The common jellyfish *Aurelia aurita*: standing stock, excretion and nutrient regeneration in the Kiel Bight, Western Baltic

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Abstract

The population dynamics, ammonia and inorganic phosphate excretion, and nutrient regeneration of the common jellyfish *Aurelia aurita* was investigated from 1982 to 1984 in the Kiel Bight, western Baltic Sea. During summer 1982, medusae abundance ranged between 14 and 23 individuals 100 m^{-3}, biomass was estimated at about 5 g C 100 m^{-3} and the mean final diameter of individuals was 22 cm. Abundance, based on numbers, in 1983 and 1984 was an order of magnitude lower; biomass was less than 2 g C 100 m^{-3} and jellyfish grew to 30 cm. During the summers of 1983 and 1984, *A. aurita* biomass constituted roughly 40% of that of the total zooplankton > 200 μm. In 1982, for which zooplankton data were lacking, it was assumed that medusae biomass was greater than that of all other zooplankton groups. Total ammonia excretion ranged between 6.5 and 36 μmol h^{-1} individual^{-1}, whereas inorganic phosphate release was 1.4 to 5.7 μmol h^{-1} individual^{-1}. Allometric equations were calculated and exponents of 0.93 for NH$_4$-N release and 0.87 for PO$_4$-P excretion were determined. Nitrogen and phosphorus turnover rates were 5.4 and 14.6% d^{-1}, respectively. In 1982, the medusae population released 1 100 μmol NH$_4$-N m^{-2} d^{-1}, about 11% of the nitrogen requirements of the phytoplankton. The inorganic phosphate excretion (150 μmol m^{-2} d^{-1}) sustained 23% of the nutrient demands of the primary producers. In the other two years the nutrient cycling of the medusae was much less important, and satisfied only 3 to 6% of the nutrient demands. It is suggested that in some years *A. aurita* is the second most important source of regenerated nutrients in Kiel Bight, next to sediment.

Introduction

Gelatinous predators are common members of neritic ecosystems. Both scyphomedusae as well as ctenophores can occur in high numbers, with their biomass contributing a large portion of the total zooplankton biomass (Möller 1978, 1980 b, Shushkina and Musayeva 1983, Shenker 1984, van der Veer and Sadee 1984). Since jellyfishes are predators of zooplankton, their occurrence leads to rapid decreases in densities of other zooplankton taxa (Cronin et al. 1962, Herman et al. 1968, Williams et al. 1968, Sage and Herman 1972, Möller 1978, Deason and Smayda 1982, Lindahl and Hernroth 1983, Feigenbaum and Kelly 1984). They are also thought to be predators of, and food competitors with, larval fish (reviewed by Purcell 1985).

Knowledge of the metabolic rates of jellyfish is scanty compared to that for other zooplankton taxa. Biggs (1977) presented data on respiration and ammonia excretion rates of many gelatinous species and detailed investigations on ctenophore metabolism were carried out by Kremer (1976, 1977, 1982) and Kremer et al. (1986). Respiration of scyphomedusae, predominately *Aurelia aurita* has been examined by Thill (1937), Krüger (1968), Biggs (1977), Kerstan (1977), Kuz'micheva (1980), but few measurements have been made on ammonia excretion (Biggs 1977, Muscatine and Marian 1982), and data for phosphate release from large scyphomedusae are still lacking. Consequently, we have no consistant ideas about nutrient cycling by large scyphomedusae.

Aurelia aurita is a characteristic component of summer plankton in the Kiel Bight, western Baltic Sea (Möller 1978, 1980 a, b). Since abundance of *A. aurita* can be high during this period, the medusae dominates the pelagic system at a stage when primary production is essentially fuelled by regeneration of nutrients (Smetacek et al. 1984). Excretion by *A. aurita* probably constitutes a significant portion of the regenerated nutrients excreted by zooplankton. Ammonia and phosphate excretion rates in *A. aurita* medusae were measured in order to evaluate it's role in nutrient regeneration in summer.

