Respiration and Ammonium Excretion by Open Ocean Gelatinous Zooplankton

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Respiration and ammonium excretion by open ocean gelatinous zooplankton[1]

Douglas C. Biggs[2]
Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543

Abstract

Warm-water species of siphonophores, medusae, ctenophores, heteropods, pseudothecosomatous pteropods, salps, and doliolids were individually collected in jars by SCUBA divers in the western North Atlantic Ocean. In situ rates of oxygen consumption and ammonium excretion were estimated by difference from control jars of seawater enclosed simultaneously. The cystonect siphonophores *Rhizophysa filiformis* and *Bathyphysa sibogae* had low respiration and excretion rates [4–7 μl O_2 (mg protein-h)$^{-1}$ and 0.3–0.5 μg NH_4^+ (mg protein-h)$^{-1}$], while several calycophore siphonophores, heteropods, and salps had high rates [19–192 μl O_2 (mg protein-h)$^{-1}$ and 1.0–3.1 μg NH_4^+ (mg protein-h)$^{-1}$]. Most O : NH_4^+ ratios ranged from 16–38 and suggest that both protein and lipid are important metabolites in tropical and subtropical gelatinous zooplankton. Many physonect siphonophores, scyphomedusae, heteropods, and salps excreted ammonium at rates exceeding 0.3 μg-atom NH_4^+-N h^{-1} and may play an important role in recycling nitrogen in the upper mixed layer of oligotrophic ocean regions.

Most of the macrozooplankton encountered on daytime SCUBA dives in the upper 30 m of the western North Atlantic Ocean are gelatinous, transparent forms (*see* Gilmer 1972; Madin 1974*a*; Swanberg 1974; Harbison and Gilmer 1976). Gelatinous zooplankton comprise representatives of several phyla and span two or three trophic levels (Hamner et al. 1975). Despite their widespread occurrence in open ocean regions, however, there is little quantitative information on the energy requirements of gelatinous animals. Measurements of respiration or excretion for gelatinous zooplankton are mostly limited to nearshore ctenophores (Miller and Williams 1972; Hirota 1972) and medusae (Kruger 1968). There are a few respiration measurements on open ocean gelatinous animals (e.g. Rajagopal 1962; Nival et al. 1972; Gilmer 1974), but simultaneous measurements of respiration and excretion have been reported for only a dozen species (Mayzaud and Dallot 1973; Ikeda 1974).

Because of their fragility, gelatinous animals make poor subjects for classical laboratory respiration and excretion measurements. For example, turbulence, abrasion, or prolonged contact with surfaces causes ctenophores and siphonophores to fragment and can cause salps to shed their tests. Nevertheless, previous investigators have collected gelatinous animals with nets and held them without food in small laboratory aquaria for up to 2 days before measuring oxygen consumption or nitrogenous excretion. Although neritic species might survive this treatment, it will kill most open ocean forms.

To minimize damage to them, I collected oceanic gelatinous zooplankton individually in handheld jars while SCUBA diving and measured oxygen and subsampled ammonium in the jars within 6 h of collection. Here I report measurements of respiration and excretion on over 350 open ocean gelatinous zooplankton. The results indicate that interspecific differences in metabolism are related to differences in their morphology and ecology.

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[2] Present address: Marine Sciences Research Center, State University of New York, Stony Brook 11794.

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Methods

SCUBA divers collected gelatinous plankton in 130–980-ml glass jars fitted with screwtop plastic lids with polypropylene liners. Before collecting a specimen, divers flushed the open jars by shaking them vigorously. Divers were careful not to damage animals by direct contact. Siphonophores were usually allowed to swim into the jars to minimize shearing turbulence and also to obtain the entire fishing network.

