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RESPIRATION AND CARBON TURNOVER RATES OF MEDUSAE FROM THE NE PACIFIC

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- Abstract**—1. Weight-specific respiration rates of medusae (10 hydromedusae species and two scyphomedusae species) from the NE Pacific ranged from 0.1 to 0.9 $\mu\text{l O}_2/\text{hr}/\text{mg DW}$.
2. The range is comparable to rates determined for other species of medusae.
3. The value of the mass exponent (b) in the equation describing respiration rate as a power function of biomass ($RR = a X^b$) ranged from 0.7 to 1.4 in the medusae. However, most values were not significantly different from $b = 1$.
4. The value of Q_{10} for respiration rates equalled 1.4–5.3, with a mean of ~ 3 , suggesting that medusae lack thermal compensation, at least over short time-spans.
5. Daily turnover of carbon due to respiration was estimated to equal 2–10% of total body carbon.

INTRODUCTION

The rate at which zooplankton oxidize carbon during metabolism is a fundamental concern when evaluating carbon cycling in the marine environment. Since medusae are significant predators in some pelagic food webs (e.g., Möller, 1979, 1980; Fulton and Wear, 1985; Larson, 1985), it is essential to have data on their respiration rates.

One of the first of such studies was that of Vernon (1899) who measured oxygen uptake by medusae, ctenophores, and salps. Recently, with increased interest in the ecology of gelatinous zooplankton, there have been a number of studies on their metabolism (e.g. Biggs, 1977; Gyllenberg and Greve, 1979; Kremer, 1977, 1982; Mayzaud and Dallot, 1973; Reeve *et al.*, 1978). Some of this work has shown that environmental factors (i.e. temperature and food supply) significantly affect metabolic rates (Kremer, 1977, 1982; Reeve *et al.*, 1978; Kremer *et al.*, 1986).

Recent investigations of O_2 uptake rates of medusae (Mangum *et al.*, 1972; Ikeda, 1974; Biggs, 1977; Kerstan, 1977; Kuzmicheva, 1980; Arai, 1986), have significantly increased our knowledge of the physiology of this group. However, little is known about the relationship between body weight and metabolism. Also, few studies have quantified metabolic carbon turnover rates for medusae.

The present paper provides respiration data for 12 species of medusae (10 hydromedusae, and two scyphomedusae) which are common in neritic waters of the NE Pacific. Also examined were the value of the slope of the regression line of weight specific respiration vs biomass and daily carbon turnover due to respiration.

MATERIALS AND METHODS

Collection and maintenance

Specimens were collected in Saanich Inlet, British Columbia from April to November (1982 and 1983) by dipping them from the surface with a small bucket. Medusae were kept in the laboratory in 20-l. plastic buckets filled with filtered sea-water. Temperatures were maintained at 10 or 15°C; salinities were 28–30 PPT. Medusae were used within 1–2 days after collection.

Respirometry

Respiration (= O_2 uptake) measurements were made on single specimens using a polarographic O_2 sensor (POS). A number of different sized respiration chambers were used (30, 58, 280, 690, or 2075 ml, total volume including pump) and consisted of a clear acrylic cylinder, sealed by a lid with an o-ring (Fig. 1). Water within the chamber was recirculated by a centrifugal stir-bar pump driven by a constant-speed, 300 rpm synchronous motor with a shaft-mounted bar magnet. Pumping rates (6 l/hr for the 30 and 58 ml chambers; 24 l/hr for the larger chambers) were such that water was completely recirculated through the entire chamber within 5 min. Water in the chambers slowly circulated, with little turbulence (as noted by motion of a contained specimen).

During the O_2 uptake measurements, the chamber/POS/pump-assembly was placed in a 70-l. water-bath where temperature was regulated within 0.5°C by a thermostatically-controlled, refrigeration unit.

Sea-water used in the experiments was first filtered through 1.5- μm membrane filters, then autoclaved (250°C for 15 min); after cooling to room temperature, 10 mg/l of streptomycin sulfate plus 10 mg/l neomycin sulfate were added to retard bacterial growth (the effects of antibiotics on respiration rates of medusae were not examined). The water was air-saturated prior to use. O_2 levels were estimated from solubility tables (Forstner and Gnaiger, 1983).

