



Synthesis toward a global model of metabolism and chemical composition of medusae and ctenophores

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ARTICLE INFO

Article history:

Received 8 October 2013

Received in revised form 8 March 2014

Accepted 10 March 2014

Available online 12 April 2014

Keywords:

Ammonia excretion

CN composition

Ctenophores

Medusae

O:N ratio

Respiration

ABSTRACT

Respiration and ammonia excretion data and chemical composition data [water content, ash, carbon (C), nitrogen (N) and C:N ratios] of a total of 28–72 species of hydromedusae, scyphomedusae, siphonophores and ctenophores from various depths of the world's oceans were compiled. Multiple regression analyses revealed that body mass and habitat temperature but habitat depth were significant predictors for respiration and ammonia excretion rates. The scale exponents of body mass (0.66–1.05) and temperature coefficients (1.7–3.1 as Q_{10}) of the empirical regression models varied greatly by the choice of body mass units (DM, C or N). The O:N ratios (median: 15.0) were independent of these parameters. Body C and N compositions (% of DM) decreased with the increase in either DM or habitat temperature, showing a stable C:N ratio of 3.8 (by mass). Comparison of the present results with global-bathymetric features of chaetognaths, copepods, euphausiids and mysids revealed that the medusae and ctenophores are unique in that they maintain high metabolic rates per unit body N, lack significant effects of habitat depth on metabolic rates, have high specific growth rates, and have little accumulation of energy reserves (lipids) in the body.

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1. Introduction

Medusae of the phylum Cnidaria (hydromedusae, siphonophores, scyphomedusae) and the phylum Ctenophora are collectively often called “jellyfish” and they are typical members of the gelatinous zooplankton which occurs in coastal waters and at various depth horizons of the world's oceans (Raymont, 1983). Medusae and ctenophores are planktonic predators, feeding on diverse zooplankton taxa (especially crustaceans) and they have been described as apex predators for “low-energy” food chains (small flagellates—jellyfish) in contrast to traditional “high-energy” food chains (large diatoms—fish) (Mills, 1995; Parsons and Lalli, 2002; Purcell, 1991). Since 1960s, blooms of medusae and/or ctenophores have been reported from many locations of the world (Brotz et al., 2012; Purcell et al., 2007). The reasons for jellyfishes blooms (leading to “low-energy” food chains) has been linked to human activities associated with pollution, eutrophication, overfishing, construction, and climate change but causes remain unresolved. Jellyfish is characterized by high water content, and have long been considered that their physiological rate processes per body mass are low. However, recent studies have shown that jellyfish exhibit foraging capacity and growth potential similar to or even greater than those of other zooplankton or fish of equivalent body carbon (Acuña et al., 2011; Pitt et al., 2013).

Information about metabolism (respiration rates, ammonia excretion rates, and O:N as $\text{NH}_4\text{-N}$ ratios) has proved useful in understanding the

energy demand, metabolic substrates and nutritional condition of marine zooplankton (Ikeda et al., 2000). Historically body mass and temperature have been regarded as the two major parameters for defining the metabolic characteristics of marine epipelagic animals (Ikeda, 1985; Ivleva, 1980), yet habitat depth has emerged as an additional parameter since metabolic rates decrease rapidly with depth for larger pelagic animals with image-forming eyes such as micronektonic fishes, crustaceans, and cephalopods (Childress, 1995; Seibel and Drazen, 2007). Reduced metabolic rates have also been reported on deep-living copepods and chaetognaths which lack functional eyes (Brey, 2010; Ikeda and Takahashi, 2012; Ikeda et al., 2006a; Kruse et al., 2010). For medusae and ctenophores, data are available in the literature on the effects of body mass and temperature within and between species (Biggs, 1977; Kremer et al., 1986; Larson, 1987a; Pitt et al., 2009; Scolardi et al., 2006; Purcell, 2009 and others), but data on the effect of habitat depth on metabolism are currently limited (Bailey et al., 1994a, 1995; Thuesen and Childress, 1994).

Accumulation of lipids in the body is a widespread phenomenon across marine zooplankton taxa (such as copepods and euphausiids) living in the cold temperature regimes of high latitudes and the deep sea, and lipids are considered as an important energy reserve for coping with food scarcity, for reproduction or energy savings while swimming via neutral buoyancy (Lee et al., 2006). Deep-living micronektonic crustaceans and pelagic copepods are characterized by low protein or N content, suggesting reduced musculature for locomotion (Childress and Nygaard, 1974; Ikeda et al., 2006b). Reduced locomotion at depth may reflect reduction in predation pressure with depth (Childress, 1995; Ikeda et al., 2006b). Larson (1986) described the chemical

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composition (water content, ash, C and N) of shallow-water medusae, and Larson and Harbison (1989) surveyed visible lipid droplets for Arctic and Antarctic medusae and ctenophores and they discussed the origin and fate of lipids under starved conditions. Bailey et al. (1995) and Clarke et al. (1992) reported proximate composition and C and N composition of 5 mesopelagic and bathypelagic species of medusae and 2 species of ctenophores off Cape Hatteras, North Carolina, USA, and 4 medusae from the Southern Ocean. Lucus et al. (2011) compiled published data of proximate and elemental compositions of a total of 102 species of medusae, ctenophores and thaliaceans. Although these results have contributed substantially to our understanding of body chemical composition of medusae and ctenophores, no attempt has been made to analyze these data within the context of global-bathymetric models.

As part of the project to establish metabolic and body compositional responses of major marine zooplankton/micronekton taxa, therefore, I have compiled published data of metabolism (respiration, ammonia excretion, and O:N ratios) and chemical composition (water content, ash, C, N and C:N ratios) of medusa and ctenophore species living at various depths in polar, temperate and tropical/subtropical seas, and significant parameters affecting the variance were explored. The present results are compared with those of the global-bathymetric models reported previously for pelagic copepods (Ikeda et al., 2007), chaetognaths (Ikeda and Takahashi, 2012; Kruse et al., 2010), euphausiids (Ikeda, 2013a), mysids (Ikeda, 2013b) and amphipods (Ikeda, 2013c) to highlight unique features of medusae and ctenophores.

2. Materials and methods

2.1. The data compilation

For the present analyses, the data compiled were those which met the following criteria:

1. Data represented post-larvae collected from the field and used for experiments without considerable time delay (<24 h) with exceptions of <8 days delay (Morand et al., 1987), 4–5 days delay (Ikeda and Hirakawa, 1998) or unspecified (Thuesen and Childress, 1994).
2. Measurements were made in the absence of food at near in situ temperatures in the dark or under natural light regimes for epipelagic or shallow-living medusae and ctenophores. For delicate deep-sea species, the data were those derived from in situ capture and incubations by the use of submersibles (Bailey et al., 1994a, 1994b, 1995; Smith, 1982). For robust deep-sea species, the data are those recovered to the surface (1 atm) on the premise that hydrostatic pressure affects little to the metabolism of deep-sea medusae and ctenophores (Childress and Thuesen, 1993; Thuesen and Childress, 1994). The metabolic rate measured on pelagic animals at uncontrolled but minimum motor activity is defined as “routine metabolism” (Ikeda et al., 2000). The ratio of “routine metabolism” to “standard metabolism” (anesthetized immobile specimens) has been reported as 2.1 for a scyphomedusa *Pelagia noctiluca* (Davenport and Trueman, 1985), 2 for *Stomolophus meleagris* (Larson, 1987a) and 4.5 for a ctenophore *Beroë ovata* (Svetlichny et al., 2004).
3. O:N ratios were computed from simultaneous measurements of respiration rates and ammonia excretion rates.
4. Body mass in terms of wet mass (WM), dry mass (DM), carbon (C), nitrogen (N) or protein (PRO) units were given alone, or together with metabolic data. (Note: body mass specific rates without body mass data are not useful).
5. The depth of sampling of specimens was described or deducible (the depth of near surface collections was assigned as 1 m for regression analyses).
6. Body composition (water content, ash, C and N) were derived with standard methods (Omori and Ikeda, 1984; Postel et al., 2000) (Note: percent composition without body mass data is not useful).

As a result, a total of 93 datasets on 72 species (55 and 18 species from datasets A and B, respectively) plus 3 size categories of siphonophores, and 38 datasets on 30 species plus 3 size categories of siphonophores were selected in the present study, and these were analyzed for respiration and ammonia excretion rates (Table 1). For siphonophore data, a colony was treated as an individual based on experimental observations on colonial ascidians (Nakaya et al., 2005). The same medusae or ctenophores but from different locations or seasons (when differences in thermal conditions were appreciable) were treated as independent datasets, though mere repetition of the data on the same species from the same or nearly habitats was carefully avoided. The data expressed in the form of regression equations only were converted to the metabolic rates of a specimen at mid-body mass ranges (= geometric means). For chemical composition, 47 datasets of water content, 38 datasets of ash, and 61–62 datasets of C, N and C:N ratios were available on 35, 28 and 44 medusae and ctenophores, respectively (Table 2). Missing habitat temperature data in some of the literature in Table 2 were substituted by those in the World Ocean Atlas of the National Oceanography Data Center (NODC) Homepage by knowing the location, season and depth. Study sites of all medusae and ctenophores are plotted on the world map (Fig. 1) to illustrate the worldwide coverage of the datasets in the present study.

Thuesen and Childress's (1994) data (Dataset B, Table 2) were treated separately from the other published datasets because their “minimum-depth of occurrence” (MDO; below which 90% of the population can be found) is difficult to translate to the sampling depth (= habitat depth) because of the broad vertical distribution of each medusa or ctenophores. For comparative purposes, MDO was assumed to be equivalent to mid-sampling depth, and body WM was converted to DM, C or N by using appropriate conversion equations established in the present study (see Section 3.3 below).

2.2. Regression models

To analyze metabolic data, two regression models were adopted according to the mathematical form of the temperature and body mass effects. One was a theoretical model characterized by the Arrhenius relationship and the other was an empirical (or log/linear) model characterized by the Van't Hoff rule (Q_{10}) (Ikeda, 2013a, 2013b, 2013c; Ikeda and Takahashi, 2012; Ikeda et al., 2007);

$$\text{Theoretical model: } \ln Y = a_0 + a_1 \ln X_1 + a_2 \left(1000X_2^{-1} \right) + a_3 \ln X_3 + a_4 X_{SC} + a_5 X_{SI} + a_6 X_{HY}$$

$$\text{Empirical model: } \ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3 + a_4 X_{SC} + a_5 X_{SI} + a_6 X_{HY}$$

where, Y is the respiration rate ($\mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) or ammonia excretion rate ($\mu\text{g N ind.}^{-1} \text{ h}^{-1}$), X_1 is the body mass, X_2 is the habitat temperature ($1000/K$ for the theoretical model, and $^{\circ}\text{C}$ for the empirical model), X_3 is the mid-sampling depth (m), and X_{SC} , X_{SI} and X_{HY} are the dummy variables on scyphomedusae, siphonophores and hydromedusae, respectively (for the definitions of these dummy variables, see Appendix). In order to make between-taxa comparison of marine zooplankton with diversified body composition possible, DM, C or N was used in the present analyses. For the datasets in which body mass was reported as WM without information about water content, DM was estimated assuming a grand mean of water content obtained in the present study (96.0% of WM), then converted to C or N mass by means of conversion equations established in the present study (see Section 3.3). It is noted that a_1 was 0.75 (= 3/4, cf. Gillooly et al., 2001) and a_2 was $-E_a / (k \times 1000)$ [E_a : activation energy, k: Boltzmann's constant ($8.62 \times 10^{-5} \text{ eV/K}$)] for the theoretical model. As an index of temperature effects, Q_{10} of the empirical model could be computed as $Q_{10} = \exp(10 \times a_2)$. The attributes of these variables were analyzed simultaneously by using stepwise

Table 1

A list of medusa and ctenophore species of which metabolic and chemical composition data were analyzed.

