Metabolism and chemical composition of zooplankton and hyperbenthos from the Great Barrier Reef waters, North Queensland, Australia

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Abstract: Rates of oxygen consumption (R) and ammonia excretion (E) of a total of 22 species of zooplankton and hyperbenthos, which weighed 0.0012 to 26.7 mg dry mass (DM), from inshore and slope waters of the Great Barrier Reef were determined at *in situ* temperatures (23 to 30°C). R s ranged from 0.0048 to 118.3 $\mu\text{L O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ and E s from 0.00051 to 15.9 $\mu\text{g NH}_4\text{-N ind.}^{-1} \text{ h}^{-1}$. Stepwise regression analyses in which the differences in body mass are taken into account revealed that zooplankton and hyperbenthos exhibited comparable R , but the latter showed lower E than the former. As a result, the atomic ratio of R to E (O:N) of hyperbenthos (geometric mean: 53.1) was greater than that (16.4) of zooplankton. No appreciable differences were evident in C and N composition of the bodies between zooplankton-hyperbenthos; total carbon (C) ranged from 18.0 to 47.2% of DM and total nitrogen (N) from 2.4 to 12.7% of DM, with C:N ratios of 3.1–7.5. Judging from C and N composition, protein was the major component of body organic matter of both zooplankton and hyperbenthos. In terms of N-specific R and N , the present zooplankton data are comparable to those published on tropical zooplankton and small fishes with similar body N. Compared with zooplankton, lower specific E s and higher O:N ratios of hyperbenthos were interpreted to reflect their partial or entire dependence on diets characterized by lower N composition (detritus).

Key words: C:N ratio, hyperbenthos, metabolic rate, O:N ratio, zooplankton

Introduction

Hyperbenthos is a distinct assemblage of small animals occurring in the water layer adjacent to the sea bottom, and is analogous to “benthopelagic” plankton in the open ocean or to “demersal” zooplankton in reef systems. The hyperbenthos includes resident species, demersal zooplankton during their downward excursion and endo- or epibenthic species that emerge into the water column as part of their diel cycles (see review of Mees & Jones 1997). The most common representatives of the hyperbenthos are amphipods, mysids, decapods, and isopods. From a trophodynamic viewpoint, hyperbenthos, together with zooplankton, are important dietary components of a variety of fishes and large invertebrates (McCall & Fleeger 1995, Mees & Jones 1997).

Information about oxygen consumption, ammonia excretion rates and resultant O:N (as $\text{NH}_4\text{-N}$) ratios of zooplankton has proved to be useful to provide a wide perspective for understanding their energy demand, metabolic balance and nutritional condition (cf. Ikeda et al. 2000). Data sets on these metabolic parameters for tropical marine zooplankton are presently available for copepods (Ikeda 1974, Gaudy & Boucher 1983), ctenophores (Kremer et al. 1986), salps (Cetta et al. 1986) and “gelatinous” zooplankton including siphonophores, hydromedusae, scyphomedusae, heteropods and pteropods (Biggs 1977). However, no comparable data sets are currently available for the hyperbenthos, with the notable exception of those in the deep benthic boundary layer (1,300–2,600 m deep) of the East Pacific (Smith 1982, 1985).

In this study, we determined oxygen consumption and ammonia excretion rates and computed O:N ratios of tropical zooplankton and hyperbenthos from inshore/slope waters of the Great Barrier Reef. The results are compared

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with published data on zooplankton, small teleost fishes and benthic animals from tropical regions to explore unique features, if any, of the metabolism and body composition of the zooplankton and hyperbenthos in this study.

Materials and Methods

Sampling

Zooplankton and hyperbenthos were collected from the jetty of the Australian Institute of Marine Science (AIMS) located at Cape Ferguson, North Queensland, coastal reefs off Mackay within the Great Barrier Reef (GBR), and the slope water of the GBR (Coral Sea) during the period September 2009 and April 2010. Samples were taken with a conical plankton net (mouth opening: 50 cm, mesh size: 0.2 mm), a Bongo net (mouth opening: 50 cm, mesh size: 0.5 mm), a modified Issac-Kidd midwater trawl net (IKMT) (mouth opening: 2.2 m × 2.4 m, mesh size: 1 mm), a handheld scoop net or a light trap (37 cm × 37 cm × 82 cm) (Table 1). For the basic design of the light-trap, see Meekan et al. (2001). The conical net and the IKMT were towed through the surface layer, and the Bongo net towed obliquely from 50 m depth to the surface. Samplings with the IKMT and the light trap were made at night and those with the plankton net and the Bongo net during daytime. Animals collected were placed into plastic buckets filled with fresh seawater and sorted into species. At each collection of zooplankton, seawater was collected from the surface with a plastic bucket or from 2 m depth with 10-liter Niskin bottles, filtered through GF/F filters, and well oxygenated prior to use for experiments.