Dissolved oxygen concentrations were measured with a meter. Temperatures and O_2 concentrations were indicated on an analog-type meter. Readings were taken at 10-min intervals for 1 hr, or at 15-min intervals for 1.5–2 hr, depending on the respiration rate of the animal (O_2 levels

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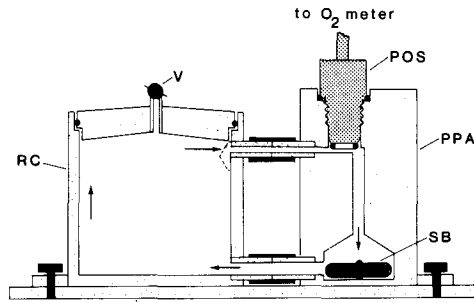


Fig. 1. Diagrammatic cross-section of respiration chamber. (Arrows indicate water circulation). POS = polarographic O₂ sensor; PPA = POS-pump-assembly; RC = respiration chamber; SB = magnetic spin bar; V = valve.

were always >80% of saturation values). Meter readings were checked over a range of O₂ levels and were found to be within 2% of replicated Winkler values.

Respiration rates were calculated from least-squares regressions of O₂ vs time (hr). Rates were constant with time. Average blank (sea-water only) O₂ consumption rates (determined from daily measurements) were subtracted from measured O₂ consumption rates to obtain a corrected rate.

Weight measurements

Dry weights were measured after specimens were blotted to remove superficial water and then freeze-dried to a constant weight.

RESULTS

Respiration rates

Respiration rates (RR) were measured at 10°C

Table 1. Respiration rate parameters* ($Y = aX^b$)

Taxon	T (°C)	a	b †, SE	N	r ‡
Hydromedusae					
<i>Aequorea victoria</i>	10	0.07	1.07, 0.06	45	0.94
<i>Aglantha digitale</i>	10	1.38	0.71, 0.05	22	0.96
<i>Eperetmus typus</i>	10	0.36	0.91, 0.18	11	0.86
<i>Eutonina indicans</i>	10	0.29	0.97, 0.08	25	0.92
<i>Gonionemus vertens</i>	10	0.35	1.14, 0.16	12	0.92
<i>Mitrocoma cellularia</i>	10	0.16	0.87, 0.08	32	0.89
<i>Mitrocoma cellularia</i>	15	0.18	0.87, 0.13	20	0.87
<i>Phialidium gregarium</i>	10	0.30	0.93, 0.14	24	0.81
<i>Phialidium gregarium</i>	15	0.20	1.30, 0.10	20	0.95
<i>Phialidium lomae</i>	15	0.33	1.00, 0.14	25	0.82
<i>Sarsia princeps</i>	10	0.05	1.40, 0.15	8	0.96
<i>Stomatoca atra</i>	10	0.29	0.95, 0.29	14	0.68
<i>Stomatoca atra</i>	15	0.21	1.10, 0.23	13	0.82
Scyphomedusae					
<i>Aurelia aurita</i>	10	0.20	0.92, 0.05	18	0.98
<i>Aurelia aurita</i>	15	0.39	0.91, 0.04	26	0.97
<i>Cyanea capillata</i>	10	0.47	1.00, 0.06	16	0.98
<i>Cyanea capillata</i>	15	0.72	1.04, 0.06	7	0.99

*a = Y intercept, b = slope, X = DW (mg), Y = μl O₂/hr per ind.

†Determined from least-squares regression.

‡P = < 0.05 for all cases.

and/or at 15°C on 10 hydromedusae species and two scyphomedusae species. The weight dependence of oxygen consumption was significant at the 0.05 level, although there was considerable variance from individual to individual as evidenced by the scatter of points and large SE values (Table 1, Figs 2-4).

The slopes of log DW (mg) vs log RR (μl O₂/hr/ind.) for the different species were compared using the GT2-Method (Sokal and Rohlf, 1981). Although a few species had significantly different slope values, most confidence limits overlapped, indi-