Data set	Phylum/Class	Genus and species	Code	Collection site	Date	Reference
Cnidaria A	Hydrozoa	<i>Aeginura grimaldii</i>	1	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
		<i>Aequorea victoria</i>	2	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Aglantha digitale</i>	3a	Usujiri coast, Hokkaido, Japan	May 1971	Ikeda (1974)
		<i>Aglantha digitale</i>	3b	Barents Sea	May/Jun 1987	Ikeda and Skjoldal (1989)
		<i>Aglantha digitale</i>	3c	W. subarctic Pacific Ocean	Mar 2006	Ikeda (unpublished data)
		<i>Aglantha digitale</i>	3d	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Benthocodon pedunculata</i>	4	Off Sweeting Cay, the Bahamas	Dec 1990, Mar 1991	Bailey et al. (1994a)
		<i>Botrynema brucei</i>	5	Off South Georgia, Southern Ocean	Jan 1987	Clarke et al. (1992)
		<i>Bougainvillia muscus</i>	6	North Inlet, S Carolina, USA	Jan, Jul 2006	Marshallones and Pinckney (2007)
		<i>Calycopsis borchgrevinki</i>	7a	Off Enderby Land, Antarctica	Oct 1985	Ikeda (unpublished data)
		<i>Calycopsis borchgrevinki</i>	7b	Off South Georgia, Southern Ocean	Jan 1987	Clarke et al. (1992)
		<i>Clytia hemisphaerica</i>	8	North Inlet, S Carolina, USA	Jan, Jul 2006	Marshallones and Pinckney (2007)
		<i>Colobonema sericeum</i>	9	off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
		<i>Crossota</i> sp.	10	W. subarctic Pacific Ocean	Dec 2004	Ikeda (2012)
		<i>Earleria cellularia</i> (formerly <i>Mitrocoma cellularia</i>)	11a	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Earleria cellularia</i> (formerly <i>Mitrocoma cellularia</i>)	11b	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Eperetmus typus</i>	12	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Eutonia indicans</i>	13	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Gonionemus vertens</i>	14	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Liriope tetraphylla</i>	15	Tropical Indian/Atlantic Ocean	Nov/Dec 1971	Ikeda (1974)
		<i>Nemopsis bachei</i>	16	North Inlet, S Carolina, USA	Jan, Jul 2006	Marshallones and Pinckney (2007)
		<i>Pantachogon haeckeli</i>	17	W. subarctic Pacific Ocean	Mar 2003	Ikeda (2012)
		<i>Phialidium gregarium</i>	18a	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Phialidium gregarium</i>	18b	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Phialidium lomae</i>	19	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Sarsia princeps</i>	20	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Solmissus incisus</i>	21	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
		<i>Stomatoca atra</i>	22a	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Stomatoca atra</i>	22b	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
	Siphonophora	<i>Abylopsis tetragona</i>	23	Villefranche-sur-Mer, France	Jul 1960, Jul–Oct 1970	Nival et al. (1972)
		<i>Chelophyes appendiculata</i>	24	Villefranche-sur-Mer, France	Jul, Oct 1970	Nival et al. (1972)
		<i>Diphyes antarctica</i>	25a	Off Enderby Land, Antarctica	Oct 1985	Ikeda (unpublished data)
		<i>Diphyes antarctica</i>	25b	Off South Georgia, Southern Ocean	Jan 1987	Clarke et al. (1992)
		<i>Diphyes</i> sp.	26	Cape Ferguson Coast, N Queensland, Australia	May 1978	Ikeda (unpublished data)
		19 species	27	Subtropical N Atlantic Ocean		Biggs (1977)
	Scyphozoa	<i>Atolla wyvillei</i>	28	Off South Georgia, Southern Ocean	Jan 1987	Clarke et al. (1992)
		<i>Aurelia aurita</i>	29a	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Aurelia aurita</i>	29b	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Aurelia aurita</i>	29c	Seto Inland Sea, Japan	Jul–Aug 1991, May–Jun 1992	Uye and Shimauchi (2005)
		<i>Aurelia aurita</i>	29d	Kiel Bight, W. Baltic Sea	Mar–Oct 1982, 1983, 1984	Schneider (1989)
		<i>Cassiopea xamachana</i>	30a	Florida Keys, Florida, USA	Sep 1992	Verde and McCloskey (1998)
		<i>Cassiopea xamachana</i>	30b	Florida Keys, Florida, USA	Jan 1993	Verde and McCloskey (1998)
		<i>Catostylus mosaicus</i>	31	Smiths Lake, NSW, Australia	Feb 2003	Pitt et al. (2005)
		<i>Chrysaora quinquecirrha</i>	32	Chesapeake Bay, Maryland, USA	May–Oct 1990	Nemazie et al. (1993)
		<i>Cyanea capillata</i>	33a	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
		<i>Cyanea capillata</i>	33b	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Cyanea capillata</i>	33c	Saanich Inlet, BC, Canada	Apr–Nov 1982, 1983	Larson (1987a)
		<i>Mastigias</i> sp.	34	Eil Malk Jellyfish Lake, Palau	Feb–Mar 1982	McCloskey et al. (1994)
		<i>Pelagia noctiluca</i>	35a	Off W Africa	Aug 1983	Davenport and Trueman (1985)
		<i>Pelagia noctiluca</i>	35b	W. Mediterranean Sea	Jun–Dec 1984, 1985	Morand et al. (1987)
		<i>Periphylla periphylla</i>	36	Lurefjorden, W coast of Norway	Mar, Nov 1999	Youngbluth and Båmstedt (2001)
		<i>Poralia rufescens</i>	37a	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
		<i>Poralia rufescens</i>	37b	Off S. California, USA		Smith (1982)
		<i>Poralia rufescens</i>	37c	Off S. California, USA		Smith (1982)
		<i>Stomolophus meleagris</i>	38	NE Gulf of Mexico, USA		Larson (1987b)
Ctenophora		<i>Agmayeria tortugensis</i>	39	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
		<i>Bathocyroe fosteri</i>	40a	Bahamian waters, WN Atlantic Ocean	May, Sept, Oct 1983, 1984	Youngbluth et al. (1988)
		<i>Bathocyroe fosteri</i>	40b	Off Cape Hatteras, N. Carolina, USA	Jul 1991	Bailey et al. (1995)
		<i>Bathocyroe fosteri</i>	40c	Off Sweeting Cay, the Bahamas	Dec 1990, Mar 1991	Bailey et al. (1994a)
		<i>Beroe abyssicola</i> (formally <i>Beroe</i> sp.)	41	S. Japan Sea	Nov 1991	Ikeda and Hirakawa (1998)
		<i>Beroe cucumis</i>	42a	Oshoro Bay, Hokkaido, Japan	Jul 1970	Ikeda (1974)
		<i>Beroe cucumis</i>	42b	Oshoro Bay, Hokkaido, Japan	Jun 1970	Ikeda (1974)
		<i>Beroe cucumis</i>	42c	Kosterfjorden, W. Sweden	Jul 1981	Båmstedt (1985)
		<i>Beroe ovata</i>	43a	Bahamian waters, WN Atlantic Ocean	1982–1984	Kremer et al. (1986)
		<i>Beroe ovata</i>	43b	Black Sea	Sep/Nov 1999	Finenko et al. (2001)
		<i>Beroe</i> sp. A	44	Off Wilkes Land, Antarctica	Jan 1980	Ikeda and Mitchell (1982)
		<i>Beroe</i> sp. B	45	Prydz Bay, Antarctica	Nov 1982	Ikeda and Bruce (1986)

Table 1 (continued)

Data set	Phylum/Class	Genus and species	Code	Collection site	Date	Reference
Cnidaria B	Hydrozoa	<i>Bolinopsis infundibulum</i>	46	Gulf of Maine, USA	Sep 1989	Bailey et al. (1994b)
		<i>Bolinopsis mikado</i>	47	Tateyama Bay, Chiba, Japan	Jul–Dec 1992, Oct–Nov 1993	Kasuya et al. (2000)
		<i>Bolinopsis vitrea</i>	48	Bahamian waters, WN Atlantic Ocean	1982–1984	Kremer et al. (1986)
		<i>Callianira antarctica</i>	49	Marguerite Bay, Antarctica	Apr–May 2001, 2002, Jul–Aug 2001, Jul–Sep 2002	Scolari et al. (2006)
		<i>Eurhamphaea vexilligera</i>	50	Bahamian waters, WN Atlantic Ocean	1982–1984	Kremer et al. (1986)
		<i>Mertensia ovum</i>	51	Frobisher Bay, Baffin Island, Canada	Aug 1984	Percy (1988)
		<i>Mertensiidae</i> sp.	52	Prydz Bay, Antarctica	Nov 1982	Ikeda and Bruce (1986)
		<i>Mnemiopsis leidyi</i>	53a	Narragansett Bay, Rhode Island, USA		Kremer (1977)
		<i>Mnemiopsis leidyi</i>	53b	Chesapeake Bay, Maryland, USA	May–Oct 1990	Nemazie et al. (1993)
		<i>Mnemiopsis mcradyi</i>	54	N. Biscayne Bay, Florida, USA	Nov 1979	Kremer (1982)
		<i>Ocyropsis maculata</i>	55	Bahamian waters, WN Atlantic Ocean	1982–1984	Kremer et al. (1986)
		<i>Ocyropsis</i> spp.	56	Bahamian waters, WN Atlantic Ocean	1982–1984	Kremer et al. (1986)
		<i>Pleurobrachia pileus</i>	57a	Usujiri coast, Hokkaido, Japan	May 1971	Ikeda (1974)
		<i>Pleurobrachia pileus</i>	57b	Kosterfjorden, W. Sweden	Jul 1981	Båmstedt (1985)
		<i>Pleurobrachia</i> sp.	58	Cape Ferguson Coast, N Queensland, Australia	May 1979	Ikeda (unpublished data)
		UC-1	59	Off Sweeting Cay, the Bahamas	Dec 1990, Mar 1991	Bailey et al. (1994a)
	Scyphozoa	<i>Aegina citrea</i>	TC1	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Botrynema brucei</i>	TC2	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Colobonema sericeum</i>	TC3	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Crossota alba</i>	TC4	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Crossota rufobrunnea</i>	TC5	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Crossota</i> sp. A	TC6	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Eirene mollis</i>	TC7	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Halicsera bigelovi</i>	TC8	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Halitrephes maasi</i>	TC9	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Pantachogon</i> sp. A	TC10	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Tetrorchis erythrogaster</i>	TC11	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Vallentinia adherens</i>	TC12	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Vampyrocrossota childressi</i>	TC13	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Atolla vanhoeffeni</i>	TC14	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Atolla wyvillei</i>	TC15	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Nausithoe rubra</i>	TC16	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Paraphyllina ransoni</i>	TC17	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)
		<i>Periphylla periphylla</i>	TC18	Off S. California, USA	Sep 1988, Jun 1990, Feb–Jun 1991	Thuesen and Childress (1994)

multiple regression (forward selection) method (Sokal and Rohlf, 1995). Independent variables were added and removed at the $p = 0.05$. The calculation was conducted using SYSTAT version 10.2.