Metabolic measurements

Within 2–4 hours of collection, oxygen consumption and ammonia excretion rates were measured simultaneously by a sealed-chamber method (Ikeda et al. 2000). The specimens were rinsed briefly 3–4 times with filtered seawater and an individual or a batch of individuals was placed into glass bottles (60, 100, 300 or 550 mL capacity depending on the size of specimens) filled with filtered seawater. Control bottles without specimens were prepared concurrently. In a typical experiment with six experimental bottles, two control bottles were prepared before the first experimental bottle and two after the last experimental bottle. All bottles were incubated for 2–12 h in the dark at near *in situ* temperatures (23 to 30°C). At the end of the incubations, duplicate 15 mL (or 70 mL for larger capacity bottles) and 5 mL (or 10 mL) water samples were siphoned out for the measurements of dissolved oxygen and ammonia, respectively. Dissolved oxygen and ammonia were determined by the Winkler titration method and the phenol-hypochlorite method, respectively (Strickland & Parsons 1972). Based on replicate measurements on homogenous samples, the precision expressed as coefficient of variation (CV) was 0.2% for dissolved oxygen determinations and

6% for ammonia determinations in this study. Specimens left in experimental bottles were rinsed briefly with a small amount of distilled water, blotted on a filter paper to remove water adhering to the body, weighed (wet mass, WM) and frozen for experiments conducted at AIMS. At sea, the specimens were rinsed briefly with a small amount of distilled water, blotted on the filter paper then stored at –20°C, and the frozen specimens were weighed (WM) in the laboratory after the cruise. For some small crustaceans, weighing of frozen specimens could not be done.

Chemical composition

In the laboratory, frozen specimens were freeze-dried, then oven dried at 60°C overnight to remove residual water for the estimation of dry mass (DM) and water content. The dried specimens were pooled by species (*Leptochela* sp. was separated to two size groups). Samples of large species (>1 mg DM ind.^{–1}) were finely ground with a ceramic mortar and pestle or cut into several portions. Samples thus prepared were used for analysis of total CN composition with an elemental analyzer (TruSpec CN Determinator, LECO Corp., USA) or a total carbon analyzer (TOC-Vcsh, Shimadzu, Japan) and a total nitrogen measuring unit (Shimadzu), using ethylenediaminetetraacetic acid (EDTA) as a standard. For ash determination, weighed fractions of samples were incinerated at 450°C overnight and reweighed. All measurements were done in duplicate. From replicate determinations of the same sample, the precision of these analyses (CV) was 3% for C and N, and 14% for ash. Water content was expressed as percent of WM, whereas the contents of ash, C and N were expressed as percent of DM.

Multiple regression analysis

Designating the body mass, temperature and life modes (zooplankton or hyperbenthos) as independent variables, the attributes of these variables to oxygen consumption and ammonia excretion rates were analyzed by using stepwise multiple regression (Sokal & Rohlf 1995). Linear regression models adopted were; $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 X_3$, where Y is oxygen consumption rate or ammonia excretion rate, X_1 is body mass (DM, C or N), X_2 is temperature, and X_3 is a dummy variable on the life mode (zooplankton or hyperbenthos). The dummy variable is defined as 0 for zooplankton and 1 for hyperbenthos. Independent variables are added if $p \leq 0.05$ and removed if $p > 0.10$. The calculation was conducted using SYSTAT J 10.2.

Metabolic data for tropical zooplankton

To facilitate analysis of metabolic features of zooplankton and hyperbenthos, published data on tropical zooplankton were combined with the present data. The data for a chaetognath *Sagitta hispida* Conant (Reeve et al. 1970), six copepods (Gaudy & Boucher 1983), four ctenophores (Kremer et al. 1986), four salps (Cetta et al. 1986), and three size-groups of “gelatinous” zooplankton (Biggs

Table 1. Sampling data of zooplankton (ZP) and hyperbenthos (HB) from inshore and offshore waters of the Great Barrier Reef. Within species the data were separated into two body mass groups for *Leptochela* sp.

Animal group	Species/larval name	Life mode	Sampling site	Sampling method
Decapoda	<i>Leptochela</i> sp. A	HB	off Mackay	Bongo net
	<i>Leptochela</i> sp. B	HB	off Mackay	Bongo net
	<i>Atyidae</i> sp.	HB	Cape Ferguson coast	Scoop net
	<i>Acetes sibogae australis</i> Colefax	ZP	Cape Ferguson coast	Light-trap
	<i>Sergestes atlanticus</i> H.Milne Edwards	ZP	Coral Sea	IKMT
Amphipoda	<i>Synopia scheeleana</i> Bovallius	HB	off Mackay	Bongo net
	<i>Barubius batei</i> (Haswell)	HB	off Mackay	Bongo net
	<i>Oxycephalus clausi</i> Bovallius	ZP	Coral Sea	IKMT
Mysidacea	<i>Siriella media</i> Hansen	HB	off Mackay	Bongo net
Euphausiacea	<i>Thysanopoda tricuspidata</i> Milne-Edwards	ZP	Coral Sea	IKMT
	<i>Euphausia gibba</i> G.O. Sars	ZP	Coral Sea	IKMT
	<i>Euphausia mutica</i> Hansen	ZP	Coral Sea	IKMT
Stomatopoda	alima larva*	ZP	Coral Sea	IKMT
Copepoda	<i>Labidocera farrani</i> Greenwood & Othman	ZP	off Mackay	Bongo net
	<i>Undinula vulgaris</i> (Dana)	ZP	off Mackay	Bongo net
	<i>Paracalanus indicus</i> Wolfenden	ZP	Cape Ferguson coast	Plankton net
	<i>Macrosetella gracilis</i> (Dana)	ZP	Cape Ferguson coast	Plankton net
	<i>Oithona nishidai</i> McKinnon	ZP	Cape Ferguson coast	Plankton net
Ostracoda	<i>Leuroleberis</i> sp.**	HB	Cape Ferguson coast	Light-trap
Chaetognatha	<i>Sagitta bedoti</i> f. <i>minor</i> Tokioka	ZP	Cape Ferguson coast	Plankton net
	<i>Sagitta neglecta</i> Aida	ZP	Cape Ferguson coast	Plankton net
	<i>Sagitta</i> sp.	ZP	Cape Ferguson coast	Plankton net
Cephalopoda	<i>Ideosepius pygmaeus</i> Steenstrup	ZP	Cape Ferguson coast	Light-trap

*from Ikeda et al. (2011b).