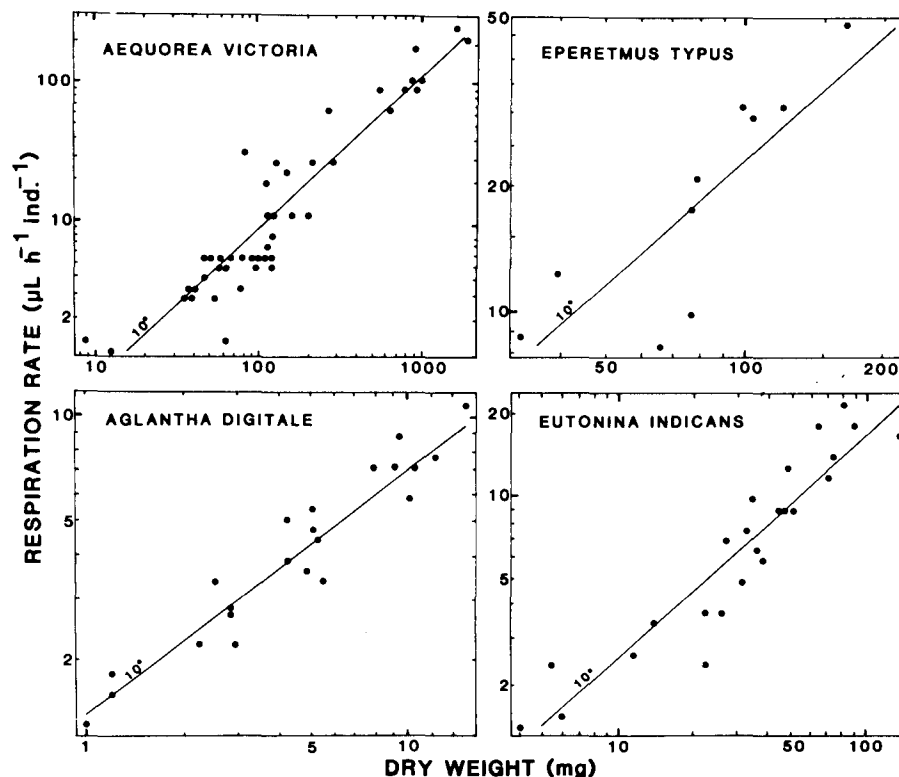


Fig. 2. Scatterplot of dry wt vs respiration rate for *Aequorea victoria*, *Aglantha digitale*, *Eperetmus typus*, and *Eutonina indicans* at 10°C.

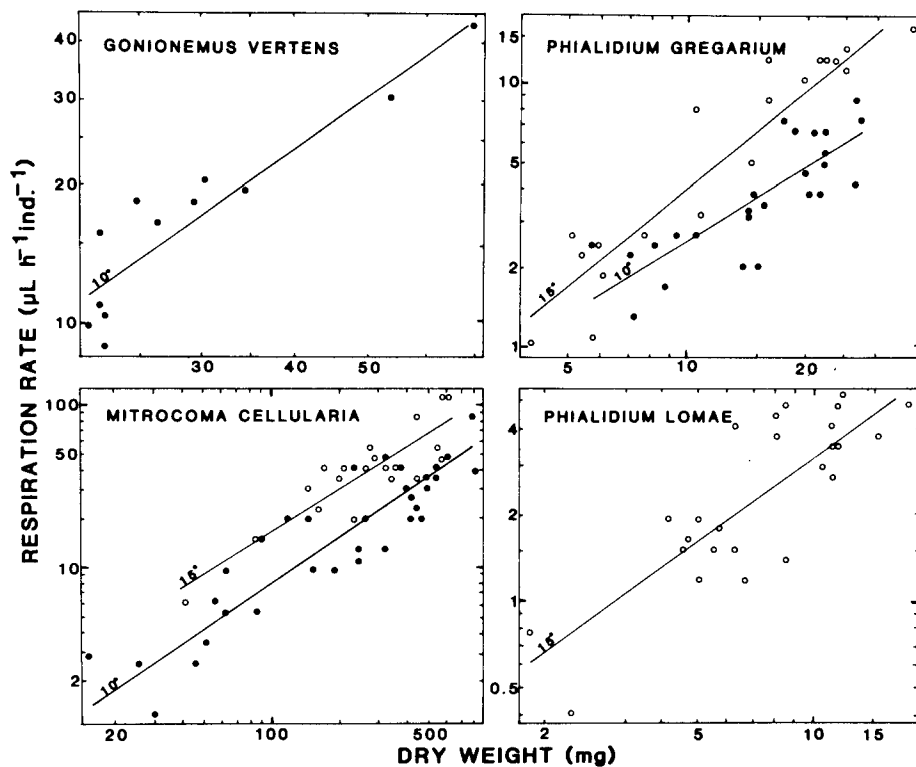


Fig. 3. Scatter lot of dry wt vs respiration rate for *Gonionemus vertens*, *Mitrocoma cellularia*, *Phialidium gregarium*, and *Phialidium lomae*. Closed circles = measurements at 10°C, open circles = measurements at 15°C.