Materials and methods

In 1982, 1983 and 1984, *Aurelia aurita* medusae were sampled approximately bi-weekly from March to October at
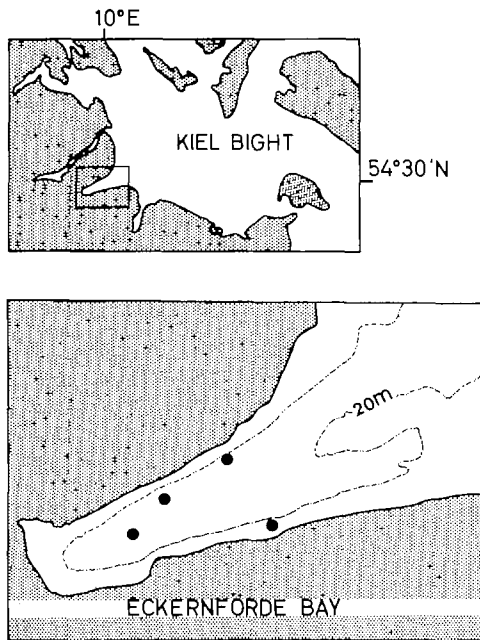
Fig. 1. Kiel Bight and Eckernförde Bay, showing sampling stations
(●)

Fig. 2. *Aurelia aurita.* Average abundance, 1982 to 1984

four stations in Eckernförde Bay, Western Kiel Bight, FRG
(Fig. 1). Oblique hauls were taken from the surface to
1.5–2 m above the seabed with a Cal COFi net of 1 m
mouth diameter (500 μm gauze). Water depth was about
20 m at three stations, but only 12 m at one station. The
volume of water filtered ranged from 300 to 400 m^3
station^{-1}. To estimate the average abundance of medusae,
the numbers of all individuals caught during the cruises were
divided by the total volume of water filtered.

After recovery of samples, medusae were counted,
weighed with a Sartorius balance (Model 2 357) and their
diameters measured. Size-frequency distributions were
established and tested for normality (chi^2, $n > 60$). In
samples of less than 60 individuals, the procedure described
by David et al. (1954) was adopted. Size-frequency distribu-
tions were found to be normally distributed, and mean
medusae size was calculated for each cruise.

The carbon biomass of the medusae were calculated
from the wet-mass carbon-mass regression given in
Schneider (1988a).

To compare the biomass of the medusae with that of
other zooplankton, in 1983 and 1984 additional plankton
samples were obtained at the four stations with a 60 cm
plankton net fitted with 200 μm gauze. Vertical hauls were
made from about 1.5 m above the sea bottom to the surface.
Zooplankton were filtered through precombusted Whatman
GF/C glass-fibre filters, dried at 60 °C, and thereafter ana-
lyzed for carbon biomass in a Perkin Elmer 240 C CHN-
analyzer.

For excretion experiments, individuals of *Aurelia aurita*
were caught with a dip net in Kiel Fjord in summer 1984,
and incubated in two 100 litre glass aquaria, one as a con-
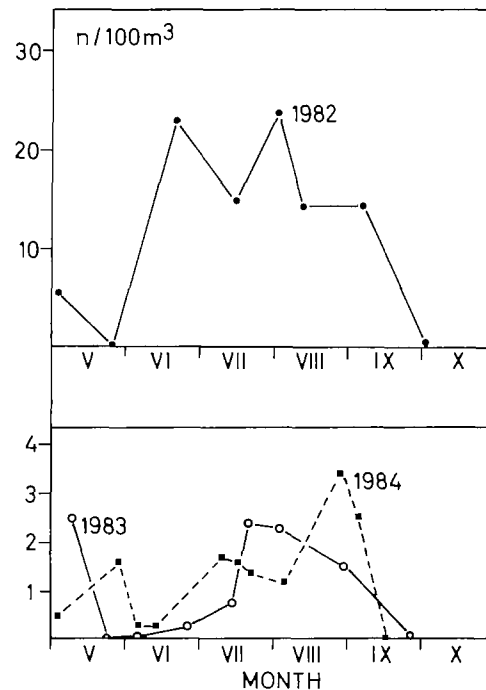trol. In a first set of experiments ($n = 12$), filtered sea water

was used. Due to the high phosphate content of the water,
only ammonia excretion rates could be determined, and
therefore in a second set of experiments ($n = 11$) artificial sea
water of 15‰ S was used. Incubation temperature was
15 °C ± 1 C°, the approximate summer temperature of the
water column during the investigations (range per cruise:
11.4 °C to 16.7 °C; mean: 14.3 °C). The duration of the exper-
iments was between 17 and 27 h. At the beginning and end
of incubations, three replicates of each nutrient were taken
from the aquaria. Ammonia and inorganic phosphate were
measured according to the methods described in Grasshoff
(1976). Results were calculated as the difference between
experimental and control aquaria at the end of experi-
ments. Wet weight of experimental medusae was determined
using the Sartorius balance mentioned above. To relate ex-
cretion rates to body constituents, the following values (de-
termined for *A. aurita* earlier: Schneider 1988a) were used:
dry wt = 1.8% of wet wt, nitrogen = 1.4% of dry wt, phos-
phorus = 0.14% of dry wt.