At most stations where animals were collected (Fig. 1), temperature in the upper 30 m was 23–29°C. Animals in their collecting jars were incubated aboard ship in a flowing seawater bath at surface temperature for 1–6 h after enclosure. Oxygen consumption and ammonium excretion were estimated by difference from control jars of seawater collected simultaneously. The tension of dissolved oxygen in each jar was measured with a polarographic oxygen electrode (Kanwisher 1959) connected to a portable, battery-powered amplifier which allowed oxygen to be measured with a maximum deviation of ±0.035 ml O_2 liter^{-1} from the mean at 4.800 ml O_2 liter^{-1}. The amplifier was designed and constructed at WHOI by K. Lawson. Oxygen electrodes were calibrated by Winkler titration (Strickland and Parsons 1972) or standardized against oxygen-saturated surface water.

Laboratory experiments were performed to investigate the effect of short term changes in temperature on oxygen consumption. After measuring the oxygen consumption of two colonies of *Forskalia edwardsi* by the method outlined above, I placed them and five other colonies of *Forskalia* in a water bath 5°C below in situ collection temperature for 1 h. All

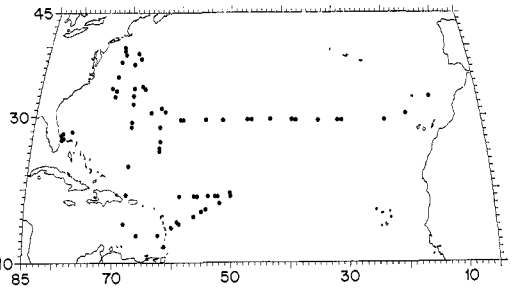

Fig. 1. Stations where SCUBA divers collected gelatinous zooplankton for measurements of respiration and excretion.

were then transferred gently into new jars of water at this temperature, sealed, and incubated for 1–6 h. Oxygen consumption was measured by difference from jars of water enclosed simultaneously.

For determination of ammonium, 100 ml of water was decanted from each collecting jar and control and filtered under low vacuum (0.7 atm) through Gelman type A glass fiber filters. A new filter was used for each filtration; to remove residual ammonium each was prerinsed with 20 ml of sample. The filtrate was immediately fixed with phenol (Deggobis 1973) and refrigerated. Ammonium was determined in duplicate by the phenolhypochlorite method (Solórzano 1969) within 1–2 weeks. There was no measurable change in ammonium concentration in fixed, refrigerated samples during this time. I used 50% less sodium nitroprusside than specified by Solórzano (1969) and also allowed color to develop in the dark for 2 h at room temperature. At sea, using a 5-cm path-length in a Bausch and Lomb model 710 spectrophotometer, precision was equal to that ashore: ±0.1 μg-atom N at 3.0 μg-atoms NH_4^+-N liter^{-1}.

Incubation times for oxygen consumption and ammonium excretion experiments were chosen to correspond to the size of an animal relative to the size of its collecting jar. Concentration of ammonium in control jars of seawater was <0.4 μg-atom NH_4^+-N liter^{-1}. Six hours was sufficient for the smallest gelatinous animals to pro-

Table 1. Oxygen consumption at 26 ± 3°C of some of the more abundant tropical and subtropical gelatinous zooplankton, estimated by linear regression: $\log y = a + b(\log x)$, where y = oxygen consumption (μl O_2 h^{-1}), x = body protein (mg), $a \pm s$ and $b \pm s$ = regression coefficients ± SE, s_{yx} = standard error of the estimate (of y on x), and r^2 = coefficient of determination.