As regression models of body composition components, percent data of water, ash, C and N (Table 2) were converted to mg per specimen, then were substituted into the stepwise multiple regression model (empirical model) mentioned above to explore significant variables (body mass, habitat temperature, sampling depth and taxa) which affect them.

3. Results

3.1. Metabolic rates

Of the medusae and ctenophores considered in the present study, *Diphyes* sp. (0.48 mg DM) and *Catostylus mosaicus* (86,440 mg DM) were the smallest and largest species, respectively (Table 2). Respiration rates at in situ temperature ranged from $0.46 \mu\text{L O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ (*Crossota* sp. from the western subarctic Pacific) to $3504 \mu\text{L O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ (*Cassiopea xamachana*), and ammonia excretion rates from $0.019 \mu\text{g N ind.}^{-1} \text{ h}^{-1}$ (*Diphyes antarctica*) to $1787 \mu\text{g N ind.}^{-1} \text{ h}^{-1}$ (*C. mosaicus*) (Table 2).

Prior to the stepwise multiple regression analyses, a preliminary analysis was performed to test the effects of temperature and sampling depth on the rates of respiration (R) and ammonia excretion (E) by first plotting the rates standardized to 1 mg DM ($R_0 = R \times \text{DM}^{-0.75}$ or $E_0 = E \times \text{DM}^{-0.75}$) against temperature ($1000/K$ or $^{\circ}\text{C}$) where the scale coefficient of body mass was assumed as 0.75 (as in the theoretical model) (Fig. 2). No appreciable differences were seen between Datasets A and B. To facilitate the analysis, the data (Dataset A) were separated into two groups depending on the depth of sampled (<500 m and

≥ 500 m). Since the effect of sampling depth to respiration or ammonia excretion rates was unclear at this stage, only the data of <500 m were used for the analysis of temperature effects on R_0 or E_0 . The resultant slope (-4.672 for respiration rates, and -5.569 for ammonia excretion rates, Fig. 2) of the regression lines was used to compute R_0 or E_0 at a given temperature (designated as 10°C) of the medusae and ctenophores from these sampling depths (<500 m + ≥ 500 m), which were plotted against the mid-sampling depth (Fig. 3). The standardized rates (R_0 or E_0 at 10°C) of these medusae and ctenophores were correlated negatively with the sampling depth ($p < 0.01$ or 0.05), and this result was not affected with or without the addition of the dataset B of Thuesen and Childress (1994) for R_0 . From these results, Datasets A and B were combined in the following regression analyses of respiration rates.

The overall results of stepwise multiple regression analyses showed that X_1 (body mass) and X_2 (habitat temperature) were significant variables regardless of the choice of models or body mass unit. The new variable X_3 (sampling depth) was not significant ($p > 0.05$) for respiration rates and ammonia excretion rates (Table 3). Higher respiration and ammonia excretion of scyphomedusae than those of hydromedusae, siphonophores and ctenophores were evident in both theoretical and empirical models when body mass was expressed by DM units. Conversely, lower respiration rates of hydromedusae were the case in the theoretical models when body mass was expressed by C and N. For either respiration rates or ammonia excretion rates, the regression coefficient a_2 of the empirical models significantly differed from unity (1.0) when body mass was expressed by DM units, but the difference was not significant when body mass was expressed by C or N. As judged by R^2 values, the empirical model was superior to the theoretical model, accounting for 78.6–85.6% and 36.1–46.5%, respectively, of the variance in respiration and ammonia excretion (Table 3). As body mass units, C

Table 2
Sampling depth, temperature, body mass, rates of respiration and ammonia excretion, ON ratios, water content, ash, C, N and CN ratios of medusae and ctenophores. Values are means or means \pm 1SD. For species codes, see Table 1. Italic values for sampling depth denote “minimum depth of occurrence” defined as the depth below which 90% of the population found (Thuesen and Childress, 1994). When the number of replicates (N) is different for respiration and ammonia excretion rates, respective numbers are given. Blank = no data.

Data set	Species code	Mid-sampling depth (range) (m)		T (°C)	N	Body mass (mg DM ind. ⁻¹)	Ammonia			Body chemical composition				
							Respiration rate ($\mu\text{l O}_2$ ind. ⁻¹ h ⁻¹)	Excretion rate ($\mu\text{g N}$ ind. ⁻¹ h ⁻¹)	ON ratio (by atoms)	Water (% of WM)	Ash (% of DM)	C (% of DM)	N (% of DM)	CN (by mass)
A	1	600	(430–760)	6	6	80 \pm 30	49.0 \pm 21.6			95.6 \pm 0.4	72.0	6.7	1.7	4.0
	2	1		10	45	290	31.9			96.5	77.0	[3.6] ^a	[0.96] ^b	
	3a	2		8.5	2	3.39 \pm 0.58	4.74 \pm 0.91	0.24 \pm 0.057	24.8 \pm 1.1			30.2	11.0	2.7
	3b	150	(0–400)	1.1	8	14.0 \pm 6.3	2.27 \pm 0.80	0.08 \pm 0.05	44.2 \pm 28.3	94.7 \pm 0.1	56.5 \pm 0.0	16.7	4.3	3.9
	3c	125		3	8	5.74 \pm 3.67	0.52 \pm 0.34			95.7 \pm 0.1	60.3 \pm 0.0	13.6	3.9	3.5
	3d	1		10	22	6	5.58			95.3	58.0	16.0	4.7	3.4
	4	767	(685–850)	9	17,8	200 \pm 100	114 \pm 61	9.2 \pm 9.6	17.8 \pm 7.5	95.3 \pm 0.1		8.2	2.7	3.1
	5	1100	(1000–1200)	2		136.0				95.8	73.2	5.6	1.6	3.4
	6	1	(0.5–1.5)	28	15	[0.70 \pm 0.27] ^d	0.38 \pm 0.20			[95.8] ^d		11.3	3.6	3.1
	7a	100	(0–200)	−0.7	5	136.0 \pm 24.1	1.7 \pm 0.4	0.15 \pm 0.06	17.6 \pm 11.8	95.7 \pm 0.3	68.3 \pm 0.0	9.5	2.5	3.9
	7b	595	(190–1000)	2		135.0				95.3	67.2	10.8	2.6	4.2
	8	1	(0.5–1.5)	28	3	[1.08 \pm 0.32] ^d	0.90 \pm 0.40			[95.8] ^d		9.6	3.0	3.2
	9	600	(430–760)	6	3	660 \pm 120	65.3 \pm 15.5			95.2 \pm 0.1	63.7	16.9	4.4	3.8
	10	750	(500–1000)	3	9	6.22 \pm 8.51	0.46 \pm 0.43			95.2 \pm 0.5	59.7 \pm 0.0	19.8	3.7	5.4
	11a	1		10	32	280	25.2			96.4	81.0	2.8	0.80	3.5
	11b	1		15	20	310	49.6			96.4	81.0	2.8	0.80	3.5
	12	1		10	11	99	24.8			96.0	69.0	8.6	2.5	3.4
	13	1		10	25	43	12.0			96.2	77.0	8.9	2.5	3.6
	14	1		10	12	31	18.0			95.4	52.0	13.7	4.1	3.3
	15	2		27	2	2.27 \pm 0.51	1.31 \pm 0.71	0.09 \pm 0.04	18.7 \pm 2.6			7.2	2.9	2.5
	16	1	(0.5–1.5)	12	22	[5.05 \pm 2.62] ^d	2.84 \pm 1.48			[95.8] ^d		14.3	4.0	3.5
	17	1125	(500–1500)	3	3	38.78 \pm 7.83	4.19 \pm 3.28			92.6 \pm 0.1	30.1 \pm 0.0	37.7	7.4	5.1
	18a	1		10	24	16	4.16			96.1	77.0	9.4	2.5	3.8
	18b	1		15	20	14	6.44			96.1	77.0	9.4	2.5	3.8
	19	1		15	25	7	2.45			96.3	79.0	6.8	1.7	4.0
	20	1		10	8	15	2.40			96.2	64.0	6.7	1.8	3.7
	21	600	(430–760)	6	4	1040 \pm 790	322 \pm 575			95.9 \pm 0.1	81.6	1.5	0.42	3.6
	22a	1		10	14	15	3.90			95.7	75.0	9.6	2.6	3.7
	22b	1		15	13	24	7.44			95.7	75.0	9.6	2.6	3.7
	23	1		15	5	12.5 \pm 2.9	3.1 \pm 0.8					[85] ^a	[2.4] ^b	
	24	1		15	2	5.0 \pm 0.4	1.70 \pm 0.70					[11.8] ^a	[3.4] ^b	
	25a	100	(0–200)	−0.7	2	37.10 \pm 2.18	0.96 \pm 0.14	0.019	67.5 \pm 29.4	95.7 \pm 0.3	64.0 \pm 0.0	9.9	3.2	3.1
	25b	2050	(1800–2300)	0.5		34.20				95.4	60.0	9.2	2.6	3.5
	26	2		25	3	0.48 \pm 0.11	1.08 \pm 0.37	0.07 \pm 0.02	19.3 \pm 3.3			[15.6] ^a	[4.9] ^b	
	27	15	(0–30)	26	8	[4.7] ^c	14.50	0.75	24.2			[8.7] ^c	[2.3] ^c	
	27	15	(0–30)	26	8	[47.4] ^c	60	5.0	15.0			[8.7] ^c	[2.3] ^c	
	27	15	(0–30)	26	8	[474] ^c	300	30	12.5			[8.7] ^c	[2.3] ^c	
	28	1650	(1200–2100)	1		1252				95.1		15.6	4.0	3.9
	29a	1		10	18	490	68.6			96.2	79.0	4.3	1.3	3.3
	29b	1		15	26	470	113			96.2	79.0	4.3	1.3	3.3
	29c	1	Surface	20	24	25,200	2862			96.4		3.7	1.0	3.7
	29d	1	Surface	15	12	6054		182				[5.2] ^d	1.4	
	30a	1		30	27	[7583] ^c	2488					[87] ^c	[2.3] ^c	
	30b	1		24	40	[7583] ^c	3504					[87] ^c	[2.3] ^c	
	31	1		25		[90,762] ^d		1787 ^e				[0.67] ^d	[0.18] ^d	
	32	1	Surface	23		195		12.4				11.1	2.8	4.0
	33a	600	(430–760)	6	4	6710 \pm 3740	470 \pm 280			95.5 \pm 0.1	68.5	10.0	2.5	4.0
	33b	1		10	16	240	115			95.8	68.6	12.8	3.7	3.5
	33c	1		15	7	130	114			95.8	68.6	12.8	3.7	3.5
	34	1		29		4000	1177					[1.6] ^a	[0.48] ^b	