Results

Standing stock data

The population structure of *Aurelia aurita* medusae was
quite different between 1982 and the other two years. From
mid-June to September 1982, average abundance ranged
from 15 to 23 medusae 100 m^{-3} (Fig. 2), whereas in 1983
and 1984 only 0.5 to 4 individuals 100 m^{-3} were recorded.
Growth showed a similar pattern to that described by
Möller (1980b): after poor growth in early spring, medusae
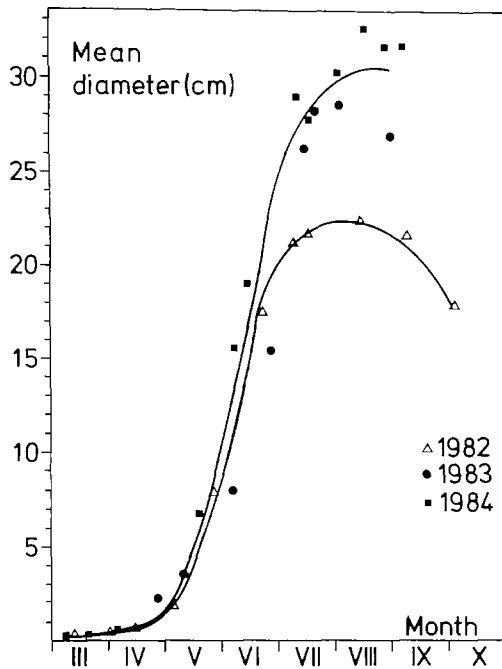size increased in May, reaching its maximal diameter in

Fig. 3. *Aurelia aurita.* Growth of medusae 1982 to 1984; data points show mean diameters for each cruise. To avoid confusion standard deviations are not given. Variability was ±30% in ephyrae and small medusae and 15 to 20% in larger specimens

Table 1. Biomass (g C 100 m^{-3}) of zooplankton > 200 μm and *Aurelia aurita* medusae during summer 1982 to 1984. nd: no data

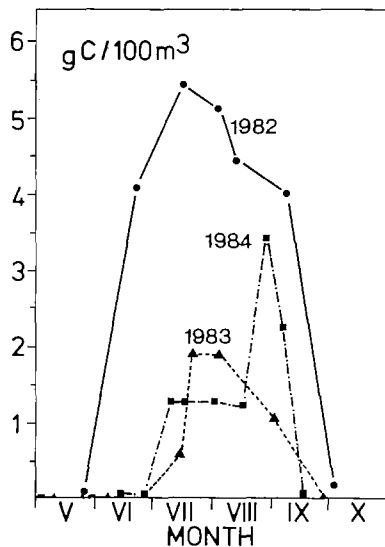| Date	Zoo-plankton	Medusae	Total	Medusae % of total
1982				
26 May	nd	0.13	–	–
22 June	nd	4.07	–	–
16 July	nd	5.48	–	–
3 August	nd	5.14	–	–
13 August	nd	4.44	–	–
8 September	nd	4.01	–	–
3 October	nd	0.19	–	–
1983				
7 June	nd	0.02	–	–
27 June	1.23	0.06	1.29	5
15 July	2.25	0.59	2.84	21
21 July	2.67	1.88	4.55	41
4 August	2.59	1.86	4.45	42
1 September	1.82	1.06	2.88	37
28 September	1.74	0.00	1.74	0
1984				
14 June	1.19	0.07	1.26	6
10 July	1.41	1.26	2.67	47
17 July	2.24	1.23	3.47	35
2 August	1.99	1.23	3.22	38
16 August	0.59	1.20	1.79	67
28 August	1.25	3.43	4.68	73
6 September	nd	2.25	–	–
17 September	0.99	0.06	1.05	6

Fig. 4. *Aurelia aurita.* Average carbon biomass, 1982 to 1984

August (Fig. 3). The average maximum size of medusae was 22 cm in 1982, and about 30 cm in 1983 and 1984. Maximum-sized medusae weighed 430 g in 1982, but 1 000 g in 1983 and 1984. Biomass attained values between 4 and 5.5 g C 100 m^{-3} in 1982, whereas in the other two years all values were less than 2 g C 100 m^{-3} (Fig. 4). The exceptional peak in September 1984 was probably due to advection of medusae caused by an inflow of less saline Baltic waters recorded at that time.