Group	n	a ± s	b ± s	s_{yx}	r^2
Siphonophora: Physonectae					
Agalma okeni	58	1.07±0.04	0.87±0.06	0.20	0.77
Nanomia bijuga	19	1.36±0.02	0.70±0.04	0.08	0.93
Forskalia edwardsi; F. tholoides	20	1.26±0.03	0.89±0.06	0.13	0.94
Athorybia rosacea; Athorybia sp.	13	1.51±0.05	0.34±0.06	0.12	0.81
Siphonophora: Cystonectae					
Bathyphysa sibogae; Rhizophysa filiformis	13	0.80±0.16	0.87±0.15	0.18	0.72
Siphonophora: Calycophorae					
Rosacea cymbiformis	13	0.75±0.08	1.24±0.19	0.19	0.79
Diphyes dispar	17	1.08±0.05	0.65±0.06	0.18	0.88
Sulculeolaria quadrivalvis	10	1.61±0.08	0.79±0.15	0.18	0.78
Hydromedusae					
Aequorea, Orchistoma, Cunina spp.	14	0.81±0.08	1.27±0.15	0.23	0.87
Ctenophora					
Eurhamphea vexilligera, Cestum sp.	10	1.28±0.07	0.73±0.13	0.15	0.80
Heteropoda					
Pterotrachea hippocampus	8	1.32±0.03	0.86±0.08	0.05	0.95
Pteropoda: Pseudothecosomata					
Corolla spectabilis; Gleba cordata	17	1.22±0.03	0.86±0.04	0.09	0.97
Thaliacea					
Salpa cylindrica, solitary	13	1.61±0.04	0.71±0.08	0.10	0.88
Pegea confederata, aggregate	21	1.30±0.04	1.06±0.09	0.16	0.88

duce a measurable change in both ammonium and oxygen. I disregarded incubations in which oxygen tension fell to <70% of saturation.

Experimental animals were frozen on Gelman type A glass fiber filters. Within 1–6 months after freezing, they were homogenized individually in 1.0 N NaOH for protein analysis by the Lowry method (Lowry et al. 1951). Freeze-dried bovine serum albumin (BSA) was the reference standard.

All measurements of respiration and excretion were standardized to protein, rather than dry weight. The carbon content of gelatinous plankton is only 3–16% of their dry weight (Beers 1966). Previous investigators have confirmed that protein is the major organic fraction in marine zooplankton (Reeve et al. 1970; Ikeda 1972; Mayzaud and Martin 1975).

Results

Individual measurements of collection temperature, size of collecting jar and duration of incubation, animal size and protein content, oxygen consumption (μl O_2 h^{-1}), ammonium excretion (μg-atoms NH_4^+-N h^{-1}) and $O:NH_4^+$ ratio are available in table form from me.

There was no measurable change in oxygen or ammonium content of replicate control jars of seawater after a 6-h incubation at ambient temperature. Moreover, when a siphonophore (*Athorybia rosacea*) was placed in unfiltered seawater and ammonium measured hourly for 4 h in the laboratory, cumulative ammonium

Table 2. As Table 1, but for ammonium excretion at 26 ± 3°C and y = ammonium excretion (μg-atoms NH_4^+-N h^{-1}).

Group	n	a ± s	b ± s	s_{yx}	r^2
Siphonophora: Physonectae					
Agalma okeni	22	-1.21±0.07	0.82±0.10	0.23	0.79
Nanomia bijuga	8	-1.13±0.07	0.71±0.14	0.21	0.82
Forskalia edwardsi; F. tholoides	14	-1.20±0.04	1.10±0.08	0.15	0.93
Athorybia rosacea; Athorybia sp.	11	-0.88±0.08	0.48±0.09	0.19	0.77
Siphonophora: Cystonectae					
Bathyphysa sibogae; Rhizophysa filiformis	13	-1.55±0.18	0.80±0.17	0.22	0.66
Siphonophora: Calycophorae					
Rosacea cymbiformis	13	-1.43±0.08	0.95±0.19	0.20	0.71
Diphyes dispar	10	-1.39±0.08	0.68±0.09	0.18	0.88
Sulculeolaria quadrivalvis	10	-0.91±0.13	0.84±0.25	0.27	0.59
Hydromedusae					
Aequorea, Orchistoma, Cunina spp.	14	-1.64±0.10	1.49±0.18	0.28	0.86
Ctenophora					
Eurhamphea vexilligera, Cestum sp.	5	-1.22±0.03	1.03±0.06	0.04	0.99
Heteropoda					
Pterotrachea hippocampus	8	-0.76±0.11	0.77±0.30	0.20	0.53
Pteropoda: Pseudothecosomata					
Corolla spectabilis: Gleba cordata	6	-1.68±0.28	0.86±0.24	0.30	0.69
Thaliacea					
Salpa cylindrica, solitary	9	-0.85±0.13	0.64±0.24	0.26	0.51
Pegea confederata, aggregate	16	-1.38±0.08	1.22±0.17	0.27	0.79

excretion was linear with time. These results suggest that there was minimum growth of microorganisms in the collecting jars.