**probably a new species (I. Karanovic, personal information).

1977) were selected since rates of oxygen consumption (R) and ammonia excretion (E) were determined simultaneously in these studies and yielded O:N ratios comparable to those of the present study. Predicted relationships between body mass (DM and N) and oxygen consumption rate (R), ammonia excretion rate (E) and O:N ratios of “general zooplankton” at the mean experimental temperature of this study (27°C) from the “global zooplankton model” (Ikeda 1985), which was established by analyzing a comprehensive collection of data on diverse zooplankton taxa from the world oceans, were computed. The data on 29 small teleost fishes, which comprise a mixture of different life modes (planktonic, hyperbenthic and micronektonic) (Ikeda et al. 2011a) were also selected on the basis that ammonia is the major end product of protein metabolism (Wright & Fyhn 2001) as is the case for zooplankton. Experimental procedures in measuring R and E in these previous studies are similar (sealed chamber method) though the collection method of the test animals differed; nets (Reeve et al. 1970, Ikeda 1985, this study), light traps (Ikeda et al. 2011a, this study) and SCUBA (Biggs 1977, Cetta et al. 1986, Kremer et al. 1986).

DM body masses of the chaetognaths and copepods were converted to N masses by multiplying by 0.062 (Beers 1964) and 0.11 (Ikeda 1974), respectively. Since R and E data of salps were given as a function of body length

or body C only, R and E at a mid-body C range (1 mg) were computed and body C was converted to DM or N first by using conversion factors of C:DM=0.08 (Madin et al. 1981) and C:N=4.4 (Cetta et al. 1986). Protein biomass of “gelatinous” zooplankton was converted to DM by using a conversion factor of DM=2×Protein, and N=0.08×DM (Postel et al. 2000). Thus, body mass data of each species or size group were standardized to DM and N.

Results

Oxygen consumption and ammonia excretion

Zooplankton including two decapods, one amphipod, three euphausiids, one stomatopod larva, five copepods, three chaetognaths and one cephalopod, and hyperbenthos including two decapods, two amphipods, one mysid and one ostracod were studied (Table 1). Among 16 species classified as zooplankton, *Acetes sibogae australis* Colefax has been observed to be distributed only in the surface layer of shallow coastal waters and can be regarded as either zooplankton or hyperbenthos. The copepod *Macrosetella gracilis* (Dana) is reported to be associated with the colonial cyanobacterium *Trichodesmium* preferentially to other phytoplankton (O’Neil 1998). Hyperiid amphipod *Oxycephalus* spp., including *O. clausi* Bovallius, are

Table 2. Summary of experimental conditions, resultant rates of oxygen consumption (R) and ammonia excretion (E), and calculated metabolic O:N ratios of zooplankton and hyperbenthos from inshore and offshore waters of the Great Barrier Reef. Values are mean $\pm$ SD of N replicates.