In the summers of 1983 and 1984 the biomass of *Aurelia aurita* contributed roughly 40% (and occasionally more) to

the biomass of the total zooplankton > 200 μm (Table 1). Unfortunately, no zooplankton sampling was carried out in 1982. However, if we assume the standing stock of zooplankton > 200 μm to have been in the same range as in 1983 and 1984, or even lower due to enhanced predation, *A. aurita* biomass exceeded that of the remaining zooplankton stock by several times.

Excretion measurements

Ammonia-nitrogen excretion rates varied between 6.5 and 35.8 μmol h^{-1} individual^{-1}, whereas inorganic phosphate-phosphorus was excreted in the range 1.39 to 5.67 μmol h^{-1} individual^{-1}. However, excretion is a weight-dependent process, usually described by the allometric equation $E = a \ W^b$, where E = excretion rate individual^{-1} unit time^{-1}, W = body weight, a is the constant for species and experimental conditions, and b is the exponent relating excretion to body weight. Estimates of coefficients (Table 2) were derived from linear regressions of logarithmic transformed excretion and weight measurements. The wet weight of the medusae in the excretion experiments ranged from 102 to 1 109 g.

There were strong correlations between ammonia excretion and body mass, with b values of about 0.93, indicating that ammonia excretion rates per unit body weight were almost independent of size. A broad scattering of data in comparatively few observations resulted in a poorer correla-

tion between PO_4-P excretion and body mass ($p < 0.05$) with the calculated b value of 0.87 being slightly lower, but not significantly so, than in the ammonia excretion experiments (Student's t-test $= 0.541$, $p < 0.05$).

Table 3 presents weight-specific rates for ammonia-N and phosphate-P excretion, atomic ratios, element content of medusae, and element turnover rates. Phosphate excretion was about one order of magnitude lower than ammonia release. The low N:P ratio of 9.1 and the estimated O:N ratio of 7.6 imply that metabolism is protein-dominated, a characteristic of carnivorous organisms (Ikeda 1977). Phosphorus turnover was about three times higher than nitrogen cycling. Ecologically, therefore, phosphate-P excretion is more important than ammonia-N release.

Table 2. *Aurelia aurita.* Coefficients of allometric excretion equation $E = a W^b$, where $E =$ excretion rate in μmol h^{-1} individual^{-1}, $W =$ body wt in g, a and $b =$ coefficients, $n =$ number of determinations, and $r =$ correlation coefficient. Wet weight of experimental medusae $= 102$ to 1109 g (13 to 31 cm diam.). Regression (1) is for the first set of experiments with filtered sea water ($n = 12$); regression (2) for the second set using 15‰ S artificial sea water ($n = 11$); regression (3) is for both experiments combined; regression (4) is for the second set (phosphorus excretion; $n = 9$)

Excretion	a	b	r	n	p
Ammonia-N					
Regression (1)	0.058	0.93	0.874	12	< 0.001
Regression (2)	0.062	0.92	0.720	11	< 0.01
Regression (3)	0.058	0.93	0.856	23	< 0.001
Inorganic phosphate-P excretion					
Regression (4)	0.010	0.87	0.693	9	< 0.05

Nutrient regeneration

Using the regressions of Table 2 (Regression 3 for ammonia), the abundance and body weight data, it was possible to calculate nutrient excretion of the medusae population m^{-2} water column (20 m depth). From June to September 1982, ammonia-N excretion by *Aurelia aurita* medusae ranged between 1 000 and 1 300 μmol m^{-2} d^{-1} ($= 14$ to 18 mg N m^{-2} d^{-1}), whereas in 1983 and 1984 ammonia release was generally less than 500 μmol m^{-2} d^{-1} ($= < 7$ mg N m^{-2} d^{-1}: Fig. 5). Mean values were 1 133 $\pm$ 125 μmol m^{-2} d^{-1} in 1982 and 323 $\pm$ 161 μmol m^{-2} d^{-1} in 1983 and 1984, respectively. The corresponding values for phosphate-P were 150 to 190 μmol m^{-2} d^{-1} (4.6 to 5.9 mg P m^{-2} d^{-1}) in 1982 (mean: 150 $\pm$ 15 μmol m^{-2} d^{-1}) and < 50 μmol m^{-2} d^{-1} (< 1.6 mg P m^{-2} d^{-1}; mean: 37 $\pm$ 18) in 1983 and 1984 (Fig. 6). Assuming the daily primary production in the Kiel Bight in summer to be about 0.8 g C m^{-2} d^{-1} (Smetacek et al. 1984) and that elemental composition of phytoplankton conforms to the Redfield ratio (Redfield et al. 1963) of C:N:P $= 106:16:1$, the average ammonia excretion of the medusae population sustained 11% of the daily nitrogen requirements of phytoplankton in 1982, but only 3% in 1983 and 1984. Due to the higher phosphate-P turnover (Table 3), 23% of the phosphorus demands for primary production were fuelled per day in 1982 and 6% d^{-1} in the other two years. Total ammonia and inorganic phosphate excretion during the entire period between the increase and decrease of medusae biomass (represented by the areas under the curves in Figs. 5 and 6) are given in Table 4. The excretion of NH_4-N and PO_4-P was about four to nine times higher in 1982 than in 1983 or 1984.