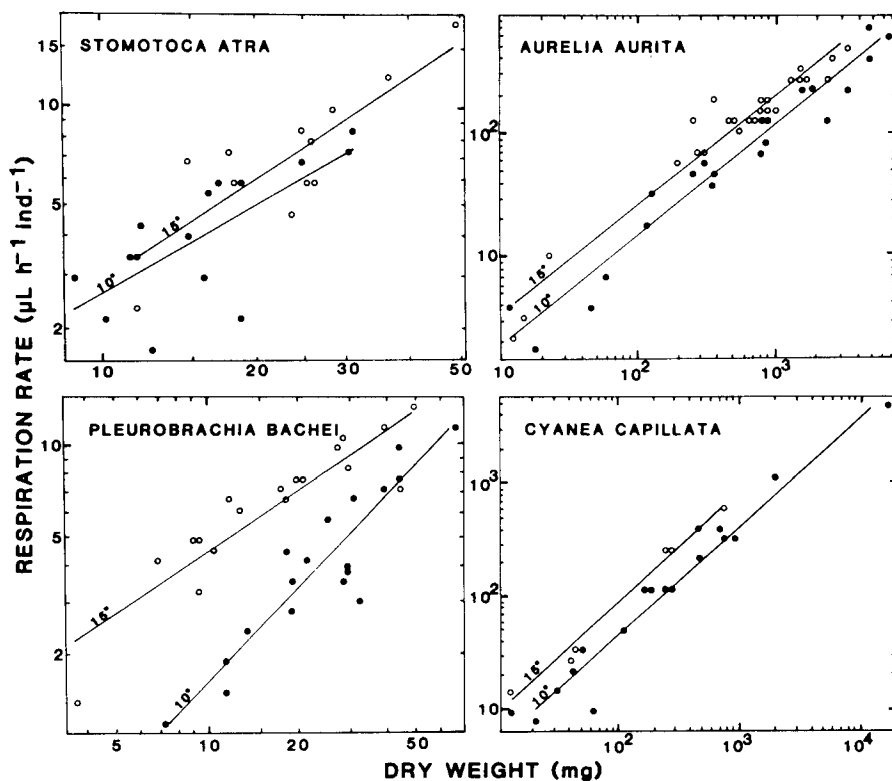


Fig. 4. Scatterplot of dry wt vs respiration rate for *Stomatoca atra*, *Pleurobrachia bachei*, *Aurelia aurita*, and *Cyanea capillata*. Closed circles = measurements at 10°C, open circles = measurements at 15°C.

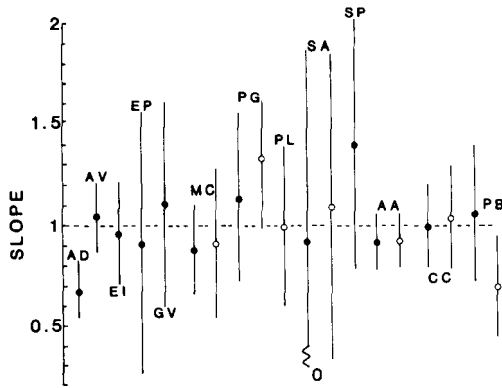


Fig. 5. Comparison of slopes of respiration rate equations by the GT2-method of Sokal and Rohlf (1981), whereby slopes with overlapping confidence limits are not different (mean and 0.05 confidence limits). AD = *Aglantha digitale*, AV = *Aequorea victoria*, EI = *Eutonina indicans*, EP = *Eperetmus typus*, GV = *Gonionemus vertens*, MC = *Mitrocoma cellularia*, PG = *Phialidium gregarium*, PL = *Phialidium lomae*, SA = *Stomatoca atra*, SP = *Sarsia princeps*, AA = *Aurelia aurita*, CC = *Cyanea capillata*, PB = *Pleurobrachia bachei*. Solid circles = measurements at 10°C, open circles = measurements at 15°C.

cating that they were not significantly different at the 95% level (Fig. 5). Also most slopes overlapped $b = 1$.

Mean values for weight-specific respiration rates equalled $<0.1\text{--}1.0 \mu\text{l O}_2/\text{hr}/\text{mg DW}$, a 10-fold range