Species/larval name	Expt T (°C)	Individual Nos. (bottle ⁻¹)	Bottle vol. (mL)	N	Body mass (mgDM ind. ⁻¹)	R (μ LO ₂ ind. ⁻¹ h ⁻¹)	E (μ gN ind. ⁻¹ h ⁻¹)	O:N ratio (by atoms)
Zooplankton								
<i>Acetes sibogae australis</i>	30	1–3	550	8	26.7 $\pm$ 5.6	99.6 $\pm$ 20.8	2.8 $\pm$ 0.9	46.1 $\pm$ 10.4
<i>Sergestes atlanticus</i>	27.5	1	550	3	23.5 $\pm$ 9.2	58.5 $\pm$ 12.1	5.4 $\pm$ 2.1	14.6 $\pm$ 5.0
<i>Oxycephalus clausi</i>	27.5	1	550	1	14.0	26.6	2.4	13.7
<i>Thysanopoda tricuspidata</i>	26	1	300	6	12.8 $\pm$ 3.5	32.3 $\pm$ 7.5	1.5 $\pm$ 0.8	30.7 $\pm$ 13.2
<i>Euphausia gibba</i>	28	1	300	7	3.3 $\pm$ 0.7	11.5 $\pm$ 1.7	0.70 $\pm$ 0.24	22.6 $\pm$ 7.0
<i>Euphausia muica</i>	28	1–2	100	10	1.8 $\pm$ 0.7	5.9 $\pm$ 1.4	0.79 $\pm$ 0.48	11.3 $\pm$ 4.3
alima larva	27.5	1	550	6	20.0 $\pm$ 7.3	26.9 $\pm$ 10.3	2.2 $\pm$ 0.9	16.7 $\pm$ 6.7
<i>Labidocera farrani</i>	25	5–7	300	4	0.16 $\pm$ 0.02	1.73 $\pm$ 0.46	0.16 $\pm$ 0.13	16.7 $\pm$ 5.8
<i>Undinula vulgaris</i>	25.5	4–7	300	4	0.22 $\pm$ 0.03	1.14 $\pm$ 0.18	0.08 $\pm$ 0.01	19.0 $\pm$ 3.3
<i>Paracalanus indicus</i>	23	34–55	60	6	0.0072 $\pm$ 0.0005	0.033 $\pm$ 0.0006	0.0019 $\pm$ 0.0001	22.2 $\pm$ 4.0
<i>Macrosetella gracilis</i>	25	16–25	60	3	0.0065 $\pm$ 0.0013	0.0423 $\pm$ 0.0049	0.0029 $\pm$ 0.0003	18.0 $\pm$ 1.8
<i>Oithona nishidai</i>	24	52–225	60	6	0.0012 $\pm$ 0.0000	0.0048 $\pm$ 0.0008	0.00051 $\pm$ 0.00011	12.2 $\pm$ 2.6
<i>Sagittia bedoti</i> f. minor	24	1	60	10	0.084 $\pm$ 0.022	0.28 $\pm$ 0.08	0.037 $\pm$ 0.014	10.1 $\pm$ 3.2
<i>Sagittia neglecta</i>	23	1	60	6	0.224 $\pm$ 0.080	0.30 $\pm$ 0.09	0.050 $\pm$ 0.0129	7.7 $\pm$ 2.3
<i>Sagittia</i> sp.	25	1	60	5	0.29 $\pm$ 0.13	0.79 $\pm$ 0.45	0.066 $\pm$ 0.048	16.0 $\pm$ 3.3
<i>Ideosepius pygmaeus</i>	30	1	550	8	26.6 $\pm$ 10.5	118.3 $\pm$ 53.9	15.9 $\pm$ 12.0	11.5 $\pm$ 3.8
Hyperbenthos								
<i>Leptochela</i> sp. A	25	1	300	7	17.6 $\pm$ 1.3	36.1 $\pm$ 8.2	2.8 $\pm$ 0.9	17.1 $\pm$ 4.1
<i>Leptochela</i> sp. B	25	1	300	8	11.7 $\pm$ 2.9	24.9 $\pm$ 11.7	1.1 $\pm$ 0.4	28.6 $\pm$ 9.6
<i>Aydae</i> sp.	28	1	300	6	1.7 $\pm$ 0.2	4.6 $\pm$ 0.7	0.07 $\pm$ 0.02	87.3 $\pm$ 24.6
<i>Synopia scheelena</i>	25	4–5	300	6	0.8 $\pm$ 0.1	2.5 $\pm$ 0.4	0.081 $\pm$ 0.022	39.9 $\pm$ 10.5
<i>Barubius batei</i>	28.5	5–7	300	6	0.9 $\pm$ 0.1	2.1 $\pm$ 0.5	0.027 $\pm$ 0.008	104 $\pm$ 39
<i>Siriella media</i>	28.5	3	300	6	4.09 $\pm$ 0.38	16.5 $\pm$ 1.1	1.1 $\pm$ 0.3	19.6 $\pm$ 5.0
<i>Leuroleberis</i> sp.	30	2	100	6	19.6 $\pm$ 0.7	6.00 $\pm$ 1.16	0.030 $\pm$ 0.020	341 $\pm$ 198

Fig. 1. Relationship between A) oxygen consumption (R) and dry mass (DM), B) R and nitrogen mass (N), C) ammonia excretion (E) and DM, and D) E and N of zooplankton (ZP) and hyperbenthos (HB) from inshore and offshore waters of the Great Barrier Reef. Data points are the means of 17 data sets for ZP and for 7 data sets of HB in Table 2. The regression line was superimposed based on the results of a significance test between ZP and HB (Table 3). The single data point enveloped by a hatched circle is an outlier (*Leuroleberis* sp.) and was excluded in the calculation of the regression line.

known to be loosely associated with ctenophores (Laval 1980). The squid *Ideosepius pygmaeus* Steenstrup is characterized by having an adhesive organ located on the posterior part of the dorsal mantle side for attachment during the day to the lower leaf surfaces of sea grasses or algae for camouflage (Boletzky et al. 2005). Despite these divergent life modes from those of typical zooplankton, all of them have been regarded as “zooplankton” in the past and we followed this practice in the present analyses. The results for the decapod *Leptochela* sp. were separated into two size groups (A and B).

Across a total of 22 species, body masses ranged from 0.0012 mg DM for *Oithona nishidai* McKinnon to 26.7 mg DM for *I. pygmaeus*. Oxygen concentration in experimental bottles at the end of the experiments was >80% of that of control bottles. Oxygen consumption (R) and ammonia-N excretion (E) rates varied from 0.0048 to $118.3 \mu\text{L O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ and from 0.00051 to $15.9 \mu\text{g NH}_4\text{-N ind.}^{-1} \text{ h}^{-1}$, respectively (Table 2).

Stepwise multiple regression analyses revealed that among the three independent variables (body mass, temperature and life modes), significant variables were body

mass only for R , but body mass and life mode for E (Fig. 1, Table 3). In the analyses of E , *Leuroleberis* sp. was identified as an outlier and was therefore removed. The choice of body mass unit (DM, C or N) had little effect on the results of this analysis. The variables identified as significant attributed 95–97% of the variance of R and 94% of the variance of E (Table 3).

O:N ratio

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 total metabolites in marine zooplankton (Mayzaud & Conover 1988, Ikeda et al. 2000). 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 is catabolized in equal quantities at the same time, O:N ratios are calculated as 21 or 13. Hence, O:N ratios of 7–17 (mid-point of 21 and 13) may be used as an index of protein-oriented metabolism and the ratios of >17 as lipid/carbohydrate-oriented metabolism.

O:N ratios ranged from 7.7 to 46.1 (geometric mean 16.4) for zooplankton and from 17.1 to 341 (53.1) for hyper-

Table 3. Stepwise multiple regression analyses of metabolic rate (Y : $\mu\text{L O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ or $\mu\text{g NH}_4\text{-N ind.}^{-1} \text{ h}^{-1}$) on body mass (X_1 : mg DM, C or N ind.^{-1}), temperature (X_2 : $^{\circ}\text{C}$) and life mode (X_3 : 0 for zooplankton and 1 for hyperbenthos).