Neither oxygen consumption nor ammonium excretion had a negative correlation with jar size or incubation time, suggesting that gelatinous animals did not respond to capture with rapid, short term increases in metabolism. However, the mobility of very active forms like doliolids, *Salpa cylindrica, Ocyropsis maculata, Pelagia noctiluca,* and species of *Sulculeolaria* may be inhibited in jars of 130–980-ml volume. Apart from these species, rates of oxygen consumption and ammonium excretion measured by in situ collection and incubation at environmental temperature probably reflect rates which undisturbed animals show in their natural environment.

Regression equations expressing oxygen consumption and ammonium excretion as power functions of body protein (mg BSA-equivalents) were calculated for 14 of the more abundant types of gelatinous zooplankton (Tables 1 and 2). I have grouped two species of *Forskalia* together because I was unable to distinguish between them. I have more arbitrarily grouped other species in Tables 1 and 2 for which individual data are limited but which had similar rates of respiration and ammonium excretion (Tables 3 and 4). The average coefficient of determination ($r^2 \pm s$) in the 14 groups was 0.86 ± 0.07 for oxygen consumption (Table 1) and 0.75 ± 0.14 for ammonium excretion (Table 2). In other words, about 14% of the variation in oxygen consumption and 25% of the variation in ammonium excretion

Table 3. Respiration [μl O_2 (mg protein-h)$^{-1}$], excretion [μg NH_4^+ (mg protein-h)$^{-1}$], and O : NH_4^+ ratio for siphonophores of three different sizes.

	Respiration [µl O_2(mg protein-h)$^{-1}$]						Excretion [µg NH_4^+(mg protein-h)$^{-1}$]						O:NH_4^+ ratio	
	0.1-1.0 mg		1.1-10.0 mg		10.1-100 mg		0.1-1.0 mg		1.1-.0.0 mg		10.1-100 mg		all sizes	
	N	Mean ± S	N	Mean ± S	N	Mean ± S	N	Mean ± S	N	Mean ± S	N	Mean ± N	N	Mean ± S
Suborder Physonectae														
Agalma okeni	(7)	12±3.9	(46)	12±5.5	(5)	6±0.8	(3)	1.3±0.8	(15)	1.0±0.6	(4)	0.6±0.1	(22)	19±7.8
Agalma elegans	(4)	39±12.7	(3)	16±2.5	-		-		-		-		-	
Cordagalma cordiformis	(6)	27±4.0	-		-		(4)	2.5±0.7	-		-		(4)	16±1.9
Nanomia bijuga	(8)	31±5.1	(11)	14±3.3	-		(5)	1.5±0.7	(3)	1.0±0.5	-		(7)	38±20.5
Forskalia edwardsi; F. tholoides	(8)	20±7.1	(10)	17±4.7	(2)	15±0.1	(6)	1.1±0.5	(8)	1.3±0.2	-		(14)	25±8.0
Athorybia rosacea	(1)	86.2	(4)	11±2.3	(5)	5±2.3	(1)	0.9	(3)	0.8±0.2	(4)	0.7±0.2	(8)	17±14.1
Athorybia sp.	(3)	40±13.7	-		-		(1)	3.3	(2)	1.5±0.1	-		(3)	22±3.6
Suborder Cystonectae														
Bathyphysa sibogae	-		(1)	6.9	(4)	6±0.9	-		(2)	0.5±0.3	(4)	0.3±0.1	(5)	20±8.1
Rhizophysa filiformis	-		(2)	5±2.5	(6)	4±1.4	-		(2)	0.3±0.1	(5)	0.3±0.1	(5)	23±7.6
Suborder Calycophorae														
Stephanophyes superba	(4)	22±3.2	(13)	14±6.3	-		(2)	1.8±0.4	(4)	1.1±0.6	-		(6)	22±8.1
Rosacea cymbiformis	(2)	8±3.6	(11)	8±2.5	-		(4)	0.8±0.4	(9)	0.6±0.3	-		(11)	23±10.3
Diphyes dispar	(7)	17±7.4	(4)	12±3.8	(6)	4±0.9	(2)	0.6±0.1	(3)	1.0±0.4	(5)	0.3±0.1	(10)	25±7.4
Sulculeolaria quadrivalvis	(3)	45±17.1	(6)	36±13.9	(1)	21.3	(2)	2.1±0.3	(7)	2.4±1.7	(1)	0.8	(9)	29±9.8
Sulculeolaria monoica	(7)	32±15.2	(2)	21±2.3	-		(6)	1.5±0.9	(2)	1.6±0.3	-		(7)	36±21.0
Sulculeolaria chuni	(4)	75±25.2	-		-		(4)	2.7±1.0	-		-		(4)	50±23.9
Sulculeolaria biloba	-		(2)	13±0.5	-		-		(2)	1.2±0.2	-		(2)	17±2.3
Abyla sp.	-		(3)	5±0.5	-		-		(3)	0.5±0.2	-		(3)	17±5.5
Chelophyes appendiculata	-		(5)	8±3.3	-		-		(3)	0.5±0.2	-		(3)	26±9.5
Hippopodius hippopus	(1)	17.3	(1)	3.5	-		-		-		-		-	
eudoxid phase, *Diphyes dispar*	(2)	78±20.2	-		-		(2)	1.4±0.7	-		-		(2)	121±78.7
eudoxid phase, *Ceratocymba* sp.	(1)	75.6	(1)	2.3	-		(1)	0.8	(1)	0.1	-		(2)	88±52.9