	35a	200		18	4	147.9	151				56.6	[10.6] ^a	[3.0] ^b	
	35b	1	Surface	21	13	597	154	26.0	7.4			11.4	2.9	3.9
	36	200	(0–400)	7	162	279	95.3					19.6	2.9	6.8
	37a	600	(430–760)	6	4	12,010 ± 16,850	3495 ± 7495			96.8		0.59	0.14	4.2
	37b	1300		3	1	59.6	11.3	0.94	15.0	96.0 ± 0.0	73.1	[36.4] ^a	[9.5] ^b	
	37c	1300		3	1	214.9	25.8	5.45	5.9			[22.8] ^a	[5.9] ^b	
	38	1		30	1	2050	2460					[2.0] ^a	[0.58] ^b	
	39	600	(430–760)	6	5	2520 ± 3000	302			95.2 ± 0.7	48.1	19.5	2.5	7.7
	40a	615	(530–700)	11	23, 20	444	9.3	0.37	31.2 ± 3.8			0.74	0.20	3.7
	40b	600	(430–760)	6	4	980 ± 450	213 ± 253			96.0 ± 0.0	81.5	0.37	0.10	3.7
	40c	767	(685–850)	9	3	1900 ± 1510	144 ± 142	13.7 ± 45.8	17.8 ± 11.3	96.1 ± 0.3		0.43	0.14	3.2
	41	550	(400–700)	0.5	2	63.6 ± 31.3	2.3 ± 1.0	0.81	10.6	96.0 ± 0.4	65.3 ± 0.0	11.2	3.0	3.7
	42a	2		15	2	3.43 ± 0.81	3.02 ± 0.70					11.3	3.7	3.1
	42b	2		15	3	52.1 ± 18.9	15.8 ± 2.9	1.2 ± 0.4	17.2 ± 2.9			11.3	3.7	3.1
	42c	100	(0–200)	6	2	14.3		0.1				[9.3] ^c	[2.5] ^c	
	43a	10	(0–20)	25	22	76	20.6	2.4	10.7			3.7	1.0	3.8
	43b	5	(0–10)	21		100	31.1			97.6		[2.8] ^a	[0.79] ^b	
	44	2		−0.8	1	401.6	15.4 ± 4.7	2.21 ± 0.24	8.70 ± 24.8			9.0	2.3	3.8
	45	1		−1.6	11	1362 ± 1192	24.8 ± 14.9	2.26 ± 1.27	14.9 ± 6.0	96.1 ± 0.2	72.8 ± 0.7	5.6	1.5	3.6
	46	180	120–240	6	10	1921 ± 291	104 ± 40			96.2	80.7	2.2	0.45	4.8
	47	1	Surface	22	14, 11	224	11.7	0.95	15.4			1.1	0.34	3.2
	48	10	(0–20)	25	56	56.3	3.8	0.27	17.6			0.60	0.12	5.0
	49	5	(0–10)	1		232 ± 329	42.7	2.6	20.2 ± 18.4	95.7		8.4	1.8	4.6
	50	10	(0–20)	25	47, 52	202	12.7	1.3	12.2			0.88	0.24	3.7
	51	15	(10–20)	0	115	300	94 ^f	8.2 ^f	14 ^f	95.5		[6.5] ^a	[1.6] ^b	
	52	1		−1.6	8	93.7 ± 53.7	12.1 ± 6.26	0.76 ± 0.58	24.2 ± 9.0	95.8 ± 0.4	66.3 ± 1.3	11.2	2.4	4.7
	53a	1	Surface?	20	30	300	30.5	2.9	13.0 ± 0.9	96.6		1.7	0.50	3.4
	53b	1	Surface	23		52.3		3.1				5.1	1.3	3.9
	54	1		22		720	70.2	7.1	12.4			1.4	0.37	3.9
	55	10	(0–20)	25	3, 2	1263	150	15.9	11.8			2.3	0.64	3.5
	56	10	(0–20)	25	16	141	17.8	1.4	15.8			1.2	0.30	3.9
	57a	2		7.3	2	5.80 ± 2.40	1.1 ± 0.06					11.3	3.7	3.1
	57b	100	(0–200)	6	5	5.2		0.19				[9.3] ^c	[2.5] ^c	
	58	2		25	6	52.3 ± 70.4	8.0 ± 11.1	0.88 ± 1.18	11.2 ± 2.1			[2.8] ^a	[0.83] ^b	
	59	767	(685–850)	9	5	18,400 ± 5880	276 ± 156	27.3 ± 51.2	17.5 ± 9.3	96.0 ± 0.1		0.51	0.16	3.3
B	TC1	800		5		[212] ^c	21.0			[95.8] ^d		[5.5] ^a	[1.4] ^b	
	TC2	600		5		[55.9] ^c	4.17			[95.8] ^d		[8.9] ^a	[2.3] ^b	
	TC3	300		5		[206] ^c	10.0			[95.8] ^d		[5.5] ^a	[1.4] ^b	
	TC4	100		5		[25.1] ^c	4.46			[95.8] ^d		[11.9] ^a	[3.2] ^b	
	TC5	500		5		[24.0] ^c	1.97			[95.8] ^d		[12.1] ^a	[3.2] ^b	
	TC6	1100		5		[5.74] ^c	0.51			[95.8] ^d		[20.5] ^a	[5.5] ^b	
	TC7	10		15		[10.8] ^c	4.53			[95.8] ^d		[8.9] ^a	[2.5] ^b	
	TC8	800		5		[28.5] ^c	1.95			[95.8] ^d		[11.4] ^a	[3.0] ^b	
	TC9	500		5		[850] ^c	20.9			[95.8] ^d		[3.3] ^a	[0.84] ^b	
	TC10	800		5		[22.8] ^c	3.15			[95.8] ^d		[12.4] ^a	[3.3] ^b	
	TC11	600		5		[18.3] ^c	1.15			[95.8] ^d		[13.4] ^a	[3.6] ^b	
	TC12	10		15		[1.40] ^c	1.44			[95.8] ^d		[18.8] ^a	[5.5] ^b	
	TC13	750		5		[14.7] ^c	1.10			[95.8] ^d		[14.5] ^a	[3.9] ^b	
	TC14	450		5		[25.3] ^c	2.72			[95.8] ^d		[44.1] ^a	[11.8] ^b	
	TC15	500		5		[366] ^c	26.2			[95.8] ^d		[16.6] ^a	[4.3] ^b	
	TC16	1100		5		[285] ^c	33.3			[95.8] ^d		[18.2] ^a	[4.7] ^b	
	TC17	800		5		[11.2] ^c	1.99			[95.8] ^d		[59.5] ^a	[16.0] ^b	
	TC18	650		5		[948] ^c	47.6			[95.8] ^d		[11.8] ^a	[3.0] ^b	

^a $\ln C = -0.635 + 0.633 \ln DM - 0.060T$ (+1.313 for scyphomedusae).

^b $\ln N = -1.950 + 0.619 \ln DM - 0.054T$ (+1.328 for scyphomedusae).

^c Calculated from protein (PRO), $N = 0.218 \text{ PRO}$ (Bailey et al., 1995), $C = 3.8 \text{ N}$ (this study), $DM = N/0.023$ (this study).

^d Original body WM data were converted to DM, C or N by using these conversion factors derived from the data set A.

^e Nighttime data.

^f Summer data.

followed by N and DM yielded best fit in the theoretical models, but such performance of the body mass units was not clear in the empirical models.

Thus, with regard to the effect of sampling depth, the results from the multiple regression analyses were dissimilar to those of the simple regression analyses (Figs. 2, 3) for respiration rates and ammonia excretion rates, in which both rates standardized by body mass and temperature (e.g., R_0 or E_0 at 10 °C, respectively) were grouped based on a single criterion (mid-sampling depth).

3.2. O:N ratios

A total of 32 O:N ratios ranged from 5.9 (*Poralia rufescens* off south California) to 67.5 (*Diphyes antarctica*) (Table 2). A scatter diagram of the O:N ratios and habitat temperature is shown in Fig. 4. Simple correlation analyses indicated that none of the three independent variables was significantly correlated with the O:N ratios (Pearson correlation coefficients >0.50). Mean and median O:N ratio were 18.0 (± 11.8 , SD) and 15.0, respectively.

3.3. Chemical composition

Water content varied from 92.6 (*Pantachogon haeckeli*) to 97.6% of WM (*Beroe ovata*) with a grand mean of 95.8 (± 0.7 , SD), ash from 30.1 (*P. haeckeli*) to 81.6% of DM (*Solmissus incisus*) with a grand mean of 68.6 (± 10.9), C from 0.37 (*Bathocyroe fosteri* off Cape Hatteras, USA) to 37.7% of DM (*P. haeckeli*) with a grand mean of 8.8 (± 7.1), N from 0.10 (*B. fosteri* off Cape Hatteras, USA) to 11.0 of DM (*Aglantha digitale* from Usujiri coast, Hokkaido, Japan) with a grand mean of 2.3 (± 1.9), C:N ratios from 2.5 (*Liriope tetraphylla*) to 7.7 (*Agmayeria tortugensis*) with a grand mean of 3.8 (± 0.8). Stepwise multiple regression analyses demonstrated that 82.4–99.6% of the variance in water, ash, C and N was contributed by body mass (represented by DM), habitat temperature, sampling depth and taxa, though these variables contributed only 21.9% of the variance of C:N ratios (Table 4). Among significant variables, the standardized partial regression coefficients indicated body mass to be of prominent importance while the importance of sampling depth and taxa were modest or minor. The scale coefficient of body mass (a_2) was significantly greater than 1.0 for ash ($p < 0.05$), but significantly less than 1.0 for C ($p < 0.001$) and N ($p < 0.001$). The scale coefficient did not significantly differ from 1.0 for water ($p > 0.50$) and the sum of ash, C and N ($p > 0.50$) (Table 4). These results for C and N were consistent with those analyzed in Fig. 5 in which C and N were expressed as percent values of DM and grouped based on single criterion (body mass and habitat temperature) and where the sampling depth and taxonomic groups were treated as random variables.

4. Discussion

4.1. Respiration and ammonia excretion

While rates of respiration and ammonia excretion of marine zooplankton are well documented as a power function of body mass in general (Ikeda, 1985), the previous results on single or mixed species of hydromedusae, siphonophores, scyphomedusae and ctenophores suggest that the rates are either a power or linear function of body mass ($a_1 = 0.5$ –1.1, Table 5), and the dual functions are seen between-species as well during ontogeny within a species (*Aurelia aurita*; Kinoshita et al., 1997; *B. ovata*; Svetlichny et al., 2004). The linear relationship may be an artifact (but see Glazer, 2006), often due to the data sets characterized by narrow body mass ranges (typically 1–2 orders of magnitude); as was the case in earlier studies in euphausiids (Ikeda, 2013a) and amphipods (Ikeda, 2013c). However, the same line of explanation is not applicable to the results summarized in Table 5, as body mass ranges that span 2–4 orders of magnitude are sufficient

to yield valid rate–body mass relationships. Multiple regression analyses of the present study, in which the attributes by habitat temperature and the other variables are taken in account, showed that respiration and ammonia excretion rates of medusae and ctenophores are a power function ($a_1 < 1.0$) of DM mass but a linear function of C or N mass ($a_1 = 1.0$). Such changes in the scale exponent (a_1) by the choice of body mass units (WM, DM, ash-free DM, C or N) have never been observed in the broad analyses of the relationship between metabolic rates and body mass of non-gelatinous or largely non-gelatinous zooplankton (Ikeda, 1985; Ivleva, 1980).