Y	Body mass unit	N	Step No.	Regression model $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 X_3$				
				a_0	a_1	a_2	a_3	R^2 (Adjusted R^2)
O_2 consumption rate	DM	23	0		0.892	0.030	−0.383	0.954
		23	1		0.908		−0.381	0.954
		23	2	1.066	0.891			0.950 (0.947)
	C	23	0		0.894	0.027	−0.254	0.970
		23	1		0.908		−0.251	0.970
		23	2	1.968	0.897			0.968 (0.966)
	N	23	0		0.879	0.07	−0.201	0.978
		23	1		0.872	0.067		0.977
		23	2	3.196	0.906			0.988 (0.974)
$\text{NH}_4\text{-N}$ excretion rate*	DM	22	0		0.940	−0.031	−1.041	0.945
		22	1	−1.306	0.925		−1.031	0.945 (0.939)
	C	22	0		0.938	−0.052	−0.988	0.947
		22	1	−0.431	0.913		−0.975	0.947 (0.941)
	N	22	0		0.926	−0.027	−1.003	0.948
		22	1	0.778	0.913		−0.997	0.947 (0.942)

*An outlier (*Leuroleberis* sp.) was excluded.

benthos (Fig. 2), suggesting protein-oriented metabolism on average for the former and lipid/carbohydrate-oriented metabolism for the latter. Regression analyses of O:N ratios on body mass (DM) showed that the ratios were independent from body mass ($R^2=0.060$, $p=0.362$ for zooplankton, and $R^2=0.002$, $p=0.932$ for hyperbenthos). The differences in the mean O:N ratios between zooplankton and hyperbenthos were highly significant (Mann-Whitney U -test, $p=0.004$), which remained unchanged even if the isolated datum (341) of *Leuroleberis* sp. was excluded (U -test, $p=0.010$).

Water, ash and elemental composition

Across 17 zooplankton species, the range of variation was 62.6–91.1% (mean: 78.5%) for water contents, 7.3–43.0% (16.8) for ash, 25.5–47.2% (38.7) for C and 6.2–12.3% (10.3) for N, with C:N ratios of 3.1–4.7 (3.8) (Table 4). For 6 hyperbenthic species, the range of variation was 51.1–76.0% (64.2) for water content, 14.2–58.8% (31.0) for ash, 18.0–43.8% (34.2) for C, 2.4–11.1% (9.0) for N, with C:N ratios of 3.3–7.5 (4.2). Significant differences between zooplankton and hyperbenthos were seen only in ash (U -test, $p<0.05$), and this conclusion was unaffected by the presence/absence of the anomalous datum for *Leuroleberis* sp. from hyperbenthos data sets.

Comparison with other zooplankton data

Published data (Table 5) on tropical zooplankton and small fishes were converted first to DM-specific R and E and plotted against DM on a log-log graph (Fig. 3A, C),

Fig. 2. Relationship between O:N ratios and dry mass (DM) of zooplankton and hyperbenthos from inshore and offshore waters of the Great Barrier Reef. Data points are the means of 17 data sets for zooplankton and 7 data sets for hyperbenthos in Table 2. Since the relationship was not significant, means were superimposed. For symbols see Fig. 1.

and compared with the 95% CI belt of pooled zooplankton and hyperbenthos data (DM-specific R) or with zooplankton data only (DM-specific E) from this study (Fig. 3). While most of the data fall within or close to the 95% CI belt, both DM-specific R and E data for ctenophores and only the E data for hyperbenthos and a part of the small fish data scatter below the lower 95% CI limit. In terms of N-specific R and E , the low values for ctenophore data

Table 4. Water content, ash, total C and N composition and C:N ratio of zooplankton and hyperbenthos from inshore and offshore waters of the Great Barrier Reef. Values are mean $\pm$ SD with the number of replicates in parenthesis for water contents, and means of duplicates for others. ND: no data.