Smetacek et al. (1984) estimated the primary production in Kiel Bight during summer to be about 70 g C m^{-2}, which

Table 3. *Aurelia aurita.* Weight-specific excretion rates, atomic ratios, N and P content of medusae and element turnover rates. WW: wet wt, DW: dry wt

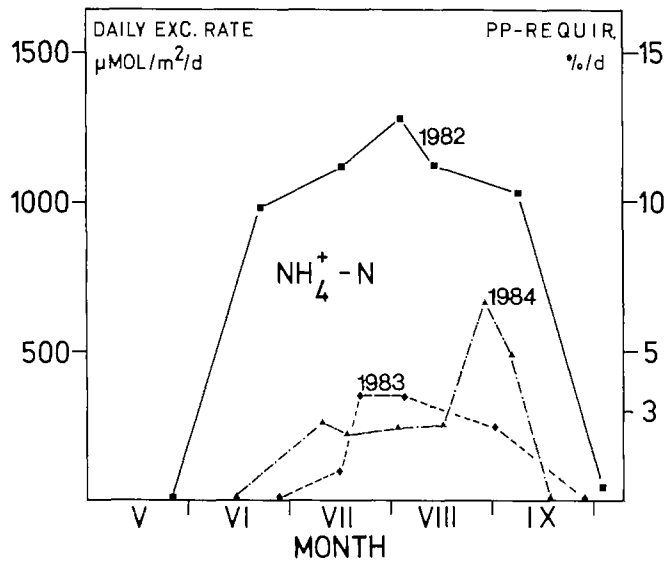| Elements	Range	x	SD	n	Source
NH_4-N excretion					
μmol g^{-1} WW d^{-1}	0.52– 1.70	–	–	23	–
μmol g^{-1} DW d^{-1}	28.8 – 94.4	–	–-	23	–
μmol mg^{-1} N d^{-1}	2.08– 6.93	–	–	23	–
PO_4-P excretion					
μmol g^{-1} WW d^{-1}	0.07– 0.17	–	–	9	–
μmol g^{-1} DW d^{-1}	3.71– 6.93	–	–	9	–
μmol mg^{-1} P d^{-1}	3.06– 7.69	–	–	9	–
Atomic ratios					
N:P	6.9– 11.4	9.1	1.8	9	
O:N (estimated)	3.9 – 14.7	7.6	2.4	23 }	Kuz'micheva (1980)
O:P (estimated)	39 – 90	62	18	9 }	
Element content of medusae					
Nitrogen (mg individual^{-1})	26 –279	–	–	23	–
Phosphorus (mg individual^{-1})	7.6 – 19	–	–	9	–
Element turnover					
Nitrogen (% d^{-1})	3.9 – 9.7	5.4	1.8	23	–
Phosphorus (% d^{-1})	9.5 – 22.5	14.6	4.4	9	–

Fig. 5. *Aurelia aurita*. Ammonia-N excretion rates of medusae population and contribution to phytoplankton nitrogen requirements (PP-REQUIR.)
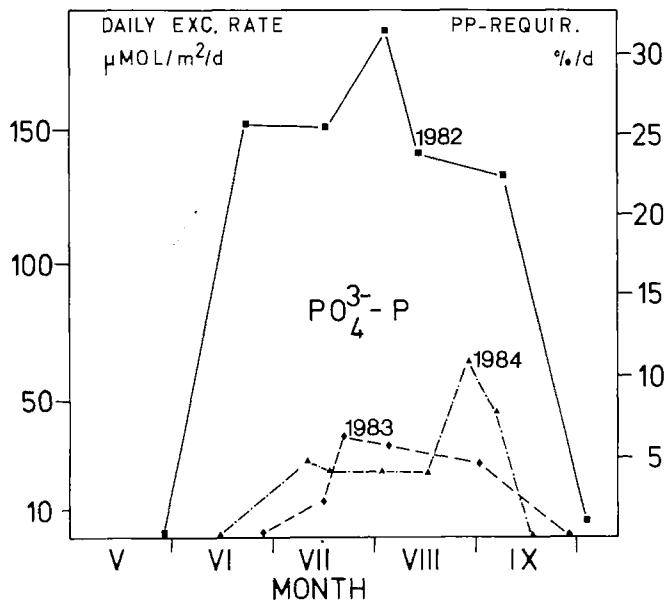