Table 4. As Table 3, but for gelatinous zooplankton, other than siphonophores, of three different sizes.

	Respiration [µl O_2(mg protein-h)$^{-1}$]						Excretion [µg NH_4^+(mg protein-h)$^{-1}$]						O:NH_4^+ ratio	
	0.1–1.0 mg		1.1–10.0 mg		10.1–100 mg		0.1–1.0 mg		1.1–10.0 mg		10.1–100 mg		all sizes	
	N	Mean ± S	N	Mean ± S	N	Mean ± S	N	Mean ± S	N	Mean ± S	N	Mean ± S	N	Mean ± S
Hydromedusae														
Aequorea sp.	–		(3)	7±0.8	(1)	12.8	–		(3)	0.7±0.4	(1)	1.1	(4)	19±12.7
Orchistoma sp.	–		(3)	14±2.8	–		–		(3)	1.5±0.6	–		(3)	16± 4.7
Cunina sp.	(5)	7±4.7	(2)	8±0.8	–		(3)	0.4±0.1	(2)	0.8±0.1	–		(5)	20±11.4
Scyphomedusae														
Pelagia noctiluca	–		(1)	16.0	(3)	16±7.7	–		(1)	0.8	(3)	1.2±0.6	(4)	23±5.4
Aurelia sp.	–		(1)	6.0	(2)	3±0.6	–		–		(1)	0.2	(1)	23.4
Ctenophora														
Eurhamphea vexilligera	(2)	21±0.9	(5)	11±2.9	–		(1)	1.0	(1)	1.2	–		(2)	22±8.5
Cestum sp.	(1)	22.6	(2)	17±3.5	–		(1)	1.1	(2)	1.0±0.1	–		(3)	27±4.5
Ocyropsis maculata	–		–		(3)	13±3.4	–		–		(3)	2.9±0.7	(3)	7±1.2
Heteropoda														
Pterotrachea hippocampus	–		(8)	19±2.5	–		–		(8)	3.0±0.9	–		(8)	13±6.1
Pteropoda: Pseudothecosomata														
Corolla spectabilis	(5)	18±2.9	(8)	16±3.0	(3)	11±2.3	–		(2)	0.2±0.1	(2)	0.3±0.2	(3)	89±37.6
Gleba cordata	–		(1)	16.5	(1)	8.7	–		(1)	0.5	(1)	0.2	(2)	54±4.6
Thaliacea														
Salpa cylindrica, solitary	(2)	55±1.4	(11)	30±6.5	–		(2)	3.1±0.6	(7)	1.8±1.1	–		(9)	31±13.6
Salpa cylindrica, aggregate	(7)	39±17.8	–		–		(7)	1.9±0.8	–		–		(7)	33±10.1
Salpa maxima, solitary	–		(3)	28±7.1	–		–		(3)	1.5±0.1	–		(5)	28±7.8
Salpa maxima, aggregate	(2)	41±1.5	(5)	14±1.9	–		–		(2)	1.2±0.1	–		(2)	18±1.8
Pegea confederata, solitary	–		(1)	35.5	–		–		(1)	0.9	–		(5)	41±14.6
Pegea confederata, aggregate	(14)	20±5.7	(7)	22±10.4	–		(11)	0.8±0.6	(5)	1.0±0.3	–		(15)	51±24.0
Thalia democratica, solitary	(6)	23±7.6	–		–		–		–		–		–	
Thalia democratica, aggregate	(9)	16±3.5	–		–		–		–		–		–	
Brooksia rostrata, aggregate	(4)	192±38	–		–		–		–		–		–	
miscellaneous doliolids	(4)	54±14.7	–		–		(3)	2.2±1.6	–		–		(6)	45±24.0