Species/larval name	Water (% of WM)	Ash (% of DM)	Total C (% of DM)	Total N (% of DM)	C:N ratio (by mass)
Zooplankton (ZP)					
<i>Acetes sibogae australis</i>	75.8 $\pm$ 0.7 (8)	13.3	42.4	12.1	3.5
<i>Sergestes atlanticus</i>	73.1 $\pm$ 1.7 (3)	16.2	40.1	10.9	3.7
<i>Oxycephalus clausi</i>	85.2 (1)	43.0	25.5	6.2	4.1
<i>Thysanopoda tricuspidata</i>	74.8 $\pm$ 0.8 (6)	13.7	42.7	12.7	3.4
<i>Euphausia gibba</i>	62.6 $\pm$ 3.6 (7)	16.1	41.7	11.3	3.7
<i>Euphausia mutica</i>	73.2 $\pm$ 4.7 (7)	13.1	40.9	11.4	3.6
alima larva	ND	14.7	45.1	9.6	4.7
<i>Labidocera farrani</i>	ND	13.8	35.4	10.2	3.5
<i>Undinula vulgaris</i>	ND	ND	42.7	11.6	3.7
<i>Paracalanus indicus</i>	ND	ND	44.9	10.9	4.1
<i>Macrosetella gracilis</i>	ND	ND	36.6	7.8	4.7
<i>Oithona nishidai</i>	ND	ND	32.4	8.9	3.6
<i>Sagitta bedoti</i> f. <i>minor</i>	83.7 $\pm$ 4.1 (10)	ND	38.4	12.3	3.1
<i>Sagitta neglecta</i>	91.1 $\pm$ 1.2 (10)	ND	31.3	8.9	3.5
<i>Sagitta</i> sp.	87.5 $\pm$ 5.2 (5)	ND	31.3	8.9	3.5
<i>Ideosepius pygmaeus</i>	78.2 $\pm$ 1.1 (8)	7.3	47.2	11.4	4.1
Grand mean	78.5 $\pm$ 8.5 (10)	16.8 $\pm$ 10.2 (9)	38.7 $\pm$ 6.1 (16)	10.3 $\pm$ 1.9 (16)	3.8 $\pm$ 0.4 (16)
Hyperbenthos (HB)					
<i>Leptochela</i> sp. A	ND	30.1	34.7	9.7	3.6
<i>Leptochela</i> sp. B	ND	26.4	36.1	10.3	3.5
<i>Atydae</i> sp.	76.0 $\pm$ 1.0 (6)	21.2	40.3	10.9	3.7
<i>Synopia scheelena</i>	ND	26.4	36.3	11.1	3.3
<i>Barubius batei</i>	59.5 $\pm$ 3.9 (6)	39.6	30.0	7.5	4.0
<i>Siriella media</i>	69.8 $\pm$ 2.9 (6)	14.2	43.8	11.0	4.0
<i>Leuroleberis</i> sp.	51.1 $\pm$ 1.8 (6)	58.8	18.0	2.4	7.5
Grand mean	64.2 $\pm$ 11.0 (4)	31.0 $\pm$ 14.5 (7)	34.2 $\pm$ 8.3 (7)	9.0 $\pm$ 3.2 (7)	4.2 $\pm$ 1.5 (7)
Grand mean*	68.5 $\pm$ 8.3 (3)	26.3 $\pm$ 8.5 (6)	36.9 $\pm$ 4.8 (6)	10.1 $\pm$ 1.4 (6)	3.7 $\pm$ 0.3 (6)
<i>p</i> for Ho: ZP=HP (<i>U</i> -test)	0.048	0.017	0.181 ^{NS}	0.284 ^{NS}	0.813 ^{NS}
<i>p</i> for Ho: ZP=HP (<i>U</i> -test)*	0.129 ^{NS}	0.034	0.376 ^{NS}	0.554 ^{NS}	0.941 ^{NS}

* *Leuroleberis* sp. data excluded.

plotted well within the 95% CI, but this was not the case for the hyperbenthos and some small fishes (Fig. 3B, D). Preliminary calculation of C-specific *R* and *E* yielded estimates close to N-specific *R* or *E* and somewhere between DM-specific and N-specific *R* and *E*; therefore the results were not shown.

The published O:N data for tropical zooplankton and small fishes (Table 5) fall within the 95% CI (6.4–41.8) belt of those of zooplankton from this study (Fig. 4), with the exception of part of the hyperbenthos data in this study and 13 out of 35 data points for small fishes (Ikeda et al. 2011a) which scattered above the upper 95% CI.

Discussion

Metabolic comparison

While no significant differences were detected in *R*–

body mass relationships between zooplankton and hyperbenthos, the latter showed significantly lower *E* than zooplankton with equivalent body masses (Fig. 1). Choice of body mass units (DM, C or N) did not affect this conclusion (Table 3). This result implies that different life modes (planktonic or hyperbenthic) affect ammonia excretion but not oxygen consumption by these animals. Coull & Vernberg (1970) observed similar or higher DM-specific *R*s of a hyperbenthic harpacticoid *Longipedia helgolandica* (Klie), as compared with a planktonic harpacticoid *Euterpina acutifrons* (Dana) at comparable temperatures. Ivleva (1980) compiled published *R*–body mass data of planktonic, hyperbenthic and benthic crustaceans from tropical waters and noted no appreciable differences among them. Thus, the present results of *R*–body mass relationships of zooplankton and hyperbenthos are consistent with those reported by Coull & Vernberg (1970) and Ivleva (1980). There is no information yet about comparisons of *E* of zoo-

Table 5. Summary of rates of oxygen consumption (R) and ammonia excretion (E) and O:N ratios of zooplankton and small fishes from tropical seas and those of "general zooplankton" predicted from the "global zooplankton model" at 27°C. It is noted that the data of Biggs (1977) were represented by the mean of 3 size categories, and those of Maden et al. (1981) from their Method A. For salps, agg= aggregate form and sol=solitary form. See text for details.