Table 2. Weight-specific respiration rates

Taxon	Dry Wt (mg) (M & R)*	T (°C)	Respiration rate	
			$\mu\text{l O}_2/\text{hr}/\text{mg DW}$	(M, SE)†
Hydromedusae				
<i>Aequorea victoria</i>	290 (99–1900)	10	0.11, 0.01	
<i>Aglantha digitale</i>	6 (1–16)	10	0.93, 0.06	
<i>Eperetmus typus</i>	99 (33–220)	10	0.25, 0.02	
<i>Eutonina indicans</i>	43 (5–133)	10	0.28, 0.02	
<i>Gonionemus vertens</i>	31 (22–67)	10	0.58, 0.03	
<i>Mitrocoma cellularia</i>	280 (16–770)	10	0.09, 0.01	
<i>Mitrocoma cellularia</i>	310 (40–580)	15	0.16, 0.01	
<i>Phialidium gregarium</i>	16 (6–27)	10	0.26, 0.02	
<i>Phialidium gregarium</i>	14 (5–37)	15	0.46, 0.04	
<i>Phialidium lomae</i>	7 (2–18)	15	0.35, 0.03	
<i>Sarsia princeps</i>	15 (7–40)	10	0.16, 0.02	
<i>Stomatoca atra</i>	15 (9–31)	10	0.26, 0.02	
<i>Stomatoca atra</i>	24 (12–49)	15	0.31, 0.02	
Scyphomedusae				
<i>Aurelia aurita</i>	490 (12–6400)	10	0.14, 0.01	
<i>Aurelia aurita</i>	470 (13–3400)	15	0.24, 0.02	
<i>Cyanea capillata</i>	240 (22–16200)	10	0.48, 0.04	
<i>Cyanea capillata</i>	130 (14–760)	15	0.88, 0.06	

*M & R = mean and range.

†M, SE = mean, standard error.

Table 3. Q_{10} values

Taxon	RR/DW ($\mu\text{l O}_2/\text{hr}/\text{mg DW}$)		Q_{10}
	10°C	15°C	
Hydromedusae			
<i>Mitrocoma cellularia</i>	0.09	0.16	3.2
<i>Phialidium gregarium</i>	0.26	0.46	3.1
<i>Stomatoca atra</i>	0.26	0.31	1.4
Scyphomedusae			
<i>Aurelia aurita</i>	0.14	0.24	2.9
<i>Cyanea capillata</i>	0.48	0.88	3.4

(Table 2). Most values, however, averaged about $0.2\text{--}0.5 \mu\text{l O}_2/\text{hr}/\text{mg DW}$, a much smaller range.

Temperature effects

Q_{10} values for temperature effects on respiration rates were determined after holding the medusae at a constant temperature for 24 hr (Table 3). Values ranged from 3 to 5, with a mean value of ~ 3.2 .

DISCUSSION

Factors affecting respiration rates

A number of factors could have affected respiration rates. Since most of the medusae were collected during the spring when food was abundant and growth was rapid (Larson, 1986a), they were in a good nutritional state. It is possible that the antibiotics used may have affected respiration rates, this was not tested for. Activity of the medusae during the O_2 uptake measurements were likely to have affected the results. Because the activity of medusae can increase when individuals are placed in small containers (e.g. respiration chambers) (Leonard, 1983; author, unpublished), laboratory-measured respiration rates may be more equivalent to active rates than to routine rates. Active metabolic rates of medusae can be twice that of basal rates (Davenport and Trueman, 1985; Larson, 1985).

Slope of the respiration rate equation

The value of the mass exponent or slope (b) in the equation describing metabolism as an exponential function of biomass ($RR = a X^b$) for a species describes the change in the metabolic rate with body wt. Its value must be < 1 , otherwise an organism would have indeterminate growth (i.e. with no upper limit). Yet there is sufficient evidence to suggest that in gelatinous zooplankton, b has a value between 0.8 and 1 (Table 4).

In short-lived invertebrates, such as most medusae and other gelatinous zooplankton, growth may be continuous and exponential for most of the life-span if sufficient food is available (Reeve *et al.*, 1978). However, a significant difference between the metabolic rates of young vs old individuals should be

Table 4. Respiration rate mass exponent values for gelatinous zooplankton

Taxon	Mass exponent	Reference
Hydromedusae	1.3	Biggs, 1977
Hydromedusae	0.8	Arai, 1986
Hydromedusae	0.7–1.4	this paper
Siphonophores	0.3–1.2	Biggs, 1977
Scyphomedusae	0.9–1.0	Krüger, 1968
Scyphomedusae	0.8–1.0	Yakovleva, 1964
Scyphomedusae	0.8–0.9	Kuzmicheva, 1980
Scyphomedusae	0.9	Shushkina and Musayeva, 1983
Scyphomedusae	0.9–1.0	this paper
Ctenophores	1	Williams and Baptist, 1966
Ctenophores	1.0	Hirota, 1972
Ctenophores	0.6–0.9	Baker, 1973
Ctenophores	0.7	Biggs, 1977
Ctenophores	1	Kremer, 1977, 1982
Ctenophores	0.8	Gyllenberg and Greve, 1979
Ctenophores	0.7–1.1	Kremer <i>et al.</i> , 1986
Ctenophores	0.7–1.0	this paper
Thaliaceans	0.7–1.1	Biggs, 1977
Thaliaceans	1.0	Ikedo and Mitchell, 1982