Fig. 6. *Aurelia aurita*. Inorganic phosphate-P release of medusae population and contribution to phosphorus requirements of primary producers (PP-REQUIR.)

Table 4. *Aurelia aurita*. Integrated excretion of nutrients during summer 1982 to 1984 and contribution to primary production. Assumed production during summer in Kiel Bight was 70 g m^{-2}. Composition of particulate matter, C:N:P = 106:16:1

Year	Excretion mmol m^{-2}		Contribution to primary production	
	NH$_4$-N	PO$_4$-P	% N	% P
1982	120	17	14	31
1983	19	2	2	4
1984	27	3	3	6

is roughly one half of the annual primary production. Taking this value, *Aurelia aurita* provided 14% of nitrogen and 31% of the phosphorus demands of the phytoplankton in 1982, whereas in 1983 and 1984 only 2 to 6% for both elements were contributed by the medusae (Table 4), provided that phytoplankton production was average in the different years.

Discussion

Growth, abundance and biomass of *Aurelia aurita* in the Kiel Bight

Although *Aurelia aurita* dominates the Kiel Bight pelagic system in summer, strobilation and release of ephyrae occurs between late autumn and early spring (Thiel 1962). During early spring there is no significant growth of ephyrae (Möller 1980 b). An increase in size begins in April or May and may be caused by the nearly synchronous increase in water temperature and mesozooplankton biomass. Growth is very fast. Möller (1980 b) reported weekly growth rates of up to 4 cm diam., and Schneider (1985) reported a maximum increment of 2.6 cm diam. and 70 g wet wt wk^{-1} in 1982. Growth ceases in summer after maximal diameters are reached. However, the final size displays considerable inter-annual variation. It is improbable that final size depended on water temperature in the present study, since the average water temperature for the whole water column differed only slightly between the three summers (Schneider 1985). Therefore, final size may depend on population density, smaller individuals being associated with high density and vice versa. This could result from food shortage, or from the larger effort necessary in the face of intraspecific competiton to collect sufficient food for growth.

The *Aurelia aurita* population consumed about 30% of the total Kiel Bight annual zooplankton production in summer 1982, but only 7% in 1983 and 1984 (Schneider 1988 b). Laboratory investigations on *A. aurita* showed that individuals which were offered ample food grew to a larger final size than individuals from natural populations (Hamner and Jenssen 1974). However, the relation between medusae size and abundance must remain speculative since sufficient long-term data on abundance, size and biomass variations do not exist to confirm this hypothesis. The observed inter-annual variations in abundance of medusae (Hernroth and Gröndahl 1985, van der Veer and Oorthuysen 1985, and present paper) may be induced by predation by the nudibranch gastropod *Coryphella verrucosa* on scyphistoma polyps (Hernroth and Gröndahl 1985) and/or by variations in the fecundity of female medusae and in larval release (Schneider in press, b).

Aurelia aurita contributes considerably to the total zooplankton biomass. During his survey in 1976 to 1977, Möller (1978) recorded biomass values for *A. aurita* medusae from July to September of between 3.3 and 4.5 g C 100 m^{-3}. Other zooplankton groups contributed only 1.0 to 2.1 g C 100 m^{-3}. *A. aurita* standing stock, therefore, outweighed

the rest of zooplankton by factors between 1.5 and 4 during this period.

During summer 1983, the average zooplankton standing stock > 20 μm was 120 mg dry wt m^{-3} (Weisse 1985), which corresponds to 4.8 g C 100 m^{-3} (assuming carbon content to be 40% of the dry wt). Thus, *Aurelia aurita* comprised approximately 30% of the zooplankton ranging from micro- to macroplankton in 1983. Since the high biomass values of medusae result in high predation pressure, it can be assumed that in 1982 *A. aurita* biomass exceeded that of all other zooplankton groups, including microplankton on which the medusae also prey (Stoecker et al. 1987).