Animal group	Species	Expt T (°C)	Original body size unit	Body mass		R ($\mu\text{L O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$)	E ($\mu\text{g N ind.}^{-1} \text{ h}^{-1}$)	O:N (by atoms)
				(mgDM ind. ⁻¹)	(mgN ind. ⁻¹)			
Copepods	<i>Candacia pachydactyla</i> (Dana)	28.5	DM	0.18	0.020	0.7	0.15	6.1
	<i>Pontella fera</i> Dana			0.15	0.017	0.6	0.16	4.8
	<i>Scolecithrix bradyi</i> Giesbrecht			0.13	0.014	0.8	0.10	9.7
	<i>Cosinocalanus</i> (= <i>Undinula darwini</i> (Lubbock))			0.15	0.017	1.1	0.14	10.3
	<i>Euchaeta marina</i> (Prestandrea)			0.22	0.024	1.3	0.13	12.4
	<i>Temora discaudata</i> Giesbrecht			0.034	0.004	0.2	0.02	14.4
Ctenophores	<i>Eurhamphaea vexilligera</i> Gegenbaur	25	BL, C, N, DM	202	0.485	12.7	1.30	12.2
	<i>Ocyropsis</i> spp.			141	0.423	17.8	1.40	15.8
	<i>O. maculata</i> (Rang)			1263	8.084	150	15.9	11.8
	<i>Beroë ovata</i> Bruguère			76	0.749	20.6	2.40	10.7
	<i>Cyclosalpa affinis</i> (Chamisso), agg			12.5	0.227	27.5	1.43	24.0
Salps	<i>Pegea confederata</i> (Forskål), agg	21–28	BL, C	12.5	0.227	31.6	1.04	38.1
	<i>Salpa cylindrica</i> (Cuvier), sol			12.5	0.244	81.3	4.04	25.2
	<i>S. maxima</i> Forskål, agg			12.5	0.227	21.9	1.14	24.0
	39 species			1.0	0.08	13.5	0.78	21.6
				10	0.8	70	5.25	16.7
Gelatinous zooplankton*		23–29	protein	100	8	435	37.1	14.7
Chaetognaths	<i>Sagitta hispida</i> Conant	26	DM	0.11	0.0068	0.40	0.075	6.7
Small teleost fishes	29 species	25–30	WM, DM, C, N	1.2–395	0.13–49.4	5.7–1296	0.28–64.2	17.2–104
"General zooplankton"		27	DM	0.001–500		$2.921 \times \text{DM}^{0.7886}$	$0.2208 \times \text{DM}^{0.7616}$	$16.53 \times \text{DM}^{0.027}$
		27	N	0.0001–50		$31.77 \times \text{N}^{0.8305}$	$2.238 \times \text{N}^{0.8361}$	$17.74 \times \text{N}^{0.0144}$

*siphonophores, hydromedusae, scyphomedusae, ctenophores, heteropods, pteropods and thaliaceans.

Fig. 3. Relationship between A) dry mass (DM)-specific oxygen consumption rate (R) and DM, B) nitrogen mass (N)-specific R and N, C) DM-specific ammonia excretion ratio (E) and DM, and D) N-specific E and N of small teleost fishes (Ikeda et al. 2011a), copepods (Gaudy and Boucher 1983), ctenophores (Kremer et al. 1986), salps (Cetta et al. 1986), gelatinous zooplankton (Biggs 1977) and a chaetognath (Reeve et al. 1970) all from tropical seas, and those of “general zooplankton” at 27°C (mean experimental temperature in this study, Table 1) derived from the “global zooplankton model” (Ikeda 1985) (calculated from the data in Table 5). Note that most of these fall within or close to the 95% CI calculated from pooled data for zooplankton and hyperbenthos (ZP+HB 95% CI) for A) and B), and from zooplankton data only (ZP 95% CI) for C) and D).

plankton and hyperbenthos. Smith (1982) determined R and E simultaneously and calculated O:N ratios (4–30) for mixed benthopelagic plankton (=hyperbenthos) predominated by the scyphomedusa *Poralia rufescens* Vanhöfen living at a depth of 1,300m off Southern California. However, direct comparison of his results with those of hyperbenthos of the present study is difficult because possible predation among hyperbenthos cannot be ruled out during his experiments with mixed species.

In Fig. 3, DM-specific R and E data for ctenophores, which scattered below the lower 95% CI range, fell well within the 95% CI range in terms of N-specific R and E . In contrast, DM-specific R of salps, which fell within the 95% CI range, shifted above the upper 95% CI range in terms of N-specific R . The same pattern, though much modulated, was seen in the specific R of gelatinous zooplankton and specific E of the same salps. As compared with other zooplankton, higher N (or protein)-specific R and E of salps and gelatinous zooplankton have been explained by gentle capture of test animals and immediate incubation *in situ* by

SCUBA divers (Biggs 1977, Cetta et al. 1986). The rapid decline in R and E after capture is a phenomenon that has been observed in early studies on zooplankton metabolism, and interpreted as a result of complex interactions between capture stress (which is highest at capture) and starvation effects (which increase with time after capture) (Ikeda et al. 2000). The result of interactions between these factors could vary across diverse zooplankton taxa characterized by dissimilar body size, behavior, swimming activity and nutrition, and no single method to overcome the problem is presently available.

Bearing this limitation of the methodology in mind, it is concluded that most published data of zooplankton and small fishes from tropical seas fit the N-specific R –body mass relationship of zooplankton and hyperbenthos established in this study (Fig. 3B). The same is true for the N-specific E –body mass relationship of zooplankton in this study, excluding the lower specific E of hyperbenthos and some small fishes (Fig. 3D).

Fig. 4. Relationship between O:N ratios and dry mass (DM) of small teleost fishes (Ikeda et al. 2011a), copepods (Gaudy and Boucher 1983), ctenophores (Kremer et al. 1986), salps (Cetta et al. 1986), “gelatinous” zooplankton (Biggs 1977) and a chaetognath (Reeve et al. 1970) all from tropical seas, and those derived from the “global zooplankton model” (Ikeda 1985) at 27°C (calculated from the data in Table 5). Note that most of these data fall within or close to the 95% CI range calculated from the zooplankton data (ZP 95% CI) in Fig 2. For symbols see Fig. 3.