Table 5. Respiration [μl O_2 (mg protein-h)$^{-1}$] of gelatinous zooplankton incubated at ambient temperature and 5°C below ambient temperature.

Species	Size (mg protein)	Temp (°C) ambient	Temp (°C) exp	Respiration ambient (R_0)	Respiration exp (R_1)	Ratio R_0:R_1
Forskalia tholoides	0.48	25.5	20.5	20.0*	15.2	1.3
Forskalia tholoides	3.23	25.5	20.5	16.1*	8.1	2.0
Forskalia tholoides	3.15	22.0	17.0	16.0*	5.7	2.8
Forskalia edwardsi	6.33	22.0	17.0	14.1	3.7	3.8
Forskalia edwardsi	10.66	22.0	17.0	18.1	4.1	4.4
Forskalia tholoides	6.38	21.0	16.0	14.9*	3.2	4.7
Forskalia edwardsi	7.77	21.0	16.0	14.6*	2.9	5.0

*Oxygen consumption calculated from Table 1.

cannot be accounted for by variation in body protein. All coefficients of determination were highly significant statistically ($P < 0.001$).

Respiration of gelatinous zooplankton ranged from 2–192 μl O_2 (mg protein-h)$^{-1}$ and excretion from 0.1–3.3 μg NH_4^+ (mg protein-h)$^{-1}$ (Tables 3 and 4). Individuals of smaller size had higher rates of respiration and excretion than those of larger animals. Ratios of respiration at environmental temperatures to respiration at temperatures 5°C lower varied from 1.3 to 5.0, with a tendency for the lower ratios to occur at higher environmental temperatures (Table 5).

Discussion

Rates of oxygen consumption reported for gelatinous animals taken from nets and held for 1–2 days in the laboratory without feeding (Nival et al. 1972; Ikeda 1974) are lower than most rates determined in my study. Since stresses of collection, maintenance in laboratory aquaria, and transfer to respirometer vessels may damage these very delicate animals, extrapolation of previous estimates of oxygen consumption to field populations of gelatinous animals is probably unrealistic. Although estimates of respiration and excretion in my study are not free from bias which may be induced by confinement, animals were collected in situ in the ocean in an attempt to minimize disturbance to them.

Temperature acclimation—Although most respiration measurements were made on gelatinous animals collected at temperatures from 23–29°C, those acclimated to lower habitat temperatures had similar rates of oxygen consumption. Species of *Forskalia* which had 1–10 mg protein respired 17 ± 4.7 μl O_2 (mg protein-h)$^{-1}$ at 23–29°C (Table 3). Four additional colonies (not included in Table 3), ranging in size from 3.15–8.21 mg protein but collected in surface waters of 21 ± 1°C, showed equivalent respiration [20 ± 9.1 μl O_2 (mg protein-h)$^{-1}$]. This implies that species of *Forskalia* can acclimate metabolically to a temperature range of at least 9°C.