Table 5. Weight-specific respiration rates for hydromedusae

Taxon	Respiration rate $\mu\text{l O}_2/\text{hr}/\text{mg DW}$	T ($^{\circ}\text{C}$)	Reference
<i>Aequorea victoria</i>	0.5*	10	Arai, 1986
<i>Aequorea victoria</i>	0.6*	15	Arai, 1986
<i>Aequorea victoria</i>	0.1	10	this paper
<i>Aequorea</i> sp.	0.8†	23–29	Biggs, 1977
<i>Aglantha digitale</i>	1.4	6–11	Ikeda, 1974
<i>Aglantha digitale</i>	5.3	15–18	Ikeda, 1974
<i>Aglantha digitale</i>	0.2	?	Båmstedt, 1978
<i>Aglantha digitale</i>	0.9	10	this paper
<i>Cunina</i> sp.	0.6†	23–29	Biggs, 1977
<i>Eperetmus typus</i>	0.2	10	this paper
<i>Eutonia indicans</i>	0.3	10	this paper
<i>Geryonia proboscoidalis</i>	0.3	16	Vernon, 1899
<i>Gonionemus vertens</i>	0.6	10	Vernon, 1899
<i>Gonionemus</i> sp.	1.5	29	Rajagopal, 1962
<i>Liriope tetraphylla</i>	0.5	27	Ikeda, 1974
<i>Mitrocoma cellularia</i>	0.1	10–15	this paper
<i>Orchistoma</i> sp.	1.1†	23–29	Biggs, 1977
<i>Phialidium gregarium</i>	0.4	10–15	this paper
<i>Phialidium lomae</i>	0.4	15	this paper
<i>Rathkea octopunctata</i>	3.0	15–18	Ikeda, 1974
<i>Sarsia princeps</i>	0.2	10	this paper
<i>Stomatoca atra</i>	0.3	10–15	this paper

*Assume DW/AFDW = 4.

†Assume protein/N = 4 and N/DW = 0.02.

evident. For example, respiration rates for *Cyanea* are proportional to pulsation rates (Larson, 1985) and in medusae, pulsation rates are inversely proportional to bell diameter (Romanes, 1877; Child, 1918; Arkett, 1984; Satterlie, 1985). Thus, higher respiration rates would be expected for smaller medusae. However, most respiration studies exclude small specimens because of the difficulty involved with measuring their metabolism; and old individuals are excluded because they are rare. Consequently, most of the respiration studies have probably been done on actively-growing individuals, where the weight-specific metabolic rate is more or less constant. The overall significance of this is that, in medusae and

other gelatinous species, there is only a small metabolic gain in being large (other things being equal), since weight-specific metabolism is nearly independent of size. Furthermore, the high *b*-values suggest that these species have a prolonged period of active metabolism (i.e. physiological senescence is relatively brief). This same metabolic life-history pattern has been noted for short-lived squids (DeMont and O'Dor, 1984).

Weight-specific respiration rates

Mean values for weight-specific respiration rates for medusae are reviewed in Tables 5 and 6. Most values range from 0.1 to 1 $\mu\text{l O}_2/\text{hr}/\text{mg DW}$, with a mean value of ~ 0.5 . Very low (< 0.05) or exceptionally high values (> 1.5) may be due to experimental error. Most values are fairly consistent from taxon to taxon, especially if the differences in temperatures are taken into account.

How do the respiration rates of medusae compare with those of other zooplankton? Medusae have respiration rates of ~ 0.1 – $1 \mu\text{l O}_2/\text{hr}/\text{mg DW}$. Respiration rates for ctenophores have a slightly lower per cent carbon value than medusae; they also have a lower metabolic rate (0.1 – $0.5 \mu\text{l O}_2/\text{hr}/\text{mg DW}$) (Baker, 1973; Kremer, 1977; Reeve *et al.*, 1978; Gyllenberg and Greve, 1979; Kremer *et al.*, 1986). In contrast, carbon-rich planktonic crustaceans (i.e. copepods and euphausiids) have much higher rates (~ 0.5 – $15 \mu\text{l O}_2/\text{hr}/\text{mg DW}$) (Raymont, 1983). However, when respiration rates are examined on a carbon-specific basis, a much better way to express the metabolic biomass, the rates are comparable (crustaceans = ~ 1 – $40 \mu\text{l O}_2/\text{hr}/\text{mg C}$, medusae = ~ 2 – $20 \mu\text{l O}_2/\text{hr}/\text{mg C}$).