The effect of temperature on metabolism has been studied in individual medusa and ctenophore species at graded temperatures within the range of their natural habitats (Table 5). According to the definition by Clarke (1987), this is “acclimation” (adjustment of an organism to a new temperature in the laboratory) in contrast to “adaptation” (the evolutionary adjustment of an organism’s physiology to environment). Acclimated Q_{10} is interpreted as reflecting the acute thermodynamic effect of temperature whereas adapted Q_{10} is presumably the evolutionary optimization of each species. Acclimated $Q_{10} > \text{adapted } Q_{10}$ and this has been described as an “evolutionary trade-off” by Clarke and Fraser (2004). From this view, acclimated Q_{10} values for individual medusae and ctenophores are 1.9–3.7 (excluding the data of 1.7–25.3 of 11 siphonophore species, Table 5) which partially overlap adapted Q_{10} values (1.8–2.8, depending on the choice of body mass units) derived from the global model for the medusae and ctenophores of the present study. The evolutionary trade-off hypothesis characterized by adapted $Q_{10} < 2.0$ has been supported by the global compilation of the data of teleost fishes (1.8, Clarke and Johnston, 1999), pelagic copepods (1.9, Ikeda et al., 2007), chaetognaths (1.7, Ikeda and Takahashi, 2012) and euphausiids (1.7, Ikeda, 2013a), but this is true for medusae and ctenophores only when their body mass was expressed by DM unit (1.8, this study). The only exception to this in the world literature is from Purcell et al. (2010) who reported no significant temperature effects on the respiration rates of 16 scyphomedusa species. Perhaps, the effects of temperature are masked in their analyses of the data characterized by the broad body mass range (5 orders of magnitude, which is comparable to the datasets of the present study) but relatively narrow temperature range (7–30 °C, as compared with –2 to 30 °C of the present study). In the analyses of metabolism–body size (in terms of WM, C and equivalent body diameter) of jellyfish, Acuña et al. (2011) and Pitt et al. (2013) standardized the metabolic data at an inverse absolute temperature (K^{-1}) of 0 (zero) by adopting the activation energy [$E_a = 0.65$ eV, Gillooly et al. (2001)] of aquatic invertebrates. The E_a value is equivalent to $Q_{10} = 2.5$ [$\exp(10 \times 0.65 / (k \times (273 - 2) \times (273 + 30)))$], where k is the Boltzmann’s constant, cf. Ivleva (1980)] for the temperature range of –2.0 to 30 °C, which falls within the range of 1.8–2.8, depending on the choice of body mass units (DM, C or N), of the present study.

As judged by R^2 values, the empirical models are superior to the theoretical models for the prediction of respiration rates or ammonia excretion rates of the medusae and ctenophores (Table 3). Among the three empirical models in which body mass was expressed by DM, C, or N, the best fit to the model was the case for DM for respiration rates but was C for ammonia excretion rates. The difference between C and N was small in both respiration rates ($R^2 = 0.797$ versus 0.799) and ammonia excretion rates ($R^2 = 0.855$ versus 0.849). The advantage of the use of C or N unit is the omission of a dummy variable (X_{SC} : scyphomedusae) which was significant when DM units were used as body mass unit for the prediction of respiration rates and ammonia excretion rates. Among the hydromedusae, siphonophores, scyphomedusae and ctenophores, scyphomedusae were selected as a distinct taxon characterized by higher respiration and ammonia excretion rates (Table 3), which may be due to their greater C and N composition than the rest of the three taxa (Table 4). Hydromedusae were a significant taxon in the prediction of respiration rates from the theoretical models based on C and N, but no

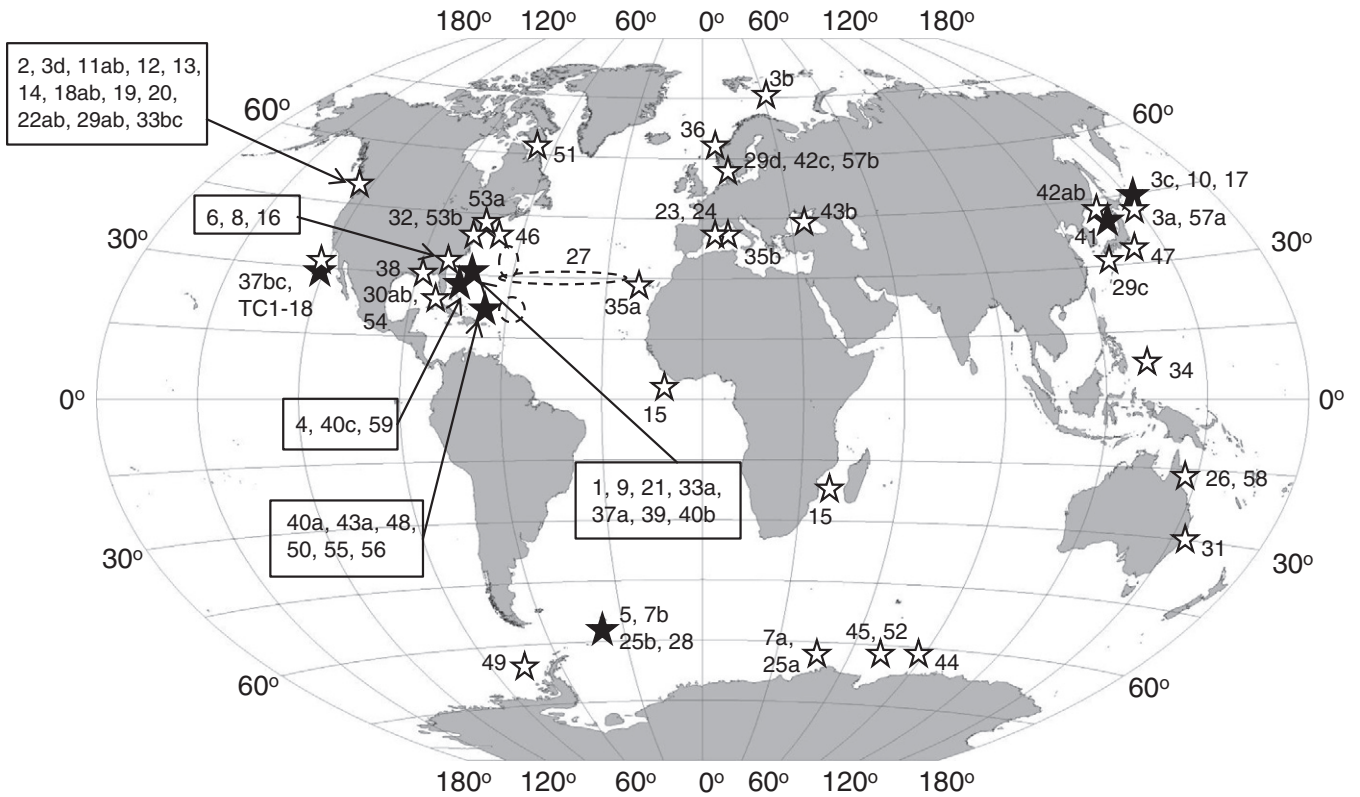


Fig. 1. Study sites of metabolic rates and chemical composition of medusae and ctenophores. The number and associated character alongside the symbol correspond to the code of each medusa and ctenophore species listed in Table 1. Open stars denote samplings from <500 m depth, and closed stars from ≥500 m depth. Enveloped by hatched lines in the subtropical North Atlantic Ocean are study areas of Biggs (1977).

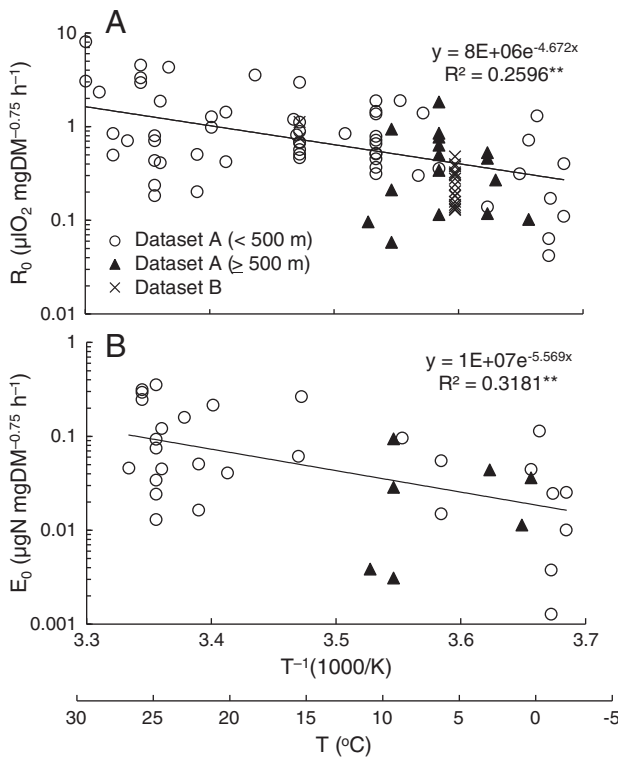


Fig. 2. Relationship between the respiration rate (A) or ammonia excretion rate (B) of medusae and ctenophores standardized to a body size of 1 mg body DM (R_0 or E_0) and temperature (T^{-1} : 1000/K, or T : °C) of the specimens from shallow (<500 m) and deep layers (≥500 m). The data points represent means from the datasets in Table 2, and the regression line is derived from shallow layer species only. $^{**}p < 0.01$.

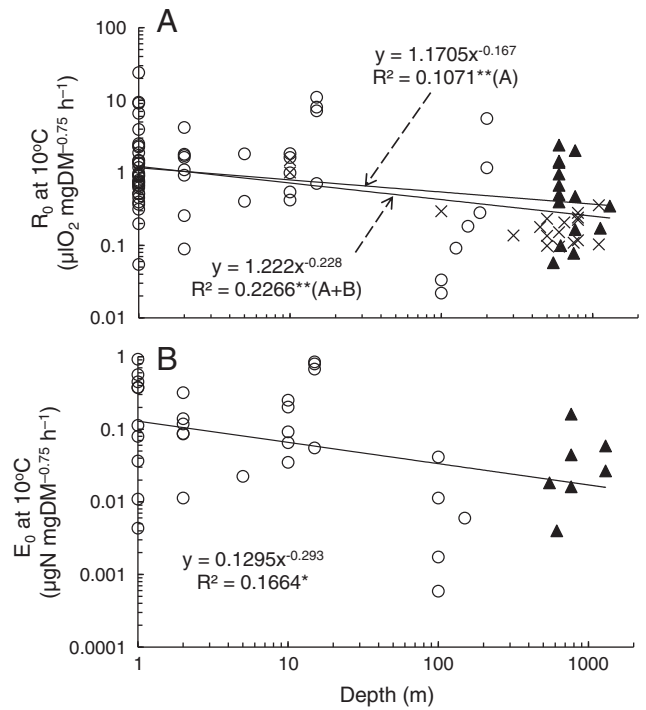


Fig. 3. Relationship between respiration rates (A) or ammonia excretion rates (B) of medusae and ctenophores standardized to a body size of 1 mg DM (R_0 or E_0) at 10 °C and mid-sampling depth. The data points represent means derived from the datasets in Table 2. Open circles and closed triangles denote the data of the species from shallow (<500 m) and deep layers (≥500 m), respectively. $^*p < 0.05$, $^{**}p < 0.01$.

