence for nutrient recycling. During

Table III. Calculated N:P ratio recycled from zooplankton for different combinations of food and zooplankton N:P ratios. For *Acartia* adults, a high and low N:P ratio are shown. For each combination, different models (Sterner, 1990; Schindler and Eby, 1997) and constants (L and K_1) are compared. A C:N ratio of 4.5, 5.4 and 7.0 was used for *Acartia*, *Bosmina* and food, respectively

Zooplankton	Zooplankton N:P	Food N:P	N:P recycled					
			Sterner model			Schindler and Eby model		
			$L = 0.3$	$L = 0.5$	$L = 0.75$	$K_1 = 0.2$	$K_1 = 0.3$	$K_1 = 0.4$
Acartia copepodites	16	15	14.6	14.1	12.6	14.6	14.2	13.6
Acartia adults	20	15	13.5	12.0	8.6	13.5	12.3	10.6
Acartia adults	25	15	12.8	10.7	6.8	12.7	11.1	9.0
Bosmina	19	15	13.8	12.4	9.2	14.0	13.2	12.2
Acartia copepodites	16	19	20.3	22.0	28.0	20.8	22.7	27.5
Acartia adults	20	19	18.6	18.1	16.5	18.6	18.2	17.6
Acartia adults	25	19	17.2	15.3	11.0	17.1	15.7	13.6
Bosmina	19	19	19	19	19	19	19	19

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the build-up of the lipid store, the N and P requirement is small, and the copepods can be expected to excrete much of their intake of nutrients, if food C:N:P ratios are close to Redfield.

The P content of copepods that do not accumulate fat was much higher, and the N:P ratio lower than in the freshwater species analysed by Andersen and Hessen (1991) and Hessen and Lyche (1991) (P content 0.4–0.7% and N:P ratio 36–52). A low P content (0.5%) was also found by Vrede *et al.* (1999). The N:P ratios obtained in this study on Baltic zooplankton, however, are nearer to those reported for marine species by Butler *et al.* (1969), Corner and Davies (1971), and Gismervik (1997). Low N:P ratios (11–17) in freshwater copepods were also found by Carillo *et al.* (1998), in a zooplankton community dominated by copepodites. Perhaps better food quality (i.e. lower C:P ratio), and higher zooplankton growth rates (see below), at marine sites can explain differences between freshwater and marine species. Another possibility is underestimation of P content due to freezing of zooplankton (Gismervik, 1997).

Acartia copepodites had higher P content than adults, possibly because of a higher growth rate. The P content of cladocerans has been shown to be positively correlated with growth rate (Main *et al.*, 1997; DeMott *et al.*, 1998), a consequence of a higher content of P-rich RNA in fast-growing individuals. The highest P content in *Acartia* was found in copepodites in spring. At this time of the year, growth may be temperature controlled and maximized by accumulation of P-rich molecules and organelles. These copepods were sampled at an exposed coastal station (B1), with a similar seston elemental composition (U.Larsson, unpublished data) as the offshore station BY31, and food elemental composition is thus rather unlikely to explain the high P content. *Bosmina* also had a higher P content than found in freshwater specimens by Andersen and Hessen (1991), while *Evadne nordmanni* had a higher C:P ratio than found by Gismervik (1997). *Bosmina* and *Evadne* were sampled only in summer, and there could be seasonal variability that has not been detected in the present study. However, summer is the only time they are abundant and could have a significant impact on nutrient recycling.

Seston C:N:P ratios at the offshore station (BY31) were close to Redfield ratios, and have been relatively similar from year to year (U.Larsson, unpublished data). This station thus conforms to the general pattern of Redfield ratios at marine sites (Hecky *et al.*, 1993). Until July, the seston N:P ratio was mostly lower than the N:P ratio of adult copepods and *Bosmina*, implying that they selectively retain N and release relatively more P (Table III). This is in accordance with the 'negative elemental imbalance' (seston N:P – zooplankton N:P), found by Hasset *et al.* (1997) at their marine stations, where copepods dominated zooplankton biomass. For copepodites, the situation would be more balanced until July, and reversed in late summer when the seston N:P increases. In late summer, the stoichiometry of adult copepods and *Bosmina* would be essentially in balance with that of the food (Table III).