Short term exposures to temperatures only 5°C lower than ambient, though, caused twofold to fivefold reductions in oxygen consumption (Table 5). Temperature changes of this magnitude could influence the metabolism of diel migrators. If some gelatinous plankton feed at night

in surface waters and migrate through the thermocline to their daytime depths, they could conserve energy (McLaren 1963), providing increases in respiration due to swimming activity and increased hydrostatic pressure are less than the decrease induced by temperature (Teal and Carey 1967; Smith and Teal 1973). In fact, individuals of many species of siphonophores migrate vertically (e.g. Alvarino 1967; Pugh 1974), and my qualitative in situ observations suggest that several species of doliolids, medusae, and salps may do so as well.

Interspecific differences—The value *b* (Tables 1 and 2) is the exponent in the relation between metabolic rate and size; if metabolism is directly proportional to weight (mg protein), $b = 1$. Actually, *b* was usually <1.0 (Tables 1 and 2), and in most species was not significantly different statistically (*t*-test; $P < 0.05$) from Hemmingsen's (1960) index of 0.73. Variation in the rate at which metabolism changes with size may reflect differences in dietary or reproductive state. However, behavioral and ecological differences between groups of gelatinous zooplankton also contribute to differences in metabolism. For example, cystonect siphonophores had lower respiration and excretion rates than physonect siphonophores (Table 3). Since cystonects lack swimming bells and are only able to writhe about in the water and rise or sink by release or secretion of gas, it is reasonable that they should have lower metabolic rates. In fact, within the physonects, respiration and excretion rates were somewhat lower in species like *A. rosacea* and *Agalma okeni* which are slow swimmers and largely inactive.

Calycophore siphonophores are highly variable in form, and the range of respiration and excretion rates in this group was correspondingly broad. In general, slow-swimming inactive species like *Hippopodius hippopus* and *Abyla* sp. had the lowest rates. *Rosacea cymbiformis*, which is a long-stem, relatively inactive species with flabby bells, had lower respiration and excretion than a faster and more active confamilial like *Stephanophyes superba*.

Most herbivores had high rates of respiration and excretion, especially small forms like the doliolids. Among aggregate salps, both *Thalia democratica* and *Pegea confederata* had lower respiration rates than *S. cylindrica* and *Brooksia rostrata*. The aggregate generations of both *T. democratica* and *P. confederata* differ in the architecture of their chains from *S. cylindrica* and *B. rostrata*, as well. Individuals in chains of *T. democratica* and *P. confederata* are oriented perpendicular to the major axis of the chain, and chains of these species are unable to swim as rapidly as chains of *B. rostrata* and *S. cylindrica*, whose aggregates are oriented at an angle <45° to the major axis (Madin 1974*b*). Moreover, rates of respiration and excretion of all aggregate salps showed a tendency to be less than those of solitary salps of similar size.

Cydippid and cestid ctenophores, along with many medusae, had low rates of respiration and excretion. Other medusae, like *P. noctiluca*, and lobate ctenophores like *O. maculata*, which are muscular, active swimmers, had respiration and excretion rates 1.1–2.7 times higher (Table 4).

The high excretion rates measured in *O. maculata* and *Pterotrachea hippocampus* were reflected in low ratios of $O:NH_4^+$. Pseudothecosomatous pteropods, like *Corolla spectabilis* and *Gleba cordata*, which had very low rates of ammonium excretion, had some of the highest $O:NH_4^+$ ratios (Table 4).