Table 3
Stepwise (forward selection, $p_{in} = p_{out} = 0.05$) multiple regression statistics of theoretical and empirical models of respiration rates (Y : $\mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) or ammonia excretion rates (Y : $\mu\text{gN ind.}^{-1} \text{ h}^{-1}$) of medusae and ctenophores on body mass (X_1 : mg ind.^{-1}), habitat temperature (X_2 : re-defined as $1000/K$ for the former, $^{\circ}\text{C}$ for the latter), depth sampled (X_3 : m), and taxa (X_{sc} , X_{sl} and X_{HY} are dummy variables on scyphomedusae, siphonophores and hydromedusae, respectively). The coefficient $a_2 = 1$ was tested for the empirical model. ** $p < 0.001$.

Regression model	Body mass unit	N	Step no.	Regression equation: $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3 + a_4 \ln X_{sc} + a_5 X_{sl} + a_6 \ln X_{HY}$							R^2 (adjusted R^2)	p for t-Test $H_0: a_1 = 1.0$
				a_0	a_1	a_2	a_3	a_4	a_5	a_6		
Respiration Theoretical	DM	93	1		0.75	−5.186					0.282	
			2	16.380	0.75	−4.875		0.865			0.396 (0.383)	
	C	93	1		0.75	−7.650					0.379	
			2	26.155	0.75	−6.956				−0.604	0.426 (0.414)	
	N	93	1		0.75	−7.330					0.354	
			2	25.863	0.75	−6.587				−0.645	0.410 (0.397)	
Empirical	DM	93	1		0.817						0.776	
			2		0.822	0.063					0.841	
			3	−1.436	0.754	0.059		0.854			0.861 (0.856)	−6.000**
	C	93	1		0.862						0.641	
			2	−0.132	0.950	0.102					0.802 (0.797)	−0.962
	N	93	1		0.893						0.654	
Ammonia excretion	Theoretical	38	1		0.75	−4.953					0.246	
			2	13.341	0.75	−4.755		1.380			0.396 (0.361)	
			1	25.904	0.75	−7.641					0.481 (0.466)	
	Empirical	38	1	26.529	0.75	−7.543					0.464 (0.449)	
			1		0.792						0.676	
			2		0.800	0.061					0.756	
	C	38	3	−3.917	0.718	0.058		1.461			0.804 (0.786)	−3.570**
			1		0.913						0.622	
			2	−2.891	1.072	0.109					0.863 (0.855)	0.960
	N	38	1		0.924						0.621	
			2	−1.496	1.080	0.108					0.857 (0.849)	1.026

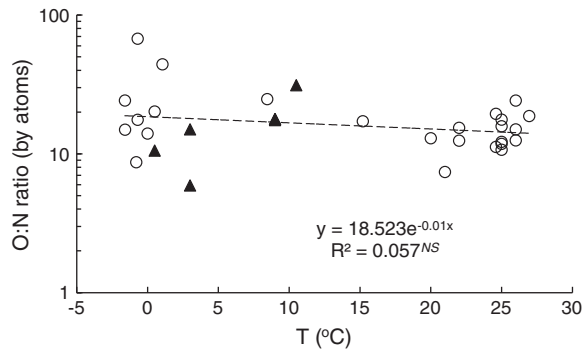


Fig. 4. Relationships between O:N (as $\text{NH}_4\text{-N}$) ratios and habitat temperature (T) of medusae and ctenophores from various regions of the world's oceans. The data points represent means in Tables 2. Open circles and closed triangles denote the data of the species from shallow (<500 m) and deep layers (≥ 500 m), respectively. $^{NS}p > 0.05$.

immediate reason for this is seen in their C and N composition data as compared with these of the other taxa.

For the progressive decline in respiration rates in deeper-living micronekton and zooplankton, the “visual-interactions hypothesis” (Childress, 1995) or “predation-mediated selection hypothesis” (Ikeda et al., 2006a) have been proposed respectively. These two hypotheses are similar as both interpret the phenomena as a result of lowered selective pressure for high activity at depth because of the decrease in visual predation in the dark. However, these two hypotheses are different in that the former applies strictly to micronekton with functional eyes whereas the latter applies to both micronekton and zooplankton irrespective of presence/absence of functional eyes. The present results showing no significant depression effects of habitat depth on respiration rates and ammonia excretion rates of the medusae and ctenophores (Table 3) are consistent with those of Thuesen and Childress (1994), and can be interpreted by the absence of functional eyes in them (visual-interactions hypothesis), or very weak predation pressure on them (predation-mediated selection hypothesis).

4.2. O:N ratios

The atomic ratio of oxygen consumption rate to ammonia–nitrogen excretion rate (O:N ratio) has been used as an index of the proportion of protein in the diet of marine zooplankton (Ikeda et al., 2000; Mayzaud and Conover, 1988). When only protein is metabolized, the O:N ratio is 7 (Table 10.3 in Ikeda et al., 2000). When protein and lipid or carbohydrate are catabolized in equal quantities O:N ratios are calculated as 21 or 13, respectively (mid-point: 17). Hence, O:N ratios of 7–17 may be used as an index of protein-oriented metabolism and ratios of >17 as lipid/carbohydrate-oriented metabolism. Metabolic O:N ratios (median; 15.0) of the medusae and ctenophores favor protein-oriented

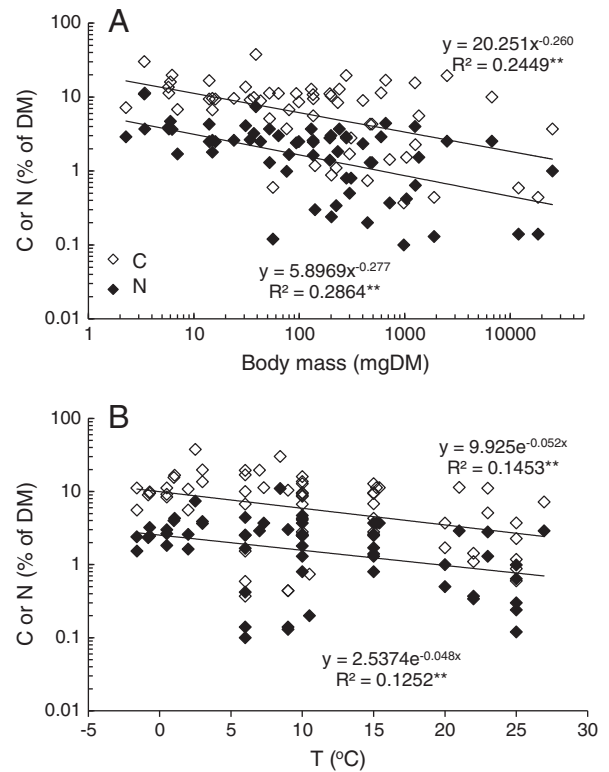


Fig. 5. Relationship between C and N composition and body mass (A) or habitat temperature T (B) of medusae and ctenophores from various regions of the world's oceans. The data points represent the datasets in Table 2. $^{**}p < 0.01$.

metabolism in general. It is noted that the O:N ratios of the medusae and ctenophores listed in Table 2 are derived from experiments in which they were placed in filtered seawater, a common practice when using the sealed-chamber method (Ikeda et al., 2000). The use of filtered seawater is imperative to determine the rates of respiration and ammonia excretion accurately without any corrections for complex uptake/release of oxygen and ammonia by food organisms, but starvation of animals has been reported to reduce the normal metabolism of various zooplankton taxa (Ikeda et al., 2000). Ammonia excretion is more susceptible to food deprivation than respiration, hence high O:N ratios in starved animals have been documented in *Pleurobrachia pileus* (Ikeda, 1977) and *Mnemiopsis mcradyi* (Kremer, 1982). The same phenomenon has also been noted in the global-bathymetric models of the metabolism of euphausiids, mysids and amphipods (Ikeda, 2013a, 2013b, 2013c).

Table 4

Final multiple regression equations derived from stepwise (forward selection, $p_{in} = p_{out} = 0.05$) multiple regression analyses of body components (Y: water, ash, C or N, all in mg; and C:N ratio with no dimension) of medusae and ctenophores on body mass (X_1 : mg DM ind. $^{-1}$), habitat temperature (X_2 : °C), depth sampled (X_3 : m), and taxa (X_{SC} , X_{SI} and X_{HY} are dummy variables on scyphomedusae, siphonophores and hydromedusae, respectively). Values in parentheses denote standardized partial regression coefficients as a measure of relative contribution to the variance. $^*p < 0.05$, $^{**}p < 0.01$.

Body component	N	Regression equation: $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3 + a_4 X_{SC} + a_5 X_{SI} + a_6 X_{HY}$						Adjusted R^2	p for t-test $H_0: a_1 = 1.0$
		a_0	a_1	a_2	a_3	a_4	a_5		
Water	47	3.087	0.997 (0.981)	0.016 (0.044)				0.996	−0.273
Ash	38	−0.469	1.034 (1.001)		−0.027 (−0.042)			0.993	2.267*
C	61	−0.649	0.635 (0.735)	−0.060 (−0.250)		1.310 (0.271)		0.824	−7.019**
N	62	−1.964	0.622 (0.735)	−0.054 (−0.226)		1.317 (0.282)		0.835	−7.560**
C:N	61	1.257			0.035 (0.482)			0.219	
Ash + C + N	36	4.359	0.999 (1.001)	0.006 (0.015)				0.999	−0.200

Table 5
Effects of body mass (as the scale exponent of body mass = a_2 of the regression model adopted in the present study) and temperature (= a_3) on respiration rates of medusae and ctenophores. The a_3 was assessed as Q_{10} of Van't Hoff rule. For body mass units, VOL = body volume, WM = wet mass, DM = dry mass, PRO = protein, and C = carbon.