The high N and P content in seston indicates that it is more probable that the zooplankton at this site are energy (C) limited, rather than limited by N or P in the food. In the model by Sterner (1990), the accumulation efficiency (*L*) of the limiting nutrient (N or P) is likely to be high when stoichiometric differences are

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large between zooplankton and the food. When zooplankton growth is C limited, L is probably closer to K_1, the gross growth efficiency in the model by Schindler and Eby (1997). Because of this, zooplankton nutrient recycling is probably best described by the Schindler and Eby (1997) model, or when using a low L in the model by Sterner (1990). Even if we assume a high gross growth efficiency (K_1) [Hansen *et al.* (1997) give maximum values for copepods and cladocerans between 0.3 and 0.4], the resulting N:P ratio of the recycled nutrients is not very different from that of the food (Table III). The largest imbalances are caused by copepods (except *Acartia* copepodites) in early summer and *Acartia* copepodites in late summer. However, for adult female copepods, the N:P ratio in the eggs would probably be a better indicator of the nutrient demand than body stoichiometry, since most of the production is allocated to eggs. Seston stoichiometry is also a crude estimate of food quality for copepods, which are known to have the ability to feed selectively (e.g. DeMott, 1988). Small differences in actual food as compared to bulk seston composition may easily accentuate or diminish estimated imbalances. For example, Lyche *et al.* (1996) found cyclopoid copepods to regenerate more P than *Daphnia*, partly because of a lower P content, but also because it fed on microzooplankton, rich in P. A skewed recycling ratio from zooplankton could also be counteracted by other factors, such as occasional nutrient inputs from deep water layers, recycling within the microbial loop, or excretion from zooplankton predators (like herring, sprat and mysids).

With the small stoichiometric difference between the investigated copepods and cladocerans, a shift in dominance between them would have little impact on the relative recycling of N and P. Still, even with similar body stoichiometry, there could be contrasting effects of copepods and cladocerans on the N:P ratio of the nutrients that are actually made available for phytoplankton. As suggested by Elser *et al.* (1988) and Balseiro *et al.* (1997), differences in N:P ratio between excretion products and faeces could be of importance, since the nutrients in the faeces are not as readily available as the excretion products, which are mainly made up of ammonium and phosphate (Båmstedt, 1985; den Oude and Gulati, 1988). If copepods have a low assimilation efficiency for P and produce faecal pellets with a low N:P ratio, the N:P ratio of the (immediately) available nutrients from excretion would be relatively high.

If the faecal pellets are lost from the photic zone by sedimentation, copepod nutrient recycling could differ from that of cladocerans, since the cladocerans produce looser faeces that disintegrate more easily, and the nutrients in their faeces would be more available for phytoplankton.

In conclusion, this study shows that Baltic copepods which accumulate lipids can undergo large annual changes in C:N and C:P ratios, but not necessarily in the N:P ratio. The observed variation in P content and N:P ratio may be related to the growth rate. The zooplankton had N:P ratios mostly above, but close to, seston N:P, which was close to the Redfield ratio of 16. The zooplankton could at certain times thus potentially enhance N limitation of the phytoplankton in the Baltic proper, but small stoichiometric differences suggest that this effect is probably weak. Apart from zooplankton and seston N:P ratios, the extent is dependent on the structure of the zooplankton community, and the gross growth

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efficiencies. Although the Baltic proper is roughly 4/5 fresh water, in this respect it seems more like a fully marine area (cf. Hasset *et al.*, 1997), primarily due to a relatively low N:P ratio of seston and copepods, and the virtual absence of daphnids. However, a proper evaluation of effects of stoichiometric imbalances between consumers and their food must consider a number of factors in a seasonal context, i.e. zooplankton community structure and biomass build-up, growth efficiency, diurnal vertical migration patterns, and species-specific effects on sedimentation of nutrients, most of which are not presently available.

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