Temperature effects

Values for Q_{10} of various gelatinous zooplankton are reviewed in Table 7. These range from 1 to 25,

Table 6. Weight-specific respiration rates for scyphomedusae

Taxon	Respiration rate $\mu\text{l O}_2/\text{hr}/\text{mg DW}$	T ($^{\circ}\text{C}$)	Reference
<i>Aurelia aurita</i>	0.3*	13–18	Thill, 1937
<i>Aurelia aurita</i>	0.2*	13–17	Nicol, 1960
<i>Aurelia aurita</i>	0.2	20	Yakovleva, 1964
<i>Aurelia aurita</i>	0.2†	23–29	Biggs, 1977
<i>Aurelia aurita</i>	0.2*	12–14	Kerstan, 1977
<i>Aurelia aurita</i>	0.1*	22	Mergner and Svoboda, 1977
<i>Aurelia aurita</i>	0.3‡	20	Kuzmicheva, 1980
<i>Aurelia aurita</i>	0.2*	20	Shushkina and Musayeva, 1983
<i>Aurelia aurita</i>	0.2	10–15	this paper
<i>A. aurita</i> ephyrae	4*	22	Mangum <i>et al.</i> , 1972
<i>A. aurita</i> planulae	3.5	20–22	Schneider and Weisse, 1985
<i>Cassiopea andromeda</i>	0.1‡	22	Mergner and Svoboda, 1977
<i>Chrysaora hysoscella</i>	0.2‡	15	Krüger, 1968
<i>Cyanea capillata</i>	0.4‡	15	Krüger, 1968
<i>Cyanea capillata</i>	0.1	5	Mangum <i>et al.</i> , 1972
<i>Cyanea capillata</i>	0.2	15	Mangum <i>et al.</i> , 1972
<i>Cyanea capillata</i>	0.7	10–15	this paper
<i>Pelagia noctiluca</i>	1.9**	23–29	Biggs, 1977
<i>Pelagia noctiluca</i>	1.0	18	Davenport and Trueman, 1985
<i>Poralia rufescens</i>	0.2	3	Smith, 1982
<i>Rhizostoma octopus</i>	0.3‡	15	Krüger, 1968
<i>Rhizostoma pulmo</i>	0.4‡	16	Vernon, 1899
<i>Rhizostoma pulmo</i>	0.4	20	Yakovleva, 1964

*Assume DW/WW = 0.03.

†Assume protein/N = 4 and N/DW = 0.01.

‡Assume DW/WW = 0.04.

**Assume protein/N = 4 and N/DW = 0.03.

Table 7. Q_{10} -values for gelatinous zooplankton

Taxon	Q_{10}	T (°C)	Reference
Hydromedusae			
<i>Geryonia proboscidalis</i>	1.8	10-24	Vernon, 1899
<i>Mitrocoma cellularia</i>	3.2	10-15	this paper
<i>Phialidium gregarium</i>	3.2	10-15	this paper
<i>Stomatoca atra</i>	1.4	10-15	this paper
Siphonophores			
<i>Forskalia</i> spp.	2-25	16-25	Biggs, 1977
Scyphomedusae			
<i>Aurelia aurita</i>	2.9	10-15	this paper
<i>Cyanea capillata</i>	2.6	5-10	Mangum <i>et al.</i> , 1972
<i>Cyanea capillata</i>	3.4	10-15	Mangum <i>et al.</i> , 1972
<i>Rhizostoma pulmo</i>	2.6	10-24	Vernon, 1899
Ctenophores			
<i>Beroe gracilis</i>	3.6	8-20	Gyllenberg and Greve, 1979
<i>Beroe ovata</i>	3.2	10-24	Vernon, 1899
<i>Bolinopsis infundibulum</i>	3.7	8-20	Gyllenberg and Greve, 1979
<i>Cestum veneris</i>	2.9	10-24	Vernon, 1899
<i>Mnemiopsis leidyi</i>	1-7	4-29	Miller, 1970
<i>Mnemiopsis leidyi</i>	3-4	10-24	Kremer, 1977
<i>Mnemiopsis mccradyi</i>	2	21-31	Baker, 1973
<i>Pleurobrachia bachei</i>	3.3	10-18	Kremer P., unpublished
<i>Pleurobrachia bachei</i>	5.3	10-15	this paper
<i>Pleurobrachia pileus</i>	2.7	2-24	Gyllenberg and Greve, 1979
Thaliaceans			
<i>Salpa tilesii</i>	2.9	10-24	Vernon, 1899
<i>Thalia democratica</i>	3.0	5-15	Mayzaud and Dallot, 1973