Taxonomic group	Species, or the number of species pooled	Body mass effect			Temperature effect			
		a ₂	Mass unit	Range (mg DM equivalent)	Q ₁₀	Range (°C)	Reference	
<i>Respiration</i>								
Hydromedusae	<i>Aequorea vitrina</i>	1.02	DM	2–800			Møller and Riisgård (2007)	
	<i>Cladonema californicum</i>	0.74	DM	0.01–0.52			Costello (1991)	
	<i>Sarsia tubulosa</i>	0.91	DM	0.3–5			Møller and Riisgård (2007)	
	11 species	1.02 ± 0.19	DM	1–1900	2.6 ± 1.0 ^a	10–15	Larson (1987a)	
Siphonophores	11 species	0.79 ± 0.26	PRO	4.4–436	1.7–25.3 ^b	16–25.5	Biggs (1977)	
Scyphomedusae	<i>Aurelia aurita</i>	1.06	WM	440–35,400			Shimauchi and Uye (2007)	
	<i>Aurelia aurita</i>	1.01	DM	20–8000	3.1	7–22	Møller and Riisgård (2007)	
	<i>Aurelia aurita</i> (15 °C)	0.63	DM	0.06–10			Kinosita et al. (1997)	
	<i>Aurelia aurita</i> (15 °C)	0.93	DM	10–1100			Kinosita et al. (1997)	
	<i>Cassiopea xamachana</i> (Jan)	0.74	PRO	100–13,080			Verde and McCloskey (1998)	
	<i>Cassiopea xamachana</i> (Sep)	0.85	PRO	100–6366			Verde and McCloskey (1998)	
	<i>Pelagia noctiluca</i>	0.95	VOL	306–1163			Morand et al. (1987)	
	<i>Periphylla periphylla</i>	0.589	C	100–6366			Youngbluth and Båmstedt (2001)	
	2 species	0.97 ± 0.06	DM	12–16,200	2.9 ^c	10–15	Larson (1987a)	
	<i>Beroe gracilis</i>				3.56	8–20	Gillenberg and Greve (1979)	
	<i>Beroe ovata</i>	0.90	DM	10–561			Kremer et al. (1986)	
	<i>Beroe ovata</i>	0.58	WM	0.03–91			Svetlichny et al. (2004)	
	<i>Beroe ovata</i>	1.04	WM	91–23,400	2.17	10–28	Svetlichny et al. (2004)	
	<i>Beroe ovata</i>	1.04	DM	10–1000			Finenko et al. (2001)	
Ctenophores	<i>Bolinopsis infundibulum</i>				3.73	8–20	Gillenberg and Greve (1979)	
	<i>Bolinopsis infundibulum</i>	0.67	DM	100–4800			Bailey et al. (1995)	
	<i>Bolinopsis mikado</i>	1.015	DM	50–2000	1.9	16–24	Kasuya et al. (2000)	
	<i>Bolinopsis vitrea</i>	0.64	DM	45–2778			Kremer et al. (1986)	
	<i>Callianira antarctica</i>	0.707	DM	2.8–1049			Scolardi et al. (2006)	
	<i>Eurhamphaea vexilligera</i>	1.12	DM	16–257			Kremer et al. (1986)	
	<i>Mertensia ovum</i> (summer)	0.655	DM	10–1000			Percy (1988)	
	<i>Mertensia ovum</i> (winter)	0.744	DM	40–700			Percy (1988)	
	<i>Mnemiopsis leidyi</i>	0.96	DM	35–562	3.67	16–25	Kremer (1977)	
	<i>Ocyropsis</i> sp.	0.97	DM	996–1575			Kremer et al. (1986)	
	<i>Pleurobrachia pileus</i>				2.72	2–24	Gillenberg and Greve (1979)	
	7 species	1.09	WM	320–1,259,000			Purcell et al. (2010)	
	6 species	0.917	WM	160–7,943,000				
	16 species	0.917	C	0.03–100,000	1.0	7–30		
	Hydromedusae/scyphomedusae	19 species	0.78	WM	1–926			Thuesen and Childress (1994)
	Hydromedusae/scyphomedusae/siphonophores/ctenophores	26 species	0.78	WM	5–1,000,000			Acuña et al. (2011)
	Hydromedusae/scyphomedusae/ctenophores	40 species	0.79	C	0.01–1000			
			0.82	C	0.03–14,330			Pitt et al. (2013)
71 species + 3 size groups of siphonophores		0.754	DM	0.5–25,200	1.80	–2 to 30	This study	
		0.950	C	0.075–932	2.77			
		0.972	N	0.024–252	2.66			
<i>Ammonia excretion</i>								
Hydromedusae	<i>Cladonema californicum</i>	1.41	DM	0.01–0.52			Costello (1991)	
Siphonophores	11 species	0.80 ± 0.18	PRO	4.4–436			Biggs (1977)	
Scyphomedusae	<i>Aurelia aurita</i>	0.93	WM	1836–19,962			Schneider (1989)	
	<i>Aurelia aurita</i>	1.09	WM	440–35,400			Shimauchi and Uye (2007)	
	<i>Chrysaora quinquecirrha</i>	0.974	DM	13–2826			Nemazie et al. (1993)	
	<i>Pelagia noctiluca</i>	0.90	VOL	306–1163	3.8	15–25	Morand et al. (1987)	
Ctenophores	<i>Beroe ovata</i>	0.82	DM	10–561			Kremer et al. (1986)	
	<i>Bolinopsis mikado</i>	1.147	DM	50–1000	4.1	16–24	Kasuya et al. (2000)	
	<i>Bolinopsis vitrea</i>	0.76	DM	45–2778			Kremer et al. (1986)	
	<i>Callianira antarctica</i>	0.487	DM	2.8–1049			Scolardi et al. (2006)	
	<i>Eurhamphaea vexilligera</i>	0.93	DM	16–257			Kremer et al. (1986)	
	<i>Mertensia ovum</i> (summer)	0.623	DM	10–1000			Percy (1988)	
	<i>Mertensia ovum</i> (winter)	0.546	DM	40–700			Percy (1988)	
	<i>Mnemiopsis leidyi</i>	0.89	DM	35–562	3.73	16–25	Kremer (1977)	
	<i>Mnemiopsis leidyi</i>	0.604	DM	7–391			Nemazie et al. (1993)	
	<i>Ocyropsis</i> sp.	1.06	DM	996–1575			Kremer et al. (1986)	
	Hydromedusae/scyphomedusae/ctenophores		0.84	C	0.14–69,780			Pitt et al. (2013)
	Hydromedusae/scyphomedusae/siphonophores/ctenophores	29 species + 3 size groups of siphonophores	0.718	DM	0.658–1050	1.79	–2 to 27	This study
			1.07	C	0.075–608	2.97		
			1.08	N	0.024–163	2.94		

^a Three species.

^b *Forskalia* spp.

^c One species.

4.3. Chemical composition

According to [Larson and Harbison \(1989\)](#), medusae and ctenophores inhabiting Arctic and Antarctic waters do contain visible lipid droplets in the lumen of the gastrovascular system. However, the amount of lipids (max 6–22% of DM, [Larson and Harbison, 1989](#)) is considerably less than those being found in the copepods and euphausiids in high latitude seas (51–71% of DM, [Lee et al., 2006](#)). The present results of non-significant relationships between body C:N ratios (as an index of the ratio of lipids to proteins) and habitat temperatures in medusae and ctenophores ([Fig. 6](#)) suggest that lipid deposition is not marked in these gelatinous zooplankton, as was noted already by [Pitt et al. \(2013\)](#). The C:N ratios (grand mean: 3.8) of the medusae and ctenophores are close to those (3.3) for crustacean plankton protein ([Ventura, 2006](#)) and that (3.1) for protein derived from an average amino acid composition ([Gnaiger and Bitterlich, 1984](#)). The predominance of protein in the organic matter has been confirmed by the proximate composition analyses on jellyfish ([Arai et al., 1989](#); [Clarke et al., 1992](#); [Doyle et al., 2007](#); [Hoeger, 1983](#); [Larson, 1986](#)). At the same time, these proximate composition analyses revealed the presence of a significant amount of bound water [lost at 450–500 °C (ash measurement) but not at 50–60 °C] and unmeasured N-compounds (a glycoprotein or an amino-polysaccharide). These rather unique components may be derived from the mesoglea (composed of water and collagen-like protein) which is present in large quantities in these animals (cf. [Arai, 1997](#)).

C and N compositions decreased with the increase in body mass for the medusae and ctenophores ([Fig. 5, Table 4](#)). The decreases in C and N in larger specimens are replaced by the increase in ash since the sum of C, N and ash is independent of body mass ([Table 4](#)). The decline in percent C and N compositions with the increase in body mass, which

emerged from between-species comparison in the present study, has already been noted within-species of some ctenophores ([Finenko et al., 2006](#); [Kasuya et al., 2000](#); [Kremer et al., 1986](#); [Reeve et al., 1989](#)) and salps ([Iguchi and Ikeda, 2004](#)).

With regard to the effect of habitat depth to the chemical composition of jellyfish, [Bailey et al. \(1995\)](#) compared the data of 5 medusae and 2 ctenophores from the mesopelagic zone off Cape Hatteras, North Carolina, USA, with epipelagic counterparts. From this comparison, they concluded that several mesopelagic species were more robust than epipelagic species, but there were no appreciable differences between the two. In the present analyses, habitat depth was not a significant variable affecting the C and N composition of the jellyfish ([Table 4](#)). Habitat depth, together with body mass, was a significant variable contributing to the majority of the variance of ash ($R^2 = 0.993$). As judged by the standardized partial regression coefficients, the contribution of habitat depth to the variance of ash content was much less relative to that of body mass, however. Thus, the present results are consistent with those of [Bailey et al. \(1995\)](#) and confirmed that habitat depth is a minor variable affecting chemical composition of jellyfish. From the “predation-mediated selection” hypothesis, these results, combined with insignificant effects of habitat depth on metabolism mentioned above, underpin possible relaxation of jellyfish from predation pressure in the marine pelagic realm as compared with non-gelatinous zooplankton and micronekton.

4.4. Medusae and ctenophores as compared with other zooplankton taxa

Previous metabolic comparison of jellyfish with other zooplankton or fish has been made on the bases of equivalent C as a body mass unit and at standardized temperature assuming a common $Q_{10} = 2$ ([Schneider, 1990](#)) or $E_a = 0.65$ eV ([Acuña et al., 2011](#); [Pitt et al., 2013](#)). These comparisons revealed that the respiration rate of a jellyfish is nearly comparable to that of other zooplankton or fish. [Ikeda \(2008\)](#) argued that N instead of C is an appropriate body mass unit since N represents proteins which are of prime importance for living systems.

Defining body mass by N units, and using taxon-specific Q_{10} values revealed in the present analyses, physiological features of medusae and ctenophores were compared with those of global-bathymetric models of chaetognaths, copepods, euphausiids and mysids ([Table 6](#)). Among these taxa, the significant depth-related decline in respiration has been observed for all the taxa excepting for the medusae/ctenophores. Adapted Q_{10} value (2.66) of the medusae/ctenophores is the highest among the other zooplankton taxa compared. For a specimen with similar body mass (1 mg N) living in the epipelagic zone (10 m depth, and 100% oxygen saturation) of temperate latitudes (20 °C), predicted respiration rates from the theoretical or empirical model of the medusae/ctenophores ($22.4\text{--}29.4 \mu\text{O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$, excluding $15.4 \mu\text{O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ for hydromedusae from the theoretical model) are the highest, and those of chaetognaths and copepods ($8.4\text{--}14.8 \mu\text{O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) are the lowest, with those of euphausiids and mysids ($15.2\text{--}17.1 \mu\text{O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) being intermediate. Previous body C-based models ([Acuña et al., 2011](#); [Pitt et al., 2013](#)), converted to body N-based models by using the C:N ratios of 3.8, yielded high respiration rates of the specimen comparable to those of the present results ([Table 6](#)). For the specimen living in the mesopelagic zone (500 m, 5 °C and 10% oxygen saturation), similar calculations showed that the high-low orders of respiration rates among the five taxa remained the same.