$O:NH_4^+$ ratios and nutrition—Ratios of oxygen atoms consumed to NH_4^+-N atoms excreted by gelatinous carnivores are in accord with those reported for many nongelatinous species. For example, in tropical, subtropical, and temperate planktonic crustacea, most $O:NH_4^+$ ratios ranged between 8 and 24 (Harris 1959; Conover and Corner 1968; Ikeda 1974). Lipid and protein are probably both important metabolites. Protein is about 16% N and requires 1.04 liters of oxygen for complete

combustion of 1 g (Ikeda 1974). If ammonium was the end-product of nitrogen metabolism, the metabolic $O:NH_4^+$ ratio for protein catabolism would be about 8. Oxidation of equivalent weights of protein and lipid requires 2.02 liters of oxygen for complete combustion of 1 g and yields an $O:NH_4^+$ ratio of about 24 (Ikeda 1974), which is in agreement with most of the $O:NH_4^+$ ratios I measured for carnivorous gelatinous zooplankton (Tables 3 and 4).

The very high $O:NH_4^+$ ratios measured in four siphonophore eudoxids (Table 3) may reflect a large amount of nonprotein catabolism in these tiny reproductive forms. In fact, some eudoxids do not seem to feed after being released from the siphonophore colony and therefore may subsist on carbohydrate or lipid reserves for their relatively brief existence.

In general, mean $O:NH_4^+$ ratios in subtropical gelatinous herbivores were higher than those measured in siphonophores and medusae, ranging from 18 for the aggregate generation of *Salpa maxima* to 89 for pteropods like *C. spectabilis* (Table 4). The extremely low O:N ratios reported for salps and other macrozooplankton from areas of the Mediterranean Sea (Mayzaud and Dallot 1973) may reflect damages incurred in collection. Animals collected from plankton nets (300-μ mesh) and from IKMT hauls may have experienced significant abrasion arising from the filtering characteristics of these samplers. After being held for 12 h in the laboratory, some or all may have been dying and either catabolized or leaked unnaturally high levels of nitrogen compounds.

Nutrient cycling—Observations by Eppley et al. (1973) in the oligotrophic central gyre of the North Pacific Ocean indicate that there is close coupling between primary productivity and the excretion (and grazing) rates of zooplankton. They found that ammonium assimilation by phytoplankton populations at two stations in the upper 75 m there averaged 11 and 18 ng-atoms NH_4^+-N liter^{-1} d^{-1}. They measured ammonium excretion by unsorted zooplankton captured with a 102 μ-mesh net at these same stations and calculated excretion per unit volume of seawater. Zooplankton excretion averaged 5 and 9 ng-atoms NH_4^+-N liter^{-1} d^{-1}, or 45–50% of measured phytoplankton assimilation rates of ammonium.

Goering et al. (1964) and Dugdale and Goering (1967), who measured ammonium uptake in the Sargasso Sea at a station 28 km SE of Bermuda, reported apparent rates of microfloral assimilation of ^{15}N-labeled ammonium which averaged 10 ng-atoms NH_4^+-N liter^{-1} h^{-1}. However, as Eppley et al. (1973) pointed out, the apparent rate of NH_4^+ assimilation is strongly dependent on the NH_4^+ concentration in the system, and Goering et al. used high levels of ^{15}N-NH_4^+ in their incubations (0.3–0.5 μg-atom ^{15}N-NH_4^+-N liter^{-1}).

If one assumes that rates of ammonium assimilation by microfloral populations in the central gyre of the North Atlantic Ocean are equivalent to those measured by Eppley et al. (1973), excretion by gelatinous zooplankton could be an important source of nitrogen for phytoplankton and microbial populations there. Gelatinous animals I encountered while SCUBA diving in the Sargasso Sea frequently had 5 mg or more body protein. Most animals of this size excreted 0.3 μg-atom NH_4^+-N h^{-1} (Table 2). An average of one gelatinous zooplankter per cubic meter of seawater (excreting 7 ng-atoms NH_4^+-N liter^{-1} d^{-1}) would be sufficient to supply 39–63% of the ammonium requirements of the phytoplankton. Moreover, this density of gelatinous animals would have the same excretion impact as all of the other zooplankton present in a cubic meter measured by Eppley et al. (1973).

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