with the mean value equal to ~ 3 . Values of > 2 imply a lack of thermal accommodation, suggesting that gelatinous zooplankton have limited ability to regulate metabolism over a range of temperatures. Yet Q_{10} values are subject to considerable variance due to outside influences such as handling of the animals, seasonal effects, and other factors. For example, Mangum *et al.* (1972) found that temperature acclimation in scyphomedusae (including

their polyps and ephyrae) could reduce acute temperature effects by about 50%.

Carbon turnover and maintenance ration

Respiration rate data can be used to estimate the maintenance ration, i.e. amount of carbon or energy required to maintain an animal at a constant weight (assuming there are no other significant carbon losses). In order to calculate the maintenance ration,

Table 8. Daily respiratory carbon turnover for medusae as % of body carbon*

Taxon	C Turnover % Body C/d	T (°C)	Reference
Hydromedusae			
<i>Aequorea victoria</i>	5	10	this paper
<i>Aglantha digitale</i>	9-34†	7-15	Ikeda, 1974
<i>Aglantha digitale</i>	6	10	this paper
<i>Eperetmus typus</i>	2	10	this paper
<i>Eutonina indicans</i>	3	10	this paper
<i>Gonionemus vertens</i>	4	10	this paper
<i>Mitrocoma cellularia</i>	3-5	10-15	this paper
<i>Phialidium gregarium</i>	3-5	10-15	this paper
<i>Phialidium loma</i>	5	15	this paper
<i>Sarsia princeps</i>	2	10	this paper
<i>Stomatoca atra</i>	3	10-15	this paper
Scyphomedusae			
<i>Aurelia aurita</i>	8‡	13-18	Thill, 1937
<i>Aurelia aurita</i>	5‡	13-17	Nicol, 1960
<i>Aurelia aurita</i>	5‡	20	Yakovleva, 1964
<i>Aurelia aurita</i>	3‡	22	Mergner and Svoboda, 1977
<i>Aurelia aurita</i>	8‡	20	Kuzmicheva, 1980
<i>Aurelia aurita</i>	4-6	10-15	this paper
<i>Aurelia aurita planulae</i>	10	20-22	Schneider and Weisse, 1985
<i>Chrysaora hysoscella</i>	3**	15	Krüger, 1968
<i>Cyanea capillata</i>	3§	15	Krüger, 1968
<i>Cyanea capillata</i>	1-2§	5-15	Mangum <i>et al.</i> , 1972
<i>Cyanea capillata</i>	4-7	10-15	this paper
<i>Poralia rufescens</i>	5§	3	Smith, 1982
<i>Rhizostoma octopus</i>	4	15	Krüger, 1968
<i>Rhizostoma pulmo</i>	7	16	Vernon, 1899

*Assume RQ = 0.8, carbon values from Larson (1986b).

†Assume C/DW = 0.16.

‡Assume C/DW = 0.04.

**Assume C/DW = 0.09.

§Assume C/DW = 0.12.

||Assume C/DW = 0.07.

it is first necessary to determine the respiratory substrate, i.e. lipid, carbohydrate or protein being catabolized. Since medusae are carnivores, the respiratory quotient (RQ) (CO_2 produced/ O_2 consumed) values should be between 0.7 (lipid) and 0.8 (protein). Kremer (1977) found that the RQ for a ctenophore was 0.74.

By multiplying the RQ by the number of moles of oxygen utilized per unit time and then by the atomic weight of carbon, the weight of carbon oxidized per unit time can be calculated. The resulting carbon value would represent the carbon turnover rate. This value is best expressed as a weight-specific value.

Table 8 reviews estimated daily carbon turnover rates for medusae (assuming RQ = 0.8). Most values are < 10%, indicating that carbon equivalent to 10% or less of the total body carbon, must be replaced daily to offset carbon that was lost through respiration. Values for daily carbon turnover > 20% are questionable because it is unlikely that food intake could be that high over extended periods of time. Because only a fraction (~70–90%) of the carbon ingested is actually assimilated, carbon intake would have to exceed that lost by respiration by 10–30% to avoid weight loss.

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