As compared with those of other zooplankton or fish of equivalent body C, jellyfish have been evaluated to exhibit slow swimming speeds but near identical or greater mass specific growth rates ([Acuña et al., 2011](#); [Pitt et al., 2013](#)). My own calculations based on the data of [Hirst et al. \(2003\)](#) confirmed that specific growth rates of medusae and ctenophores (mean: 0.192 d^{-1}) were much greater than that (0.143) of copepods and that (0.103) of chaetognaths. No comparable growth rate data

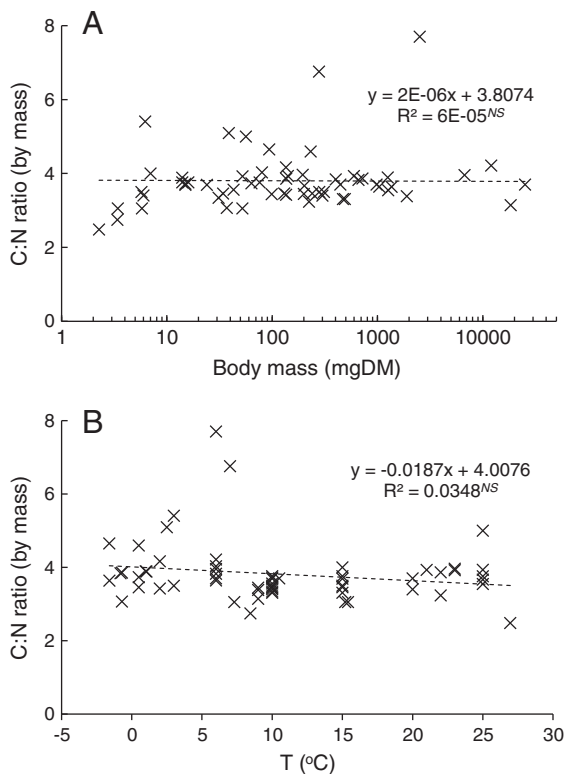


Fig. 6. Relationship between C:N ratios and body mass (A) or habitat temperature T (B) of medusae and ctenophores from various regions of the world's oceans. The data points represent the datasets in [Table 2](#). ^{NS}p > 0.05.

Table 6

Global-bathymetric comparisons of ecological and physiological features of medusae/ctenophores, pelagic chaetognaths, copepods, euphausiids and mysids living in world's oceans. For respiration rate, T and E denote Theoretical and Empirical models, respectively. For comparative purpose, the rates predicted from the models from Acuña et al. (2011) and Pitt et al. (2013) are included. Body components were compared based on the results from multiple regression analyses in which body mass, habitat temperature and depth were designated as independent variables (for the regression model, see Table 4). N is the number of data and Nsp the number of species. Modified from Ikeda (2013a, 2013b, 2013c). NS: not significant ($p > 0.05$), ND: no data.

Parameters	Medusae/ctenophores	Chaetognaths	Copepods	Euphausiids	Mysids
Food habit	Carnivore	Carnivore	Herbivore, omnivore, carnivore	Herbivore, omnivore, carnivore	Herbivore, omnivore, carnivore
Metabolism					
Respiration rate ($\mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$)					
Depression effect of habitat depth	Not significant	Significant	Significant	Significant	Significant
Body mass (mg N, range)	0.024–252	0.010–2.01	0.0005–2.38	0.029–149	0.008–66.0
Q_{10} for the temperature range of -1.8 to 30 °C (based on body N)					
Mean (95% CI range)	2.66 (2.10–3.38)	2.05 (1.60–2.63)	1.92 (1.67–1.93)	1.60 (1.39–1.60)	2.12 (1.60–2.81) ^a
N (Nsp)	93 (72)	25 (17)	253 (108)	39 (24)	42 (38)
Predicted rate for a specimen of 1 mg N body mass inhabiting 10 m depth (20 °C, O_2 saturation = 100%)					
T-model	29.4 ^b , 15.4 ^c	8.4	12.1	15.9	17.1
E-model	22.4	14.2	14.8	15.7	15.2
Acuña et al.'s model	28.4 ^d				
Pitt et al.'s model	32.4 ^d				
Predicted rate for a specimen of 1 mg N body mass inhabiting 500 m depth (5 °C, O_2 saturation = 10%)					
T-model	8.7 ^b , 4.6 ^c	1.5	2.3	5.6	4.4
E-model	5.2	1.8	2.6	5.6	3.3
Acuña et al.'s model	7.1 ^d				
Pitt et al.'s model	8.1 ^d				
O:N ratio (by atms)					
Range	5.9–67.5	6.8–36	4.8–49	11–142	8–45
Mean (\pm SD)	18.0 (11.8)	15.6 (8.9)	20.7 (11.3)	30.1 (17.4)	20.3 (10.6)
Median	15.0	12.2	16.9	27.1	18.7
N (Nsp)	32 (25)	12 (10)	37 (29)	31 (19)	15 (13)
Growth					
Weight specific rate (day^{-1})					
Range	–0.069 to 0.078 ^e	–0.013 to 0.41 ^e	0.000–1.62 ^f	ND	ND
Mean (\pm SD)	0.192 (0.198)	0.103 (0.125)	0.143 (0.209)		
N (Nsp)	103 (9)	87 (4)	2528 (69)		
Body composition component, and regression coefficients of body mass (a_2), habitat temperature (a_3) and depth (a_4)					
Water					
a_2 (\pm SD)	0.997 (0.011)	1.128 (0.055)	ND	1.002 (0.007)	0.953 (0.033)
a_3 (\pm SD)	0.16 (0.003)	NS	ND	NS	NS
a_4 (\pm SD)	NS	NS	ND	0.005 (0.004)	NS
N (Nsp)	47 (35)	18 (13)	93 (93) ^g	36 (27)	18 (14)
% of WM, mean (SD)	95.8 (0.7)	90.8 (2.9)	81.4 (5.1) ^g	76.9 (3.7)	77.6 (5.4)
C					
a_2 (\pm SD)	0.635 (0.052) ^h	0.957 (0.028)	1.045 (0.006)	1.011 (0.008)	1.038 (0.012)
a_3 (\pm SD)	–0.060 (0.013)	NS	–0.003 (0.001)	NS	NS
a_4 (\pm SD)	NS	NS	NS	NS	NS
N (Nsp)	57 (42)	27 (18)	253 (108)	41 (28)	24 (20)
% of DM, mean (\pm SD)	8.7 (7.3)	37.9 (7.3)	50.6 (6.7)	42.6 (4.4)	46.6 (6.6)
N					
a_2 (\pm SD)	0.622 (0.050) ^h	0.936 (0.027)	0.952 (0.011)	1.013 (0.012)	1.038 (0.012)
a_3 (\pm SD)	–0.054 (0.013)	NS	NS	NS	NS
a_4 (\pm SD)	NS	NS	–0.022 (0.006)	–0.028 (0.008)	NS
N (Nsp)	58 (42)	26 (18)	253 (108)	41 (28)	24 (20)
% of DM, mean (\pm SD)	2.3 (1.9)	9.6 (2.2)	8.8 (1.8)	10.1 (1.4)	8.8 (2.3)
C:N (by mass)					
Range	2.5–7.7	2.6–5.1	3.7–9.4	3.4–8.6	3.2–10.6
Mean (\pm SD)	3.8 (0.8)	4.0 (0.6)	5.4 (1.5)	4.2 (1.1)	5.8 (2.5)
N (Nsp)	57 (42)	32 (22)	94 (94)	41 (28)	24 (20)

^a Substituted by the DM-based data.

^b For siphonophores, scyphomedusae and ctenophores.

^c For hydromedusae.

^d For a specimen weighing 3.8 mg C, which is equivalent to 1 mg N (C:N ratio = 3.8).

^e Calculated from the data in Hirst et al. (2003).

^f From Hirst et al. (2003).

^g From Båmstedt (1986). Means given for six groups (3 latitudes \times 2 depths) were weighed by the number of data sets to derive a grand mean.

^h Null hypothesis: $a_2 = 1.0$ was rejected ($p < 0.01$), suggesting progressive decline in %C or %N in DM with increasing DM.

are presently available for euphausiids and mysids. Protein synthesis requires the highest energy among the processes involved in the formation of new body mass in zooplankton (Kjørboe et al., 1985; Thor,

2000). To achieve fast growth, jellyfish must capture and ingest prey animals efficiently. A recent analysis revealed that jellyfish are indeed a group of animals that evolved large, watery bodies that enhance

prey contact rates and could exhibit clearance rates as high as fish competitor of equivalent C mass (Acuña et al., 2011).

As a metabolic quotient, large standard deviations (SD) associated with the mean O:N ratios of the medusae/ctenophores and the other zooplankton taxa suggest non-normal distribution of the O:N data. Thus, the medians rather than means are thought to provide better index of the central trend. Somewhat lower median O:N ratios of the medusae/ctenophores and chaetognaths (15.0 and 12.2) than those of copepods, euphausiids and mysids (16.9–27.1) may be interpreted by the taxon-specific feeding habits; e.g. the former group is a typical carnivore characterized by protein-oriented metabolism (O:N ratio = 7–17) while the latter group is a mixture of herbivores, omnivores and carnivores characterized by protein- and lipid/carbohydrate-oriented metabolism (O:N ratio = 7–∞).

In terms of chemical body composition, the medusae/ctenophores contrast to the three crustacean taxa by extremely high water content (mean: 95.8% vs. 76.9–81.4%), but much lower C (8.7% vs. 42.6–50.6%) and N (2.3% vs. 8.8–10.1%) compositions and C:N ratios (mean: 3.8 vs. 4.2–5.8) (Table 6). The data of chaetognaths fall between these two extremes. Apart from these between-taxa differences in body composition, an important finding of the present study is the progressive decline in C and N composition (expressed as % of DM, Table 4) in the medusae/ctenophores; a phenomenon never been observed in chaetognaths, copepods, euphausiids and mysids. Implications gained from this result are that; one, in addition to taxonomic similarities, body size and habitat temperature are needed to take into account to convert WM or DM to C and N for jellyfish; two, large jellyfish are advantageous to maintain the same WM or DM mass specific growth rate to that of small ones by lower cost of organic matter under identical environmental conditions. In other words, the benefit of large, watery body of jellyfish is not limited to enhance foraging capacity (Acuña et al., 2011) but also to achieve same growth by lesser amount of organic matter input.

In conclusion, multiple-regression analyses of metabolic rates and body composition data in medusae and ctenophores from various depth horizons of the world's oceans revealed that not only the rates of respiration and ammonia excretion but also C and N compositions were a function of body mass and habitat temperature. No significant effects of habitat depth on the metabolic rates and body composition were detected. From global-bathymetric comparisons of the present results with those of chaetognaths, copepods, euphausiids and mysids, medusae and ctenophores are shown to be unique in that they exhibit at higher respiration rates per unit body N, no-significant depth-related reduction in metabolic rates, higher specific growth rates, significant decline in body C and N compositions with increasing body mass and habitat temperature, and no appreciable accumulation of energy reserves (lipids) in the body. Because of body mass-dependence of the C and N composition, the scale exponents of body mass (0.66–1.05) and temperature coefficients (1.7–3.1 as Q_{10}) in the empirical regression models of their respiration rates and ammonia excretion rates varied greatly by the choice of body mass units (DM, C or N).

Acknowledgments

I am grateful to Bill Hamner for the critical reading of early drafts of this paper, and to Graeme Hays for the comments which improved the text. [SS]

Appendix. Definitions of dummy variables. The taxa were categorized into Scyphozoa, Siphonophora, Hydrozoa and Ctenophora

Taxon category	X_{Sc}	X_{Si}	X_{Hy}
Scyphozoa	1	0	0
Siphonophora	0	1	0
Hydrozoa	0	0	1
Ctenophora	0	0	0

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