Excretion rates

Studies on excretion rates of large scyphomedusae have not been systematically carried out until the present study. Few data on ammonia excretion exist. Biggs (1977) carried out five measurements on *Pelagia noctiluca* and *Aurelia* sp., whereas Muscatine and Marian (1982) reported nine measurements on four *Aurelia* spp. held together in one experimental vessel. A comparison of weight-specific ammonia excretion rates (Table 3) with values obtained by the workers cited above and with data obtained for other coelenterates are given in Table 5. Protein-specific excretion rates of *A. aurita* were calculated using the protein content of the medusae given in Schneider (1988a). To facilitate comparison, the rates reported in the literature were converted to 15°C using the well known Q_{10} law. An overall Q_{10} of two was assumed (Ikeda 1985).

Data on phosphate-P release are scarce for coelenterates and ctenophores in general. Kremer (1977) and Ikeda and Mitchell (1982) examined phosphorus excretion in the ctenophores *Mnemiopsis leidyi* and *Beroe* sp. The results ranged between 0.7 and 4.9 (15°C: 1.7 to 3.0) μmol g^{-1} dry wt d^{-1}. Båmstedt (1985) has also published data on ctenophore P-excretion: 0.01 to 0.22 (15°C: 0.02 to 0.42) μmol mg^{-1} protein d^{-1}.

However, the comparability of such data is limited, mainly for three reasons. (1) Experimental temperatures are quite different and the temperature correction of rates (15°C in Table 5) enables only rough estimates because Q_{10} values differ between species and are not known for all coelenterates examined. (2) Another modifying agent is the nutritional state of experimental individuals; Kremer (1982) showed that after 1 d of starvation, a time period which lies within the range of incubation periods in excretion experiments, ammonia-nitrogen excretion was only about 60% that of fed individuals; similar results were obtained for *Pleurobrachia pileus* by Ikeda (1977) and appear to be a common feature in zooplankton (Ikeda 1977 and citations therein). (3) The weight of experimental individuals also influences metabolic rates; in the allometric metabolic equation, most invertebrates exhibit exponents (*b*) between 0.7 and 0.8 (e.g. Prosser 1973). Small individuals have higher weight-specific metabolic rates than larger ones. Since scyphomedusae are often considerably larger than other coelenterates, low weight-specific excretion rates might be expected. However, coelenterates often have *b* values in excess of 0.8 (Biggs 1977, Kremer 1977, 1982, Kremer et al. 1986, and present study), and similar exponents have been obtained in respiration measurements (Krüger 1968, Biggs 1977, Kremer 1977, 1982, Kuz'micheva 1980, Kremer et al. 1986).

Ammonia excretion and respiration per unit body weight of gelatinous plankters appear to be only slightly affected by medusae weight and differ from the general rule mentioned above. However, Phillipson (1981) re-evaluated the weight-dependence of metabolic rates of metzoan ectotherms, and found *b* values much closer to 0.9 than 0.7 or 0.8. Vidal and Whitledge (1982) obtained exponents of about 0.8 to 0.9 in ammonia excretion and respiration studies on crustacean zooplankton.

Overall, excretion rates and weight dependence of excretion in *Aurelia aurita* are in the same range as those reported for other coelenterate species. The same is true for elemental

Table 5. Weight-specific ammonia-N excretion rates of *Aurelia aurita* and other pelagic coelenterates and ctenophores. WW: wet wt; n: no. of measurements; n*: no. of mean values

Species	Original data	T (°C)	Data corrected for 15 °C	n	Source
μmol NH$_4$-N g^{-1} WW d^{-1}					
Aurelia aurita	29 – 94	15.0	29 – 94	23	This study
Various species	20 – 60	12.8	23 – 70	4	Jawed (1973)
Various species	23 –127	6.5–27.0	20 –209	9	Ikeda (1974)
Mnemiopsis leidyi	10 – 36	10.3–24.5	10 – 18	6*	Kremer (1977)
Mnemiopsis mccradyi	10 – 42	22.0	6 – 26	4*	Kremer (1982)
Beroe sp.	9.5	−0.8	28.3	1	Ikeda and Mitchell (1982)
Various species	2 – 14	−1.6	7 – 44	6*	Ikeda and Bruce (1986)
Ctenophore species (4)	10 – 36	25.0	6 – 26	4*	Kremer et al. (1986)
μmol NH$_4$-N mg^{-1} protein d^{-1}					
Aurelia aurita	0.5– 1.6	15.0	0.5– 1.6	23	This study
Scyphomedusae	0.3– 1.6	26.0	0.2– 0.7	3*	Biggs (1977)
Various species	0.3– 4.4	26.0	0.1– 2.1	47*	Biggs (1977)
Aurelia sp.	1.8	31.0	0.6	1*	Muscatine and Marian (1982)
Ctenophore species (2)	0.2– 0.6	5.0	0.2– 1.1	3	Båmstedt (1985)