O:N ratio

Higher O:N ratios (lipid-oriented metabolism) have been documented for large grazing copepods living in high latitude seas; the copepods deposit a large amount of energy reserves (lipids) in the body as part of their life history traits for coping with a long food-scarce winter (Conover & Corner 1968, Ikeda 1974, Mayzaud & Conover 1988, Ikeda et al. 2000). However, this explanation is not applicable for higher O:N ratios of hyperbenthos, since there is no indication of large amounts of lipids in the body as judged by their C and N composition data (see “chemical composition” section below). For some small fishes that exhibited high O:N ratios, Ikeda et al. (2011a) interpreted that this was a reflection of their partial or entire dependence on diets such as benthic algae, seaweeds or detritus, all characterized by extremely low N composition (1–2% of DM, Tenore 1983, 1988, Duarte 1990) in contrast to N-rich phytoplankton and zooplankton (3–12% or more of DM, Parsons et al. 1961, Mayzaud & Martin 1975, Ikeda 1974, Verity et al. 1992).

While no information about the diet of the hyperbenthos used in this study is presently available, it is conceivable that their diets are likely to include N-poor detritus because of their close association to the bottom. There is ample evidence to support this interpretation—high metabolic O:N ratios associated with low N composition of diets—in some benthic animals. Mukai & Koike (1984) compared O:N ratios of two mud shrimps and noted that one (*Callinassa japonica* Stimpson) feeding on mud showed a significantly higher ratio (48) as compared with that (20) of the other (*Upogebia major* (de Haan)) feeding on phytoplankton. As typical deposit feeders, tropical sea

cucumbers *Holothuria atra* Jaeger and *H. scabra* Jaeger exhibit O:N ratios of 32 and 44, respectively (Mukai et al. 1989), both of which are much higher than the mean of 16.4 observed for zooplankton in the present study.

Relevant here, higher O:N ratios (51–180) have also been observed for carnivorous phyllosoma larvae, a common member of tropical zooplankton (Ikeda et al. 2011b). The same line of explanation by low N diets cannot be applied for the phyllosomas, since higher O:N ratios of phyllosomas were also the case for larvae raised in the laboratory provided N-rich foods (*Artemia* larvae, fresh blue mussel). As an alternative, Ikeda et al. (2011b) considered that the higher O:N ratios of phyllosomas were due to a species-specific feature such as the preferential utilization of diet N to synthesize body protein rather than for fuel metabolism. Phyllosomas are different from “general zooplankton” and hyperbenthos of the present study in that they have much reduced *R* as well as lower body N contents.

Chemical composition

While ash was the only component that showed a significant difference between zooplankton and hyperbenthos (Table 4), this requires more data on a wide array of species in the light of high inter-species variations within each group. The present results of C and N composition for 7 out of 9 animal groups (decapods, amphipods, mysids, euphausiids, stomatopod alima larvae, copepods and chaetognaths) are in good agreement with those of the respective groups reported from tropical or subtropical seas by previous workers (Ikeda 1974, Gorsky et al. 1988). No C and N composition data is available for ostracods or cephalopods from tropical waters. However, the C and N values of three mesopelagic ostracods from the western subarctic Pacific (39.8–50.8% and 7.8–9.4%, respectively; Kaeriyama & Ikeda 2004) were much higher than the present results for *Leuroleberis* sp. The inorganic fraction (CaCO_3 -C) of total C in zooplankton is thought to be minor (Curl 1962), but may be substantial in calcareous ostracods such as *Leuroleberis* sp. as judged by their high ash content (58.8%). Assuming that ash is solely composed of CaCO_3 (1 mole = 100g), C and N composition of ash-free DM (=organic matter) of the ostracod is estimated as 26.6% ($= (18.0 - 12 \times 0.588) / 0.412$) and 5.8% ($= (2.4 - 0.0 \times 0.588) / 0.412$), respectively, yielding a C:N ratio = 4.6. For squids, the present results for *Ideosepius pygmaeus* fall within the ranges of 74–91% for water content, 10.3–20.1% for ash, 31.6–43.0% for C and 9.6–14.0% for N, with C:N ratios of 2.8–4.1 for 11 oceanic squids from the Northeast Atlantic (Clarke et al. 1985).

While zooplankton living in high latitude seas are often characterized by high C composition (up to 70% of DM) and C:N ratios (up to 10) due to the accumulation of C-rich lipids as mentioned above, those in low latitude seas do not deposit lipids in the body and C composition (<40% of DM) and C:N ratios (3–4) are much lower than

those of their high latitude counterparts (Ikeda 1974, Båmstedt 1986). Analyzing biochemical composition data on 182 zooplankton species (mostly crustaceans), Ventura (2006) calculated average C and N composition of protein to be 52.8% and 16.0%, and lipids (represented by triacylglycerol) to be 77.3% and 0%. With these results, the C:N ratio is calculated as 3.3 for protein alone and 8.1 for organic matter composed of equal amounts of protein and lipid. Carbohydrate in tropical zooplankton has been reported to be <1% of DM (Beers 1966) and is therefore omitted in this calculation. From this criterion, organic matter of all zooplankton (mean C:N=3.8, Table 4) and hyperbenthos (3.7, excluding *Leuroleberis* sp.) from the present study is characterized by the predominance of protein.

As a general conclusion, we demonstrated that *R* of zooplankton was comparable to that of hyperbenthos at equivalent body mass, but *E* of the latter was lower. The pattern was most evident by choosing N rather than DM as the body mass unit. As a consequence, O:N ratios of hyperbenthos were significantly higher (lipid/carbohydrate-oriented metabolism) than those of zooplankton (protein-oriented metabolism). As judged by body C:N ratio, protein is the predominant biochemical compound in both zooplankton and hyperbenthos. Despite living in the same habitat, these dissimilarities (metabolic O:N ratios) and similarities (body C:N ratios) between zooplankton and hyperbenthos may be explained by their dependence on diets characterized by N-rich matter (phytoplankton, zooplankton) for the former and N-poor composition matter (detritus) for the latter.

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