Table 6. Daily release of regenerated nutrients by different sources in Kiel Bight and contribution to nutrient demands of primary producers. Assumed daily primary production = 0.8 g C m^{-2} d^{-1}. Composition of particulate matter, C:N:P = 106:16:1

Regenerated nutrient	Excretion (μmol m^{-2} d^{-1}) of		Contribution of primary production		Source
	NH_4-N	PO_4-P	% N	% P	
Phytoplankton demands					
(total N and P)	10 000	630	–	–	
Regeneration					
Aurelia aurita					
1982	1 133	150	17	23	Present study
1983, 1984	323	37	5	6	Present study
Other zooplankton	990	75	15	11	Weisse (1985)
Sediment	1 803	176	27	26	Pollehne (1986)

turnover rates and atomic ratios of excretory products (cf. Kremer 1976, 1977, 1982, Ikeda and Mitchell 1982, Ikeda and Bruce 1986, Kremer et al. 1986, and present study).

Nutrient regeneration in the Kiel Bight

During summer a well developed pycnocline exists in the Kiel Bight between 10 and 15 m, separating a nutrient-poor euphotic surface layer from nutrient-rich but light-limited deeper water. This strong stratification results in poor contact between euphotic waters and deeper sediments. Thus, the main nutrient sources for primary production are regenerated nutrients released via excretion of pelagic heterotrophs and by sediments situated above the pycnocline. Other inorganic nutrients such as nitrate and nitrite occur only in very small amounts within the euphotic water column (Smetacek et al. 1987).

Comparison of results with nutrient regeneration rates of other zooplankton groups, as well as of bottom sediments above the pycnocline, (Table 6), suggests that *Aurelia aurita* in 1982 excreted similar amounts of ammonia as micro- and mesozooplankton and released slightly more than one half of the nutrients regenerated within the sediment. Inorganic phosphate-phosphorus recycling by medusae was twice that of zooplankton and similar to that of sediments. That phosphorus recycling of medusae is considerably higher than of other zooplankton groups is due to the lower phosphorus content of medusae tissue compared with that of the ingested food. The excreta of medusae are enriched in phosphorus so as to maintain a nutrient balance between ingested zooplankton-P and body tissue-P (see Kremer 1976, 1977).

Ammonia-N content of the euphotic water column during summer is approximately 10 mmol m^{-2}, with lower values in early and higher values in late summer, whereas inorganic phosphate occurs in concentrations of 1.5 mmol m^{-2} (von Bodungen personal communication). Medusae, other zooplankton and sediments (Table 6) recycle between 20 and 40% of these nutrients d^{-1}. Therefore, sediments situated within the mixed layer release most of the nutrients of the Kiel Bight, with micro- and mesozooplankton excretion only accounting for about one half the sediment value.

The role of *Aurelia aurita* in summer nutrient cycling in the Kiel Bight is variable. In years of high population density, excretion of medusae is correspondingly high, comprising up to 30–40% of the inorganic nutrients regenerated daily. In such years, medusae become the second most important nutrient source for phytoplankton during summer stratification, exceeding the contribution by micro- and mesozooplankton. In years of low medusae density, about 60% of the inorganic regenerated nutrients are released by sediments, 30% by micro- and mesozooplankton, and only about 10% by *A. aurita*. The total nutrient release of these three sources contributes 30 to 40% of the nitrogen and 46 to 64% of the phosphorus required by the phytoplankton.

The excretion rates in Table 6 are minimum values, since the medusae were held without food during the excretion experiments. It can be assumed that actively feeding individuals in the environment excrete more nutrients than measured experimentally (e.g. Ikeda 1977, Kremer 1982). Moreover, organic excretory products were neglected in the laboratory experiments. Release of organic nitrogen and phosphorus by zooplankton accounts for roughly 30% of the total nutrient release (reviewed in Raymont 1983), whereas in coelenterates, organic nitrogen release is as high as ammonia excretion, and organic phosphorus makes up about 25% of total phosphorus release (Kremer 1976, 1977, 1982, Kremer et al. 1986). Therefore, nutrient regeneration of medusae, other zooplankton and sediments is higher than shown in Table 6, probably exceeding 50% of the nitrogen and 70% of the phosphorus requirements of primary producers during summer in the Kiel Bight.

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